Reviews: Methods and Technologies in Fish Biology and Fisheries

Ecological and Genetic Implications of Aquaculture Activities

Edited by

Theresa M. Bert

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Cover Photo;
Salmon farming cages in the Reloncavi Estuary in Southern Chile, photograph by Fernando Jara.

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FOREWORD

This book is based on a symposium entitled "Ecological and Genetic Implications of Aquaculture Activities," which was held at the annual meeting of the World Aquaculture Society (WAS), May 4–5, 2000, in Nice, France. I organized the symposium while serving as Vice-chair and Chair of the U.S. National Committee for the International Union for the Biological Sciences (USNC/IUBS). The USNC/IUBS is a U.S. National Academies of Sciences committee that represents U.S. interests in the biological sciences in the international world of scientific organizations and is under the auspices of the U.S. National Research Council. The IUBS itself had an ongoing program, called Reproductive Biology and Aquaculture (RBA), for the application of modern technologies to animal reproduction in aquaculture. Prior to USNC/IUBS involvement in the RBA program, the program focused on the applications of modern techniques developed in the disciplines of cell biology, molecular biology, and genetics to address issues and needs pertaining to aquaculture. The USNC/IUBS involvement in the RBA program launched the program's second stage. The program expanded toward understanding the genetic, ecological, and environmental effects of these technologies and the development of solutions to those negative effects. The scope of the second stage met an important global need. It focused awareness on the development and dissemination of aquaculture approaches and methods that could increase the efficiency and quantity of food production while minimizing ecological and genetic damage to both wild populations and aquacultured animals associated with this food production.

At the time that the symposium was being planned, aquaculture industry leaders and scientists were becoming acutely aware of the increasing global attention to ecological and genetic effects of aquaculture activities. Thus, WAS scientific and industry leaders welcomed the opportunity to host a major symposium that addressed those issues at an annual WAS meeting. The objectives of the symposium were twofold: (1) bring together leaders of the science of aquaculture to identify specific national and global ecological and genetic effects that the various types of aquaculture activities brought upon the environment and its constituent ecosystems and (2) share and discuss the effectiveness of actual and attempted solutions to those effects and develop new solutions.

Twenty-eight speakers from 18 different countries gave presentations at the symposium. Toward the symposium objectives, some speakers described the types and overall level of global effects from aquaculture activities and presented directions of thinking to address those effects. Many speakers documented the principal types of effects that occur in their countries and presented specific action plans or actual modes of operation to reduce and manage those effects. Other speakers presented assessments of ongoing efforts to limit aquaculture effects and pointed out specific strengths and weaknesses of the projects and programs they evaluated. After the formal presentations, workshops were held to share additional information about ways to ameliorate or prevent aquaculture effects on native organisms and environments. Scientists and representatives of both the aquaculture industry and major funding agencies for aquaculture, such as the World Bank, attended these workshops.

IUBS leaders were keenly interested in a focus on South America for the symposium. Thus, that continent is well represented in this book. In addition, five trainees from South American countries also attended the symposium as invited guests. These trainees were selected by the symposium speakers from those countries. A special reception was held during the symposium so that the trainees could converse with the speakers in an informal atmosphere. In exchange for the financial support given to the trainees to attend the meeting, each student wrote a report that described the benefits to the student of attending the symposium and the WAS meeting.

Twenty-five speakers from 19 different countries submitted manuscripts based on their presentations for inclusion in this book. One manuscript (Alves et al., Chapter 16) was solicited from the authors at a later WAS annual meeting. Many of these authors are the leaders, or are among the leaders, of aquaculture science in their respective countries. Others are renowned aquaculture and fisheries scientists worldwide. Together, the chapters written by these authors form a comprehensive compilation of the various ecological and genetic problems faced by broad areas of the world in association with the development and expansion of aquaculture-related activities and enterprises. Their contributions allow the identification of common problems among nations; of the scope and extent of the most pervasive problems; and of common solutions, aquaculture methods, and ways of thinking about and designing aquaculture programs that enable the practice of productive aquaculture simultaneously with ecosystem conservation.

The preparation of this book obviously took a long time. Many factors contributed to the lengthy process of editing the manuscripts, compiling the chapters, and writing my own chapters. Most chapter authors submitted their chapters a number of years ago. A few chose to update their chapters as new work was accomplished and additional relevant literature was published. Thus, some chapters may appear to be lacking references to the most up-to-date published literature whereas others contain more recent references. I must take the blame for this problem and offer my most sincere apologies to the authors. I also deeply thank all of the chapter authors for their long-enduring patience while this book was in preparation. All authors except one chose to keep their chapters in this book rather than to withdraw them and publish them sooner elsewhere. On the positive side, some chapters have already been cited in the literature several times and others have already been used as teaching tools for college aquaculture classes. This is a testimony to the utility and relevance of the various authors' contributions to this book. I dedicate this book to the authors of the chapters within it. I will be indebted to them always for their support.

Funding for the symposium and publication of this book came from many sources. The USNC/IUBS, the IUBS, the Japanese National Committee for the IUBS/RBA program, the U.S. Department of Interior, and the WAS sponsored the symposium. The IUBS and the Japanese IUBS/RBA National Committee also funded travel and reception expenses for the five South American trainees who attended the symposium. All of the funding sources listed previously and the State of Florida contributed funds toward publication.

I thank Barry Chernoff for introducing me into the realm of international research organizations and activities, Kenjiro Ozato for helping me to solidify the new direction that the IUBS/RBA program took through USNC/IUBS involvement, and Devin Bartley for support, advice, and consultation throughout the development of this book. I am most grateful for the highly competent assistance of many people who helped me with the organization and execution of the symposium and with the preparation of the book. Rachel Sackett served as budget manager, communications focal person, and executive assistant to me during the process of organizing the symposium and arranging travel for the symposium participants. Staff members of the Florida Institute of Oceanography also facilitated getting symposium participants from their various locations in the world to the WAS meeting and reimbursing those individuals. Leroy Creswell and Rosa Flos, who were co-chairs of the committee to organize the WAS annual meeting, helped with many details of obtaining funding, and organizing and executing the symposium. Jennifer Nielsen, editor-in-chief of the Reviews: Methods and Technologies in Fish Biology and Fisheries book series, invited me to publish this book as a contribution to that series. The Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWRI) library staff provided incredible assistance for years. Jan Boyett, head librarian, queried library computer search engines and contacted other librarians throughout the world to ensure that the references listed in each chapter were as correct and complete as possible. She, Lawanda McCarter, and Judith Burhman copied dozens of articles and arranged interlibrary loans for tens of books that I needed to verify the accuracy of other authors' texts and references or to write my own chapters. Gil McRae, Director of the FWRI, generously found funding for the color figures. Lastly, but very importantly, Martine van Bezooijen, of Kluwer Scientific Publications (now a subsidiary of Springer), did an outstanding job of working with me and encouraging me during the publication process. Over the course of working on this book, she became a true friend. I am indebted to all of these people and sincerely thank them for their contributions to this project. I also apologize if I have forgotten anyone who helped me during the eight-year interval between the inception of the idea for expansion of the IUBS/RBA program in this direction and the publication of this book.

Some key terms and words used throughout the book warrant explanation. The aquaculture literature is replete with terms and words that have been adopted for standard use in the language of aquaculturists and those who study aquaculture. Many very similar terms have subtle differences that are defined and redefined by aquaculture scientists and policy-makers. Authors from various countries in the world refer to particular entities in different ways. Thus, when reading publications containing chapters or articles from authors of different nations, such as this book, terminology can become confusing. Rather than standardize particular terms and words in all chapters in this book, I chose to maintain the terminology used by the authors, thus preserving the genre of each article. However, this necessitates a listing of definitions and a generalization of some words and terms that have more closely defined, specific meanings in other publications. Following are words and terms used more or less synonymously in this book:

1. Alien, non-native, non-indigenous, foreign, introduced, or exotic species or organisms. All refer to animals from species or populations that do not live locally in the area under discussion and are cultured or introduced into the non-native area, either inadvertently or purposefully. In contexts where more than one of these terms is used, alien, foreign, or exotic species are usually considered to be species not found in the country under discussion; translocated or non-indigenous species are those found within the country but not in the water system under discussion; and non-native species are, collectively, species in both of those categories. Some authors define some of these terms specifically in their chapters.
2. Farmed, cultured, aquacultured, hatchery, or hatchery-reared fish or invertebrates. All refer to (1) animals that were either spawned from broodstock held in captivity in an aquaculture facility and reared in the aquaculture facility or (2) animals that were collected from the wild at young life stages and reared in an aquaculture facility. Unless the terms used in a chapter are explained in the chapter, the first definition holds.
3. Net-pens or cages. Both refer to enclosures made of strong fibrous or coated metallic nets or fencing material and suspended via floatation devices in open water (e.g., lakes, embayments, coastal waters), and used for fish culture. Cages may also be used for culture of invertebrates (e.g., scallops).
4. Ton, tonne, or metric ton. All of these terms refer to metric tons throughout the book.

5. Aquaculture or mariculture. Mariculture refers to aquatic culture in the marine environment, whereas aquaculture means all types of aquatic culture, ranging from freshwater culture to marine culture. The breadth of salinity regimes encompassed by the term "aquaculture" will depend on the scope and context in which that term is used in the chapter.
6. Stock enhancement or stock supplementation. Although experts who deal with aquaculture in which hatchery animals are used to increase numbers of individuals in wild populations differentiate these terms, the diverse array of authors in this volume use these terms essentially interchangeably. The hatchery-reared animals may or may not contribute to the next generation's breeding stock. Both stock enhancement and stock supplementation are differentiated from stock restoration, which is the reintroduction of native species into locations where they have been extirpated. Some authors of chapters dealing specifically with purposeful stocking of hatchery fish into the wild provide specific definitions of these terms in their chapters.
7. Integrated aquaculture or polyculture. Integrated aquaculture generally refers to the separate culture of at least some components of a multi-culture system (e.g., fish, various invertebrates, algae). These components are integrated through channeling of the water among culture units to facilitate its cleaning. Polyculture refers to animals (fish, invertebrates, algae) cultured within the same culture unit (e.g., pond, net-pen, tank).

Perhaps most importantly, while working with the chapter authors for this book, I learned that the term "aquaculture" itself is used in a wide variety of contexts by fisheries and aquaculture scientists in different countries. This is highly evident in the chapters in this book. To preserve the full spectrum of what aquaculture means from the worldwide perspective as it exists in this book, "aquaculture" here includes closed-system aquaculture; all types of flow-through system aquaculture; intensive or extensive aquaculture, net-pen aquaculture; aquaculture-based stock enhancement or restoration; and the aquaculture-based introduction of native or non-indigenous or alien species into open waters for the development or supplementation of fisheries (a type of aquatic ranching).

CHAPTER 1

ENVIRONMENTALLY RESPONSIBLE AQUACULTURE—A WORK IN PROGRESS

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Abstract: Aquaculture yields important benefits to humans—food, essential products used in developing new industries and maintaining current industries, and fish and shellfish used to supplement depleted natural populations. Three objectives of the aquaculture industry are to provide food and income for people in developing countries; reduce fishing pressure on wild stocks; and maintain sufficient numbers of fish to sustain commercial, recreational, and subsistence fisheries. But these benefits come with a price. The ecological and genetic effects associated with aquaculture operations have received a great deal of attention for at least 20 years. This focus has been stimulated by several factors: (1) the high-profile presence of aquaculture activities and facilities, which operate principally in inland and coastal waters where humans tend to concentrate and conduct numerous other activities that compete for space and resources; (2) the physical evidence of environmental decline in the vicinities of aquaculture operations; and (3) the promise that aquaculture products can provide considerable, reasonably priced protein throughout the world. The negative effects of aquaculture are numerous, diverse, and complex. They are not easily mitigated or alleviated because they are tied to the actual and potential benefits of the industry. The effects of aquaculture can compromise biodiversity at all levels—from genetic through ecosystem, or broader in scope—and can interfere with the interactions of organisms at all biodiversity levels. Collectively, the authors of the chapters in the four sections of this book identify many ways that aquaculture has affected biodiversity and present new perspectives on some previously documented ways. They also provide specific, applicable solutions for the effects they address. They provide detailed documentations of the status of various types of aquaculture effects in their respective countries, evaluations of the success of various aquaculture endeavors, and overviews of the type of thinking and planning that could lessen all types of ecological and genetic problems caused by aquaculture. This book is unique in that it provides in-depth evaluations of specific effects resulting from aquaculture operations in countries throughout the world and suggests specific solutions to the problems described.

Theresa M. Bert (ed.), Ecological and Genetic Implications of Aquaculture Activities, 1–31.

Key words: aquaculture, biodiversity, ecology, effects, environment, genetics, solutions, stock enhancement, worldwide

1. THE IMPORTANCE OF AQUACULTURE

A quick perusal of a literature search produced using the keywords ''aquaculture,'' ''ecology,'' and ''genetic'' will illustrate that a great deal of attention has been paid to the environmental effects[1] of all types of aquaculture activities. Numerous workshops, symposia, and conference sessions have addressed these issues (e.g., Pullin et al., 1993; Food and Agriculture Organization of the United Nations [FAO] and Government of Japan, 1995; Pullin et al., 1999; Svennevig et al., 1999; ; Network of Aquaculture Centres in the Asia-Pacific [NACA] and FAO, 2001; Subasinghe et al., 2001; Holmer et al., 2002; Stead et al., 2002; Morry et al., 2003; Nakamura et al., 2003; Phillips et al., 2003). Many national and international organizations and groups have prepared codes, recommendations, guidelines, or policies for conducting responsible aquaculture (e.g., Turner, 1988; GESAMP, 1991, 1996, 2001a, b, c; Working Group on Aquaculture, Standing Committee on Fisheries and Aquaculture (Australia), 1994; FAO, 1995, 1997; FAO and Government of Japan, 1995; ICES, 1995; Reinertsen and Halland, 1995; Bartley et al., 1996; Pullin et al., 1999; Secretariat of the CBD, 2004 [also see http://www.fao.org/documents]). Several organizations and companies award certifications or recognition for practicing environmentally conscientious aquaculture (e.g., British Columbia Innovation Council, Canadian Aquaculture Industry Alliance, FAO, Global Aquaculture Alliance, NACA, North Atlantic Salmon Conservation Organization [NASCO], World Bank, World Wildlife Fund). Many articles and books have been written that document the general environmental problems common in the practice of aquaculture and provide principals and methods for developing sustainable aquaculture systems and programs (e.g., Welcomme, 1988; Barinaga, 1990; Pillay, 1992; Pullin et al., 1993; Lassuy, 1995; Schramm and Piper, 1995; Thorpe et al., 1995; Azeta et al., 1997; Bardach, 1997; Barg and Phillips, 1997; Goldburg and Triplett, 1997; Tringali and Bert, 1998; Svennevig et al., 1999; Bert and Tringali, 2001; Bert et al., 2001; Black, 2001; Goldburg et al., 2001; Naylor et al., 2001; Read and Fernandes, 2003; Bello et al., 2004; Leber et al., 2004b). Lastly, a number of

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[1] In this chapter, I use the term ''environmental effects'' in a very broad sense—inclusive of ecological, genetic, and biodiversity effects on all living natural ecosystem components and their independent and interactive processes as well as effects on nonliving ecosystem components. This special usage allows me to dispense with longer phrases, such as ''ecological, biological, genetic, and biodiversity effects,'' when discussing the broad range of aquaculture effects that affect natural ecosystem components. Similarly, I use ''environmental'' in the broad sense, to refer to living organisms and their interactions plus the habitats in which they live. When the adverse effects under discussion are pronounced and widespread, I use the term ''impacts'' rather than ''effects.''

national and international organizations have as a focus of their attention and efforts the promotion of environmentally responsible aquaculture (e.g., Asian Wetland Bureau, European Inland Fisheries Advisory Commission, Global Aquaculture Alliance, International Union for the Conservation of Nature and Natural Resources, NASCO, United Nations through the FAO and the United Nations Environmental Program, WorldFish Center [formerly ICLARM, the International Council for Living Aquatic Natural Resources], and a number of national and international fishery commissions and oversight groups).

Aquaculture leaders and relevant governmental officials, as well as industry workers, have been acutely aware of the constant and notable attention given to the industry's activities and their sometimes negative effects on the environment. Numerous articles on reducing aquaculture effects have been published in journals such as *Aquaculture, Aquaculture International, Aquaculture Research*, and *World Aquaculture*, the trade periodical of the World Aquaculture Society. Thus, aquaculture societies and associations from the local to the international level have begun to address these problems and adhere to standards of practice that minimize environmental effects.

Why has this worldwide attention developed regarding aquaculture? Aquaculture, in some form, has been a type of farming for centuries. For example, in the 1500s in northeastern Bolivia prior to the influence of western civilization, native people constructed fish-weir habitats to constrain and farm fish that entered their savannah/forest-island homeland during the rainy season (Erickson, 2000). Their culture probably developed around building and maintaining those weirs and tending the entrained fish (Erickson, 2000). Now, the benefits associated with aquaculture extend beyond simply providing food. Aquaculture, if conducted in an environmentally safe manner, can provide many benefits to ecosystems and humans, including the following:

1. Aquaculture shows great potential for providing food to alleviate the poverty of people living in coastal areas, particularly those who are among the poorest people in the world (GESAMP, 2001b). For example, in South America, aquaculture has contributed to foreign exchange earnings and to employment in areas where employment opportunities are few, so it has slowed migration of the rural poor to outlying areas of major cities, which usually do not have the infrastructure (e.g., water, sewage, roads, power) to support them (Hernández-Rodríguez et al., 2001).
2. Aquaculture can sustain small communities where commercial fishing has severely declined (e.g., Colson and Sturmer, 2000) and can help diversify income for small agriculture farmers (Goldburg and Triplett, 1997; Pullin, 2001). In some cases, these people can raise either low-cost fish for food or high-value fish for export, depending on which products have the greatest immediate economic benefits (Williams, 1997).
3. Aquaculture helps conserve wild fishery stocks (e.g., Wang, 1999; Williams, 1999) and, thereby, helps conserve genetic and species biodiversity and ecosystem integrity (Beveridge et al., 1997).

4. Aquaculture, particularly of mollusks or aquatic plants in areas of adequate water movement, can be used to clean certain types of wastewater (Prein, 1995; Beveridge et al., 1997; Goldburg and Triplett, 1997).
5. Integrated aquaculture/agriculture (e.g., insectivorous fish/rice farming) can improve the ecological sustainability of agriculture systems (Lightfoot et al., 1993; FAO et al., 2001) by reducing the need for chemical treatments such as fertilizers or pesticides (Barg and Phillips, 1997) and can increase biological diversity of the farmed habitat.
6. Aquaculture wastewater channeled through constructed, associated wetlands and holding areas can purify the water (Mires, 1999) and provide habitat for coastal plants, birds, and other wildlife (Pullin, 1993; T.M. Bert, personal observation). Sedimentation ponds and mechanical filters, as well as constructed wetlands, can serve as aquaculture wastewater catchments that trap waste products for use as fertilizer in agriculture (Pillay, 1992; Goldburg and Triplett, 1997).
7. Integrated aquaculture and polyculture can be used to reduce eutrophication.
8. Freshwater- and sea-ranched species can be used to help control pests and predators in the wild. For example, carp are introduced and allowed to range freely in isolated water bodies (e.g., ditches) to control freshwater aquatic plants. In the marine environment, wolf fish (*Anarhichas lupus*) can be sea-ranched to prey upon the sea urchins (*Strongylocentrotus droebachiensis*) that eat Norwegian kelp forests.
9. Stock enhancement and stock restoration can assist in the recovery of depleted or extirpated fish or invertebrate stocks (e.g., Barg and Phillips, 1997; Kongkeo, 2001; Moksness, 2004; Wilbur et al., 2005).
10. Open-water mollusk farming can increase local spat supply (Beveridge et al., 1997).
11. Net-pens, cages, or mollusk farming structures can attract wild fish and serve as substrates for sessile invertebrates and aquatic plants (e.g., Soto and Jara, 2007).
12. Aquaculture stimulates research on the levels and organization of genetic variability in aquatic species and on the use of genes and genomics to develop genetically modified organisms.
13. Aquaculture products are used to control undesirable animals and plants and to produce fine chemicals and bioactive compounds.

Aquaculture is the most rapidly expanding type of farming in the world (FAO, 2004). Its growth in the past two decades has been profound. Assisted by governmental promotions and financial assistance in some countries, global production of farmed fish and shellfish doubled between 1987 and 1997, and continues to rise dramatically. Aquacultured animal products currently account for more than one-third of all seafood consumed by humans (Goldburg et al., 2001; Naylor et al., 2001). Over the past 20 years, demand for fish and shellfish has greatly increased, but in the past ten years, global production of wild fish has remained at a plateau of about 85–90 million metric tons (FAO, 2004), principally due to overfishing of selected species and degradation of critical habitat worldwide (Goldburg and Triplett, 1997; Leber et al., 2004a). Thus, wild-caught fish and shellfish cannot meet current world demands. This situation will not change in the near future because most currently harvested aquatic species are fished at the maximum sustainable levels or are overfished (Pauly and Christensen, 1995; Pauly et al., 1998; Leber et al., 2004a). As world fisheries become increasingly depleted (Pauly et al., 1998), aquaculture is increasingly seen as a way to directly replenish wild stocks and to provide food-fish and shellfish for human consumption without further depleting wild stocks, despite highly visible reservations (Masood, 1997; Naylor et al., 1998, 2000, 2001). Because this benefit could also include providing considerable food security and economic input to remote, resource-poor areas, it could contribute to the economic empowerment of the people in those areas (Jia et al., 2000). Aquaculture can also be less detrimental to ecosystems than fishing and more efficient in producing animal protein than terrestrial livestock production (Goldburg et al., 2001). For these reasons, it is important that aquaculture be conducted sustainably and with minimal negative environmental and sociological complications (FAO, 1997).

2. NEGATIVE EFFECTS ASSOCIATED WITH AQUACULTURE

Some types of aquaculture may effect the surrounding ecosystem less than others (Read and Fernandes, 2003), but all types effect native ecosystems to some degree. Overall, perhaps the most worrisome aspect of aquaculture effects is that they typically cannot be predicted until they occur; and they can be extensive, complex, and irreversible. Following is a description of many problematic aquaculture effects that have been recognized in the literature. Some are common to many types of aquaculture, whereas others are specific to, or more pronounced in, certain types of aquaculture. Consequently, the effects listed below are categorized by type of aquaculture. Many are further described in the publications cited above and in the chapters within this book.

The following problems are most commonly associated with many types of aquaculture practices:

1. Densely packing farmed aquatic organisms generates some of the same environmental contamination problems as densely packing farmed terrestrial animals such as chickens or pigs. Nearby waters can become contaminated, nearby lands can be altered, and local plant and animal communities and ecosystems can be damaged.
   a. Surrounding or recipient waters can become enriched with nutrients, organics, and chemicals (including toxins). This, in turn, can lead to eutrophication and possibly harmful algal blooms (Chua, 1993), salination and pH changes, increased turbidity, anoxia, and the death of pelagic wild larvae and juveniles (Gowen and Rosenthal, 1993). However,

    the overall effect of aquaculture on water bodies compared to the effect of agriculture has been questioned (Boyd, 1999). Incorrectly applying feeds to or overfeeding farm animals and directly discharging wastewater or wastes into open or flowing water bodies are common sources of water pollution generated by aquaculture.
   b. Sediments beneath receiving waters and net-pens can become degraded to the point of anoxia. This, in turn, can result in alterations in benthic communities and accompanying declines in their biodiversity, possibly to the extreme of azoic conditions (e.g., Gowen and Rosenthal, 1993; Yokoyama et al., 2007). Discharging wastes and wastewater into aquatic systems with little water exchange and locating net-pens in areas with low levels of water circulation are two common causes of these problems.
   c. Coastal wetlands and marshes can become degraded. This, in turn, can lead to local or regional effects on fisheries because these environments serve as nursery grounds for many economically important vertebrate and invertebrate species (Naylor et al., 1998). Damages include physical alteration of the area, degradation of the habitat, and depletion or elimination of coastal resources (e.g., wood and bamboo to construct aquaculture facilities, larval fish and invertebrates to stock culture ponds and tanks, fish and invertebrates to feed cultured animals [Beveridge et al., 1997]). These damages, in turn, result in increased siltation in neighboring areas; salinity changes in groundwater; and loss of critical habitat for young life stages of all types of species, including those that support fisheries. However, although these are frequently cited effects of coastal aquaculture, their actual extent compared to other coastal effects such as urbanization and other industrial development has been challenged (Boyd, 1999). Coastal land alteration to build aquaculture facilities and the discharge of untreated wastes and wastewater are two principal causes of these problems (see e.g., Williams, 1999).
2. Nonnative aquacultured species can escape into the environment. This can lead to a plethora of problems (e.g., Thorpe et al., 1995; FAO, 1999; Strayer, 1999) that usually cannot be remedied because escaped animals cannot be recalled. Effects include disruption of community structure and degradation of the environment, sometimes to the point of ecosystem alteration (Williams, 1999); depletion of endangered and fishery species; reduction in fitness of native-species populations; and introductions of alien parasites and pathogens through infected or infested aquacultured individuals (Phillips and Barg, 1999; Williams, 1999; Goldburg et al., 2001). However, interactions between wild fish and escaped hatchery fish are complex. For example, sometimes negative effects of hatchery fish or hatchery/wild hybrids on purebred wild fish at one life stage are offset by superior performance of the purebred wild fish at another stage (e.g., Youngson et al., 1998). The cause of these problems is the farming of species, varieties, or forms that are not indigenous to the area in which the aquaculture operation is located.

3. Wild stocks can be depleted through a variety of mechanisms.
    a. Seed individuals (e.g., larvae) are collected from the wild or wild juveniles and adults are harvested for use as food for cultured fish (Beveridge et al., 1997; Sandnes and Ervik, 1999). These practices can effect fisheries by reducing recruitment of seed stocks needed for fisheries or by depleting food sources for harvested carnivorous species. The causes of these problems are the use of wild individuals as sources of seed for aquaculture operations and the extensive use of wild fish to feed cultured fish (Pauly et al., 1998).
    b. Wild species can be preyed upon by escaped or released farmed individuals, which can, in turn, deplete native-species populations, disturb animal and plant communities, or alter ecosystems. The problems are exacerbated as the ratio of hatchery fish to wild fish increases. The hatchery fish can be native or alien to the region; the wild fish can be conspecific (individuals of the same species) or other species. The causes of these problems are the escaped hatchery species, which can have advantages in predatory or competitive ability compared with wild fish.
    c. Species attracted to the aquaculture operation, such as predatory shorebirds, seals, or large fish can be locally depleted if they are shot, speared, or entangled while trying to feed on captive aquacultured species (Beveridge et al., 1997). These species are attracted to the high concentrations of cultured fish or invertebrates in certain types of aquaculture facilities (e.g., exposed ponds, cages, or rope lines).
4. Chemicals, drugs, or poisons (e.g., chemotherapeutics, fungicides, parasiticides) can be ingested or absorbed by wild species (Phillips et al., 1993; GESAMP, 1996; Phillips and Barg, 1999). This, in turn, can contaminate animal or human food sources and lead to the mobilization of these substances throughout the aquatic ecosystem. Wild species can ingest these toxic substances directly or by consuming other organisms that have ingested and accumulated these substances (Austin, 1993). The source of this problem is heavy use of chemical substances to keep cultured species healthy and aquaculture facility water and structures free of contaminants and fouling organisms.
5. The genetic diversity[2] of wild populations can be altered after hatchery fish are added to those populations. This is a broad topic that can have long-term, irreversible effects on the genetic diversity of wild populations if cultured animals that have escaped or have been purposefully released interbreed with the wild populations. The consequences can be complicated. Because the ultimate outcome may not be expressed in the admixed population (hatchery + wild + products of their hybridization, if hatchery and wild

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[2] Here defined as *genetic variability*—the alleles collectively present in the stock, population, species, or higher taxonomic unit under consideration—and *genetic composition*—the frequencies of those alleles in the same unit.

individuals interbreed) for several generations, genetic damage can be difficult to identify (see e.g., Campton, 1995). The many causes of genetic effects to wild populations include the use of low numbers of broodstock individuals or effective population sizes (N_es; see Ryman and Laikre, 1991) to generate hatchery broods designated for release; the release of too many hatchery individuals relative to the number of wild conspecifics in the recipient population; the release of broods with significantly different levels of genetic diversity than that of the recipient population; or extensive interbreeding between hatchery individuals and wild conspecifics. More than one of these factors can act on recipient wild populations; and interbreeding between stocked hatchery fish and wild fish is not necessary for some of these factors to have an effect on recipient populations. The cause of these problems is poor genetic management of the stock enhancement project.

6. Fitness components of cultured populations can be reduced over generations. Using brood animals as the subsequent generation of broodstock, particularly small numbers of individuals or N_es, can contribute to a suite of physiological, morphological, behavioral, reproductive, or developmental abnormalities that can negatively effect the fitness of hatchery animals; including the critical components of growth, reproduction, and survival (see e.g., Bert and Tringali, 2001). Exchanging cultured animals among hatcheries over generations can only partially and temporarily mitigate this problem. The cause of reduced fitness in hatchery populations is failure to introduce new individuals into hatchery broodstocks or using small numbers of broodstock individuals each generation.
7. Aquaculture activities effect humans in several ways. Other activities of individuals or groups of humans (e.g., recreation, tourism, fishing, working) can compete with aquaculture for coastal space (Gowen and Rosenthal, 1993). Coastal environments used by humans can become degraded through aquaculture pollution. Pests, parasites, or diseases can be transmitted to humans or their animals (including fisheries species) through introduction of aquacultured species that act as vectors or intermediate hosts (King, 1993). Aquatic or terrestrial habitats can be altered by aquaculture facility development and operation. Causes of these problems are the broad array of human interests in, and advantages to, living and working near water bodies (e.g., availability of multiple living and nonliving natural resources for industrial and domestic use, consumption, and esthetic enjoyment; facilitation of transportation).
8. Strong, well-directed regulations governing aquaculture may be absent or enforcement of existing regulations may be problematic. These can be particularly difficult problems in countries with extensive subsistence and small-scale aquaculture operations and countries with substantial areas of undeveloped and sparsely populated land. Even in Taiwan, where aquaculture is common, regulations governing stock enhancement are inadequate

(Liao, 1997). Causes for these problems include influence and pressure on governmental bodies from external sources that oppose regulation; lack of physical or logistical ability to enforce existing regulations; lack of education about the rationale for regulations; and lack of knowledge, technical expertise, and financial ability to conduct environmentally responsible aquaculture.

Some types of aquaculture—stock enhancement, nonnative-species fisheries, shrimp farming, and finfish net-pen farming—are particularly predisposed toward generating certain types of effects. Stock enhancement can compromise the genetic diversity of recipient populations in several ways:

1. Overstocking can cause genetic damage to recipient wild stocks. The purposeful release of hatchery animals to supplement depleted wild stocks creates multiple avenues for genetic damage because, in many cases, hatchery broods do not possess all or most of the genetic diversity possessed by recipient populations. Wild-population genetic diversity can be reduced through interbreeding with stocked hatchery individuals. Admixed hatchery/wild populations can have significantly reduced genetic diversities without interbreeding if the ratio of hatchery animals to wild animals is sufficiently high. The sometimes complex and usually detrimental effects of reduced genetic diversity have been well documented and addressed by many aquaculture scientists (e.g., Ryman and Laikre, 1991; Campton, 1995; Tringali and Bert, 1998; Bert et al., 2007; Hindar and Fleming, 2007).
2. Wild stocks can be inadvertently overharvested. A purpose of stock enhancement is to contribute individuals to fishery stocks beyond the number recruited from the wild population because the wild population is depleted to the point at which humans believe that intervention is needed. Thus, compared to the numbers of individuals in recipient wild populations, relatively high numbers of hatchery fish can be introduced. Wild-population components can be inadvertently reduced to numbers that preclude their continued viability unless care is taken to ensure that they are not overharvested simply because large numbers of fish are harvested. If a wild population is depleted, its collective local adaptation and genetic diversity can be reduced.
3. The environment's carrying capacity can be exceeded by stocking. In both the stocked-fish and wild-fish populations, competing for food and living space beyond that which the habitat can provide could negatively effect many life history components, including growth, reproductive capacity, and survival (see e.g., Flagg et al., 1995; Cooney and Brodeur, 1998).
4. The overall fitnesses of admixed populations (including fishery stocks) can be decreased. Stocked hatchery broods can have lower fitness in some life history components than recipient wild populations (see e.g., Philipp and Claussen, 1995; Olla et al., 1998; Ranaka et al., 1998; Youngson et al., 1998). This effect typically occurs because nonindigenous strains, which usually have altered genetic diversity compared with recipient populations, are

added to locally depleted populations (Philipp et al., 1995) or because hatchery broods that have become domesticated to some extent in the hatchery have lower fitness than the recipient wild populations. The net result is reduced fitness of admixed populations.

Nonnative-species fisheries originate from two sources. (1) They are intentionally introduced into the wild for ranching or sportfishing and sometimes are only casually tracked or monitored. (2) They sometimes escape from hatchery facilities in numbers sufficient to generate feral, self-sustaining populations capable of supporting fisheries. These types of aquaculture-based fisheries are not uncommon (Bardach, 1997) and some have caused more problems than they have solved (see e.g., Courtenay, 1995; Lassuy, 1995). The following effects commonly accompany these types of fisheries:

1. Native species are purposefully eliminated to facilitate the successful introduction of the alien species (Rinne and Janisch, 1995).
2. Some species of tilapias (*Oreochromi*s spp.), salmon (e.g., *Salmo salar*) and carp (e.g., *Hypothalmichthyx molitrix*) have become nearly circumglobally distributed (Bardach, 1997). This has caused an array of sometimes complicated and drastic types of environmental damage to native ecosystem constituents and processes (Fitzsimmons, 1997; Pullin et al., 1997; Paez-Osuna et al., 2003).
3. Nonindigenous species populations predominate in some areas. In sufficient numbers, nonindigenous species can alter or destroy the structure of local ecosystems by shifting native species' relative abundances and relationships to each other or driving them to local, regional, or (in the case of endemic species with limited ranges) total extinction. The introduced species can disproportionately consume critical components of the food web (e.g., keystone or intermediate-level predators, herbivores, or plants), physically alter critical habitats, ecologically displace native species, or directly prey on native species (OTA, 1993; Lee, 1995; Rinne and Janisch, 1995; Volpe et al., 2000; NACA and FAO, 2001). If the introduced species become naturalized, these problems become permanent.

The most troubling prospect associated with introducing nonnative species into the wild is that the type, magnitude, and reversibility of the consequences are unknown. In addition, their effects may be indescribable because baseline data on the original composition and structure of the affected ecosystem are lacking (although some progress has been made in that arena; Pullin et al., 1997). A number of authors in this book document the problems their respective countries face because of the introduction and transplantation of nonnative species for fisheries development (but see Vigliano and Alonso, 2007; Pascual and Ciancio, 2007).

Of all aquaculture activities, shrimp farming, principally of M*acrobrachium rosenbergii*, *Litopenaeus vannamei*, and related genera and species, is among the most frequently cited as being environmentally destructive, particularly in some Asian and Central American countries (e.g., Boyd and Clay, 1998; Shiva, 1999).

Moreover, the destructive elements can act synergistically, resulting in spectacular failures of shrimp farms and widespread environmental damage (see e.g., Vivekanandan and Kurien, 1999). The cost:benefit ratio of shrimp farming is so high that Naylor et al. (2000) have suggested that shrimp farms do not pay for the environmental damage they cause and ocean resources they consume. The environmental effects commonly associated with shrimp farming are varied and can be extensive.

1. Wetlands and coastal mangrove forests are degraded or destroyed because the land is restructured for building aquaculture farms and associated roads, dykes, and canals (e.g., Primavera, 2005). These important natural resources protect against the wave action of tropical storms and other oceanic upheavals (e.g., tsunamis); prevent erosion of coastal land by anchoring shifting mud; serve as sources of biodiversity and nursery grounds by providing shelter, habitat, and food for fish and other marine life; and provide lumber, charcoal, tannin, dyes, and food for humans (Hossain et al., 2004). They are difficult to reclaim if the shrimp farm is abandoned (Naylor et al., 1998). In addition, the actual extent of this effect is difficult to assess because no standardized, reliable, long-term statistics exist that would allow us to compare the extent of mangrove destruction by shrimp farming with destruction caused by other sources (Bardach, 1997).
2. Diseases are transmitted both between shrimp farms and from the shrimp farm to wild populations (JSA Shrimp Virus Work Group, 1997). Shrimp viruses, which are easily transmitted between shrimp farms through the transfer of larval seed stocks, can ravage production levels in shrimp farms and devastate local wild shrimp populations. Poor management of shrimp farms is cited as the most common cause of this problem (e.g., Hossain et al., 2004).
3. Nonnative species can become established in the wild (AFS, 1997; DIAS, 1999). Because shrimp farms are located along coastal areas, any natural event that elevates sea level and generates waves that overrun shrimp aquaculture ponds will wash cultured shrimp into the ocean. In addition, shrimp are released into the sea by aquaculture workers for a variety of reasons (e.g., disease, mechanical component failure in the facility, closure of the facility).

Notably, in recent years, the aquaculture industry has put much effort into working with scientific and economic researchers to ameliorate the effects of shrimp farming.

Numerous authors have documented all types of damage in the vicinity of net-pens that house aquacultured fish, including the following:

1. Untreated waste discharge degrades the water column and sediments. Because net-pens and cages are placed in open water, they have the greatest potential to cause this type of damage (Goldburg and Triplett, 1997). The highest levels of contamination are in the near-bottom water and upper sediment layers that are in close proximity to the net-pens. Types of contaminants include high levels of precipitated or remobilized heavy metals

(Cd, Cu, Fe, and Zn); undesirable chemicals such as sulfuric acid and ammonia; algal blooms; and shellfish, fish, and human pathogens (Beveridge, 1996; Belias et al., 2003; Nash, 2003). Near to total anoxic conditions generate azoic sediment conditions. The level of effect is related to the amount of food given to the fish, method of feeding, density of fish in the cages, annual production, years of operation, local hydrology and geomorphology (Belias et al., 2003; Yokoyama et al., 2007), and proximity of the bottom of the net-pen to the sea floor (Yokoyama et al., 1997; Holmer et al., 2002).

2. Captive fish escape. Captive fish are very likely to escape from net-pens that are located directly in open water. There, the net-pens can be subject to plummeting by wave action and by large predators trying to feed on the captive fish. Escaped fish can compete with or prey upon local wild fish; become naturalized, thereby changing local or regional ecosystems and affecting existing fisheries; or interbreed with local species and disrupt locally adapted gene pools.
3. Fish diseases, pests, and parasites can be transmitted to wild species. The close packing of single fish species in net-pens promotes the spread of fish diseases and development of large populations of fish parasites and pests (NMFS and FWS, 2000), such as the sea lice that ravage salmon reared in net-pens in Chile and elsewhere (McVicar, 1997; Finstad et al., 2000). These afflicters can also invade local wild populations and cause considerable damage to them.

The effects of aquaculture on the environmental are often so intertwined that the lists above constitute only a generalized framework for the actual effects. In many cases, the effects act together, creating a unique set of complications that can be difficult to disentangle and address.

The effects of aquaculture on the environment are only one component in a complex suite of problems. Aquaculture activities can affect aquaculture operations themselves (New, 1999). The water pollution (King, 1993) and disease transmission common in high-density intensive fish cage culture and shrimp farms effect productivity. Excessive collecting of wild shrimp postlarvae for stocking aquaculture ponds depletes the stocks needed for future pond seeding. Damaging local mangrove systems to build ponds destroys the larval shrimp nursery habitat. Packing cultured animals in high densities can pollute the immediate environment around the aquaculture facility. Introducing diseased broodstock individuals or moving diseased animals among aquaculture facilities can decimate production. Most effects of aquaculture practices on aquaculture operations are the consequences of poor management and site selection (Stickney, 1997; Thia-Eng, 1997).

Aquaculture can also be affected by outside sources, sometimes to the complete demise of the aquaculture operation. Polluted intake waters threaten the life-support system that aquaculture depends on. Water contaminated with domestic sewage, municipal runoff, and agricultural or industrial wastes can be loaded with pathogens, chemicals, and poisonous organic pollutants

(Pullin, 1993; Barber, 1997; GESAMP, 2001c; Paez-Osuna et al., 2003). Even underground water used as freshwater-inflow sources can be contaminated (Thia-Eng, 1997). Cultured shellfish can be particularly susceptible to these pollutants. Trace chemical contaminants (e.g., metals, organochlorines) can be transferred to cultured fish (especially mercury) and shellfish (especially cadmium) and then to humans, who consume the contaminated animals (Phillips, 1993). Events such as outbreaks of red tide organisms and other noxious algal species can also effect aquaculture systems that use unprocessed water or that are located in open water (Austin, 1993). Physical degradation of aquatic habitats due to residential or commercial development can lead to reduced productivity, disease outbreaks, contamination of aquacultured organisms, or mass mortalities in open-water aquaculture systems that rely on these resources (Barg and Phillips, 1997). In populated or desirable coastal areas, competition with other uses of coastal and nearshore waters—such as for boating, fishing, commercial shipping, port development, or urban expansion—can eliminate opportunities for new development of aquaculture in those areas or cause existing aquaculture operations to shut down (Thia-Eng, 1997).

2.1. Biodiversity Preservation and Aquaculture

In part because of their biodiversity, aquatic environments are by far the most valuable ecosystems on earth in terms of natural capital and provision of services (Costanza et al., 1997). The value of that natural capital is becoming realized in aquaculture. However, it is the practice of growing things in water, regardless of the objectives of a specific aquaculture endeavor, that must be considered regarding its effects on biodiversity.

A common theme in discussing the environmental effects of aquaculture is reduction in biodiversity. The Convention on Biological Diversity (CBD, 1994), and the United Nations (Bartley and Pullin, 1999) recognize three levels of biodiversity—genes and their gene pools, species and their populations, and ecosystems and their communities. Others have recognized even more levels of complexity, intricacy, and interaction (e.g., Noss, 1990). Each level of the biodiversity hierarchy—from genetic, through organismal, population, species, community, and ecosystem—has specific unique functions that contribute to the overall health of biological systems by providing some defense against adverse effects and by acting an aid to recovery from those effects (Bartley and Pullin, 1999). Moreover, each level provides support for the other levels. The loss of biodiversity at any single level ultimately affects biodiversity at all levels.

Native-species genetic diversity and the hierarchical partitioning of the gene pool can be affected by intentionally or inadvertently releasing genetically limited, nonnative, or genetically altered individuals (Pauly et al., 1998; Naylor et al., 2000). Species' gene pools are particularly susceptible to alteration through the many activities associated with stock enhancement (see e.g., Bert et al., 2007). Poor hatchery breeding and rearing protocols can generate broods with restricted or altered genetic complements compared with wild conspecific populations. The release of these hatchery broods into the wild can disrupt or overwhelm native-species gene pools, with or without interbreeding between hatchery animals and wild animals. Natural species diversity and species' population structures can be altered or depleted by humans through any of the following activities:

1. inadvertently harvesting excessive numbers of individuals in particular populations to use as aquaculture seed stock;
2. introducing aquacultured broods from different populations;
3. excessively harvesting wild fish to feed cultivated fish;
4. introducing nonnative species, which can disrupt native-species' food webs, habitats, or life history cycles;
5. introducing cultured fish that harbor alien parasites and pathogens.

Ecosystem diversity and community structure can be affected by the following activities:

1. modifying or destroying habitats to construct aquaculture facilities;
2. overusing ground or surface water;
3. polluting surface water and land through disposal of solid and liquid wastes;
4. introducing nonnative cultured species.

The loss of biodiversity is far greater in freshwater aquatic systems than in terrestrial ecosystems (Johnson et al., 2001). In fresh waters, a host of other activities detrimental to aquatic systems (e.g., deforestation, aquatic mineral mining, channel dredging, pollutant dumping, overfishing) occur concurrently with the practice of aquaculture; and fresh waters are more finite, and therefore less resilient, than marine systems. Effects to biodiversity at all levels are most pronounced in freshwater environments in developing countries, where the roads can be the rivers, streams, and coastal waters and where monitoring and regulating those effects is particularly difficult.

The CBD (1994) required that policies be established for conserving and using biodiversity at each of the three levels in aquatic systems. Other prominent scientists and scientific groups (e.g., Noss, 1990; Williams, 1999; Gaston, 2000) have also advocated a hierarchical approach to biodiversity conservation. Aquaculture managers should work with natural resource scientists, policymakers, and industry associates to retain critical types and ranges of variation in natural systems to maintain their resiliency (Hollig and Meffe, 1996) because biodiversity is important for plant and animal breeding (Eldredge et al., 1999) and, therefore, for aquaculture itself.

3. CONTRIBUTIONS OF THIS BOOK TOWARD SOLUTIONS TO THE EFFECTS OF AQUACULTURE

From the above summary, it is obvious that a great deal of attention has been paid to the environmental effects of all types of aquaculture practices over at least the past decade. What, then, could another book contribute? Together, the chapters in this book address essentially all of the problems cited above, and many in specific, applicable ways. The perspective of this book is unique in that half of the chapters (Section Three) are authored by nationally or internationally recognized experts who describe in detail the specific effects of aquaculture practices in their respective countries. They provide ideas for, or practical applications of, solutions to those problems. In each country or region, each set of problems has unique properties and each set of proven or proposed solutions is customized to solve those problems.

Damian Ogburn describes the various types and practices of aquaculture in Australia from a historical perspective. He documents the effects that culturing nonindigenous species and transplanting them around Australia to establish aquaculture in new areas has had upon native Australian species, habitats, and ecosystems. He describes the various attempts to solve the problems generated by these aquaculture activities and the Australian government's participation in ensuring that aquaculture development with minimal ecological or genetic damage is advanced in that country.

Saleem Mustafa and coauthors propose that the use of repeated generations of hatchery fish, propagated originally from one or a few small founder broodstock(s), has resulted in a low but lethal level of genetically based morphological abnormalities in Malaysia's widely aquacultured Asian seabass (*Lates calcarifer*). They advocate using adequate numbers of broodstocks and regularly introducing individuals collected from the wild into broodstocks.

Tae Seok Ahn and Dongsoo Kong document in detail the ecological, limnological, and biological damages done to artificial reservoirs and their associated river systems by the Republic of Korea's burgeoning alien-fish net-pen aquaculture industry in the reservoirs. They recognize the ongoing efforts of the Korean government to reduce these damages and restore the reservoirs, provide additional ideas to further those efforts, and propose solutions to prevent damage to other reservoirs while still allowing net-pen aquaculture.

Jian-Hai Xiang summarizes the importance of mariculture to the People's Republic of China (P.R. China); describes the pollution that Chinese pond, raft, and net-pen culture operations have inflicted upon those operations themselves; and provides examples of the reductions in genetic diversity that have accumulated over generations of cultured invertebrates that are produced and used as broodstock by the mariculture industry in that country. He provides several workable solutions to these problems and additional ideas for sound mariculture management in P.R. China.

Randy Brummett describes the advantages of, and provides ample reasons for, involving all appropriate sectors of the public at the local level in the development of low-cost, cottage-industry, native-species aquaculture in the developing countries of Africa. He presents a number of ideas on how to accomplish this type of aquaculture in Africa. He describes not only the types of aquaculture operations and facilities best suited to this endeavor but also the research base, investment and marketing strategies, and educational efforts needed for empowering people to sustainably conduct this type of aquaculture.

The next several chapters describe the effects of escaped or released nonnative fishes, originally brought into South American countries for various aquaculture purposes, including stocking, on the world-class diversity of freshwater fish and invertebrate species in that continent. Many of these chapters have detailed reports of fish species diversities and distributions; thus, they are valuable baseline documentaries of South American fish biodiversity at this point in time.

Hernán Ortega and colleagues contribute an expansive documentation of the occurrence of alien (not native to their country) and translocated (native to their country but not to the river system into which they were introduced) fishes in Perú. Their chapter includes the following:

1. extensive lists documenting the locations of both native and nonnative fishes in three distinctive aquatic systems;
2. detailed information on the specific location and relative abundance of the three most commonly found alien species in one river system;
3. documentation of the apparent displacement, by the rainbow trout (*Oncorhynchus mykiss*), of the three high-altitude native species occurring in a World Heritage national park;
4. documentation of the uses for aquaculture and spread in the wild of alien fishes in Perú, based on historical records and publications, as well as their own research;
5. descriptions of two complex incidents in which alien species were introduced into areas and then a cascade of introductions were made in attempts to mitigate the effects of the initial introductions.

Ortega et al. then provide a comprehensive and diverse list of attainable solutions designed to address the following:

1. mitigating the effects of feral, problematic, alien species in Perú;
2. reducing the probability of escape and spread of aquacultured alien species;
3. reducing the use of alien species for aquaculture and fisheries;
4. better organizing and monitoring ongoing and future aquaculture operations in Perú.

Their chapter will serve as a landmark paper for future reference on the distribution of both native and nonnative fishes in Perú.

Héctor López-Rojas and Ana Bonilla-Rivero describe the general evolutionary relationships between the native fish faunas of Venezuelan river systems and document the distribution of escaped, naturalized (feral) alien freshwater fishes and invertebrates and of translocated freshwater fishes among rivers and lakes in those river systems. They note that little detail is known about species compositions, distributions, ecologies, or life histories of the native aquatic faunas of these river systems. Thus, it is nearly impossible to adequately assess the effects of feral alien or translocated species on native Venezuelan aquatic animal communities or ecosystems. Nevertheless, where possible, they evaluate the changes in Venezuelan aquatic faunal communities due to these introductions and transplantations. They support an ongoing, increased focus on obtaining information on aquatic species composition, distribution, and abundance in South American countries so that adequate assessments of changes due to introduced species can be made. They also call for education and research on cultivating native species. Their documentation of the geographic distribution of nonnative species and list of introduced and transplanted species in Venezuela can also serve as landmarks for future comparisons.

Carlos Alves and colleagues summarize the many types of introductions and translocations of nonnative freshwater fishes that have occurred in state of Minas Gerais in Brazil and the many types of effects they have generated. These include displacement of, and predation on, native species; transmission of diseases and parasites; and hybridization between native and nonnative species. They recommend increasing regulations and enforcement, broad-based education on the effects of nonnative-species introductions and on the value of native ecosystems and aquatic species, and research on the aquaculture of native species. Their summary table of the distribution of the known introduced species in Minas Gerais state can also serve as a landmark for future comparisons.

Pablo Vigliano and Marcelo Alonso—and, in a separate chapter, Miguel Pascual and Javier Ciancio—comprehensively describe the interesting and rather spectacularly positive (from some perspectives) but complex effects of salmonid introductions that occurred up to 100 years ago in the cold waters of Patagonian Argentina. Vigliano and Alonso's chapter provides the following:

1. a history of salmonid stocking throughout the region;
2. a detailed portrait of the distribution of all introduced salmonids throughout the region;
3. a summary of the relative abundances of the various introduced salmonids in the major water bodies and drainage systems of Patagonia;
4. a description of the tangled array of sometimes competing factions (aquaculturists, businessmen, conservationists, economists, lawmakers, policymakers, researchers, and sportfishermen) who view this massive salmonid introduction and naturalization as a blessing or a curse.

Their quantitative distributional assessment combined with their detailed distributional map of the various salmonid species constitute a landmark documentation of the extent of naturalization of these introduced species—and one with which future assessments can be compared.

Pascual and Ciancio provide additional details about the history of the introductions and an ecological and genetic perspective on their uniqueness. They describe their use of the ecological information available for naturalized Patagonian chinook salmon in an evaluation of the ecological effects of a proposed new salmonid introduction. They outline their development of a multidimensional impact assessment model designed to estimate the ecological costs versus economic benefits of the proposed introduction under various scenarios of successful establishment. They then describe evidence for the ecological and genetic release that previously introduced salmonid species must have experienced and elaborate on the potential for all types of biological, ecological, and genetic research on the numerous populations of these species in Patagonian Argentina and Chile.

The next trio of chapters deals with effects of aquaculture in the USA. The authors of the various chapters describe the ecological and genetic effects associated with aquaculture in the USA; relate a story about the development of a hatchery-based stock supplementation program that is ecologically and genetically responsible and describe the effort and involvement needed to achieve the program's goals; and evaluate the accomplishments of a group of salmon stock-supplementation programs.

Robert Stickney opens with an overview of the types of problems that American aquaculturists, aquaculture scientists, and conservationists commonly address in the USA. His description of American concerns mirrors the concerns of many other countries but includes esthetic concerns not typically voiced worldwide. He provides a general overview of the principal complaints directed toward aquaculture development in the USA and of the accomplished solutions to those problems.

William Smoker and William Heard describe the development and current status of the extensive Alaskan salmon ocean ranching program. They describe the habitats in which the admixed populations live and the fisheries upon which these populations are based. They then present the battery of precautions, regulations, and technological advances woven into this program to protect the ecological integrity and genetic diversity of wild Alaskan salmon populations in these mixed-stock fisheries.

Robin Waples and colleagues examine the validity of the belief that hatchery-based stock supplementation programs promote the well-being and recovery of depleted natural North American Pacific salmon populations. They closely examine numerous salmon stock supplementation programs by submitting them to an extensive, complex evaluation. They construct a set of goals that the programs should have addressed and assess the degree to which each program achieved each goal. They then evaluate the overall achievement level of each goal for salmon stock enhancement in general by totaling the program scores for each goal. From this detailed analysis, they draw an overall conclusion about the value of salmonid stock supplementation programs in the USA Pacific Northwest. Their chapter has already been cited in publications a number of times; and this work formed the basis for more extensive explorations of the value of salmon stock supplementation programs.

The remaining chapters are divided into three sections. Section One is a series of perspectives on the scope, diversity, and pervasiveness of environmental effects attributable to aquaculture activities and the long-term directions and actions needed to sustain aquaculture while minimizing the adverse effects that it can generate. The perspectives of the authors vary widely, as do their treatments of the issues.

Devin Bartley, who was the keynote speaker at the symposium upon which this book is based, explains the application of FAO's position on managing fisheries and aquaculture from an ecosystem perspective, in which humans are integral components of ecosystems. Bartley assesses the FAO's Database on Introductions of Aquatic Species (DIAS) and other literature to evaluate aquaculture's role in introducing aquatic alien species throughout the world, the parties responsible for the introductions, and the outcomes of the introductions. His recommendations focus on the importance of worldwide cooperation in monitoring and reporting all types of effects (both positive and negative) from aquaculture activities to facilitate addressing the problems associated with aquaculture practices using the ecosystems approach.

Roger Pullin and colleagues, in a forward-thinking chapter, focus on the future of aquaculture and provide a set of biological, ecological, and socioeconomic indicators by which to measure the likelihood that aquaculture activities and production can be sustainable. They evaluate the accessibility of data to apply to these indicators and the probability that the aquaculture industry and organizations that monitor the industry's actions will use the indicators to fulfill their obligation to ensure that aquaculture continues to be a valuable, viable source of food production for world needs while minimizing its environmental footprint.

Nai-Hsien Chao and I-Chiu Liao summarize the most common types of aquaculture activities that generate ecological and genetic problems. They suggest a dual approach for minimizing those effects and for facilitating the long-term, continuous, environmentally responsible expansion of all types of aquaculture for future food production.

Although a number of chapters mention genetic issues related to aquaculture, the four chapters in Section Two deal directly with genetic concerns, and in very different ways. Together, these chapters document and illustrate the variety of genetic problems that effect aquacultured organisms and the populations they come into contact with, and they offer both long-term directions and actionable procedures and recommendations for avoiding those problems.

Dennis Hedgecock and Katharine Coykendall examine a potentially very damaging genetic effect associated with stock enhancement—the genetic swamping of recipient wild populations with hatchery-bred broods of limited genetic diversity. They use modeling applied to a California (USA) chinook salmon (*Oncorhynchus tshawytscha*) stock enhancement program to demonstrate that in some situations, hatchery-based stock enhancement can actually increase the effective size (N_e; after Ryman and Laikre, 1991) of recipient populations. To the extent possible, they apply their model to marine stock supplementation programs and offer advice on the genetic monitoring of those programs.

Peter Grewe leads a list of authors who describe a method of gene insertion that generates individuals that are sterile in the wild but fertile in the hatchery. They propose a number of applications for this technology and call attention to the potential for using these genetically modified organisms in aquaculture. They also recognize the attendant need for guidelines, policies, and regulations to govern the development and uses of organisms that have been genetically altered for aquaculture so that genetic risks to wild populations are minimized.

Kjetil Hindar and Ian Fleming focus on Atlantic salmon (*S. salar*) broods generated for stock supplementation in Norway. The broods are the products of continuous generations descended from a broodstock composed of fish collected 30 years ago. They contrast genetic changes and hatchery adaptations that have occurred in this captive population over the generations with the genetic diversity and adaptations of recipient wild Atlantic salmon populations. They then draw upon observational and experimental information to assess differences in a suite of biological and behavioral traits between broods spawned from the descendant broodstocks and released into the wild for stock supplementation. They compare the fitness estimates for those traits among the wild stock, hatchery fish, and hybrids between these two groups; speculate on the potential for continued viability of the recipient wild stocks; and pose solutions that could better ensure the maintenance of sufficient genetic diversity in the wild population for its long-term viability.

Theresa Bert and coauthors provide a review of the genetic effects of stock enhancement and describes the genetic “tools” and the effort needed to monitor genetics in stock enhancement programs. They include the following in their chapter:

1. reviews of the reasons for tracking the genetic diversity, fitness, and effective population size of hatchery broodstocks and broods during breeding and stocking, and of admixed populations after enhancement;
2. descriptions of the information needed, genetic tools available, and work required to conduct the genetic analyses for stock enhancement genetic monitoring programs;
3. a description of a stock enhancement program designed to maintain genetic diversity as much as possible and monitor for potential genetic problems.

Recognizing that a full genetic monitoring program is beyond the financial or logistical capabilities of many stock enhancement efforts, Bert et al. separate the components of a complete program and describe the effort needed and information that can be obtained from each component. From this information, smaller monitoring programs that capture information essential for evaluating whether the program’s goals are being attained in a genetically responsible manner can be developed.

Following the spirit of the symposium upon which this book is based, Section Four is devoted to the description of a variety of methods for minimizing the ecological and genetic effects of aquaculture. Two categories of solutions are offered: taking advantage of natural ecosystems and topographical configurations to minimize water column and benthic environmental contamination in open-water net-pen culture systems and structuring, locating, and designing aquaculture operations so that nutrients are cycled and wastes are processed within the systems and, thereby, external environmental damaged is minimized.

Hisashi Yokoyama and colleagues describe a procedure for quantifying environmental damage beneath and around densely packed marine net-pen fish farms located in an embayment system in east-central Japan. They use water quality, benthic invertebrate community composition, bathymetry, aquaculture fish production, and net-pen location in this system to develop a model for predicting potential environmental damage resulting from placement of marine net-pens in embayments. To develop their model and describe its potential for alleviating environmental contamination due to the Japanese marine net-pen aquaculture industry, they do the following:

1. evaluate concentrations of chemical elements diagnostic for estimating degree of anoxia in the water immediately above the sea floor and in the upper layer of benthic sediment beneath numerous net-pens;
2. describe the benthic macro-invertebrate communities beneath and around net-pens and develop an index to characterize the communities;
3. develop a standardized index for the bathymetry of the bay system;
4. examine various relationships among the concentrations of the chemical compounds, the values for the benthic community index, the values for the bathymetric index, the sizes (as estimated by annual production level) of the net-pen aquaculture operations, and the locations of the net-pens.

Environmental degradation in the vicinity of nearshore aquaculture net-pen farms in Japan should be reduced by using their model.

Marine polyculture has been recognized as an environmentally friendly mode of aquaculture by numerous aquaculture experts (e.g., Chua, 1993; Bardach, 1997; Goldburg and Triplett, 1997; NATS, 1998; Åsgård et al., 1999; Grant, 1999; Li, 1999; Pillay, 1999; Goldburg et al., 2001; Hernández-Rodríguez et al., 2001; Hossain et al., 2004). Three chapters in this section describe a number of benefits derived from polyculture in which marine algae are components of the culture systems. The authors of each chapter describe a different type of culture system, but all demonstrate some contribution to water purification and increased growth rate or quality of the animals cultured with the algae. They also discuss the added economic benefits of culturing salable algae with animals and reducing waste water cleanup costs through natural nutrient recycling.

Hachiro Harata and colleagues describe an experimental culture system in southern Japan in which, for six months, they compared the dissolved oxygen and carbon dioxide content of the water and the growth and condition of red sea bream (*Pagrus major*) co-cultured in net-pens with the green alga *Ulva pertusa* to the dissolved oxygen and carbon dioxide content of the water and growth and condition of red sea bream reared in net-pens without *U. pertusa*. The alga was also routinely harvested from the net-pens in which it was grown. It was then dried and added to the food fed to the red sea bream in the co-culture cage. Based on their results, they point out the advantages of marine polyculture systems in which macroalgae are reared in net-pens with this fish.

Muki Shpigel and Amir Neori also report on the benefits of marine polyculture systems over monoculture systems but describe more sophisticated flow-through or recirculating land-based systems that involve separate tanks or ponds for fish, micro- or macroalgae, and algivorous or phytoplanktivorous mollusks. Their systems are excellent examples of mariculture systems that can be built and operated in dry environments.

Thierry Chopin and colleagues describe two types of marine polyculture, one in which a red alga (*Porphyra* sp.) is grown in proximity to net-pen-cultured salmonids and another in which *Chondrus crispus* is cultured in close proximity to cultured mussels and oysters. They provide estimates of the amount of *Porphyra* needed to absorb the excess nitrogen and phosphorus generated per year by one metric ton of salmon and compare the growth rates of *Porphyra* grown near cultured salmonids with those of *Porphyra* grown in isolation from the salmon net-pens.

Doris Soto and Fernando Jara use information from several related innovative observational and manipulative experiments to demonstrate that in some net-pen aquaculture operations, native species and other ecosystem components can be used to assist in water and sediment purification, nutrient recycling, and bioturbation reduction. They explain how fish and benthic mollusks and crustaceans consume, and thereby mobilize and recycle, unused feed and metabolic waste products beneath and around both freshwater and marine salmon net-pens. They further suggest that these systems can generate additional economic benefit because the mollusks and crustaceans, which can be concentrated beneath the net-pens by placing artificial reefs there, and the fish, which aggregate around the pens, can be harvested.

Many chapters in this book have already proven their value. They have been cited in a number of publications and used as teaching tools in college classes. Projects they describe have formed the basis for more extensive explorations and research. Recommendations they contain have been applied to ongoing aquaculture programs or incorporated into planned aquaculture activities. Considering the aquaculture effects noted by these chapter authors together with those previously described by other experts allows identification of the aquaculture effects that are most prevalent and problematic from a worldwide perspective, as well as the most commonly recommended suggestions to reduce those effects, and the common solutions that have actually worked. These suggestions and solutions should be given priority in future legislation and policy development and in formulating plans of action for addressing the reduction of aquaculture effects throughout the world.

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SECTION ONE

OVERVIEWS OF ECOLOGICAL INTERACTIONS

CHAPTER 2

AN ECOSYSTEMS APPROACH TO RISK ASSESSMENT OF ALIEN SPECIES AND GENOTYPES IN AQUACULTURE

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Abstract: The international community is advocating an "ecosystems approach" to balance conservation and sustainable-use priorities in decision-making regarding aquaculture and fisheries development. In aquaculture, the use of alien species and genotypes, which are also known as introduced species and genetically improved species, is a valid means to increase production. However, there is concern that the species used will adversely affect local ecosystems and the people that depend on those ecosystems. The Food and Agriculture Organization of the United Nations Database on Introductions of Aquatic Species (DIAS) and other relevant literature were examined to provide information on alien species. Aquaculture was found to be the primary reason for the purposeful introduction of alien aquatic species and, overall, the majority of introductions for aquaculture that were assessed had positive results. National governments constituted the group most often responsible for the introductions. Ecological and social/economic mechanisms by which introduced species could impact the environment and human communities were identified; however, very little documentation existed on the actual impact of many introductions. The majority of the impacts reported have been from disease transmission and have mostly impacted the aquaculture industry. Improved information and monitoring and the evaluation of introductions will be necessary for informed risk assessment and decision-making.

Key words: alien species, aquaculture, ecosystem, environment, exotic species, impact assessment, introduction

1. INTRODUCTION

The international community is becoming aware of the mutual dependence between conservation and sustainable use in fisheries and aquaculture development. The "ecosystems approach" has been proposed as one means to

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balance this dependence between resource use and conservation priorities. Twelve principles of an ecosystems approach were established through meetings of the Convention on Biological Diversity (CBD, 1994) and have been discussed in general terms of aquaculture development. A working group of the CBD (1999) explained that

> An ecosystems approach is based on the application of appropriate scientific methodologies focused on levels of biological organization which encompass the essential processes, functions, and interactions among organisms and their environment, and the linkages among ecosystems. It recognizes that humans, with their cultural diversity, are integral components of ecosystems.

As a consequence of using the ecosystems approach for risk assessment, consideration must be given to both ecological and economic impacts. The use of alien species and genotypes, also known as introduced species and genetically improved species, has produced both beneficial and adverse impacts (Williams et al., 1989; Lassuy, 1995; Bartley and Casal, 1999) and is one area where it will be extremely important to balance the environmental risks and the economic benefits in aquaculture and fishery development.

In the literature on introduced species, it is the spectacular successes and disasters that receive the most attention. For example, in Chile, exotic salmon account for about 20% of the world's farmed salmon production (FAO, 1997), whereas in the USA the exotic zebra mussel, introduced through ship's ballast water, has cost the US over US$ 3.1 billion in eradication and control measures over the last ten years (CRS, 1999).

However, not all introductions produce such extreme impacts, and international instruments such as the Convention on Biological Diversity (CBD, 1994) and the FAO Code of Conduct for Responsible Fisheries (FAO, 1995) are calling for accurate assessments of the benefits and risks of using exotic species. Toward this end, the FAO Fisheries Department has put information on introductions of inland fishes (Welcomme, 1988) and other taxa, on marine species, and on ecological and socio-economic impacts into the Database on Introductions of Aquatic Species (DIAS) (DIAS, 1997; Garibaldi and Bartley, 1998).

Welcomme's (1988) original data and the recently added information were acquired through international distribution of questionnaires on introduced species and through directed literature searches (Garibaldi and Bartley, 1998). Information from DIAS on fish has been incorporated into FishBase (Froese and Pauly, 1998), a relational database for the conservation and sustainable use of aquatic resources. FishBase allows users to link together various types of information on the introduced species, such as maximum size, genetic diversity, growth rates, and commercial use.

In this paper, I focus on the impacts of alien species and genotypes used in aquaculture from the broad ecosystem perspective by including social and economic considerations. Inadvertent introductions of alien species through ship's ballast water and fouling organisms (Carlton, 1985; Bartley and Minchin, 1996) also capture many headlines, but will not be covered in this paper.

2. MATERIALS AND METHODS

To assess both environmental and economic impacts from the use of alien species and genotypes, DIAS was queried to determine the following information:

1. the reason for the introduction of aquatic species,
2. who made the introduction,
3. what species were introduced,
4. the overall ecological impact of introduced species, and
5. the overall socio-economic impact of species used in aquaculture.

Other types of biological information on an alien species that could be useful in assessing impact, such as trophic status and habitat preference, were obtained from FishBase. For taxa not covered in FishBase, habitat preference was determined by examining "environment" or "habitat" fields in Aquatic Sciences and Fisheries Abstracts.

Queries to DIAS provided summary statistics on the overall effect of the introductions: a field in the DIAS data structure allows the respondent or the person evaluating literature to simply enter "beneficial," "adverse," or "undecided" regarding the nature of the impact. Because DIAS represents a combination of responses from questionnaires and information collected from literature, the classification of an impact as either "positive" or "negative" may not be objective, but could depend on the perspective of those writing the paper or filling in the questionnaire. There are also gaps in the coverage of exotic species (Bartley and Casal, 1999; Garibaldi and Bartley, 1998) and interpretation of the results should be done carefully. Nonetheless, DIAS represents a large collection of data that can be useful in the responsible use of exotic species. Although DIAS is an important initial summary and registry of introduced species, it does not provide the information needed for a more in-depth treatment of the impacts of exotic species used for aquaculture. Therefore, selected illustrative examples from the literature were also examined.

3. FINDINGS

Basic information on why introductions are made, who is making them, and what is being introduced are important first steps toward impact assessment. Aquaculture has been shown to be the primary reason for the deliberate introduction of aquatic species (Welcomme, 1988), and this is borne out by analysis of DIAS (Figure 1). The ten species most often introduced are a combination of omnivores, herbivores, and carnivores (Table 1). The group most often responsible for introductions was composed of national governments (Figure 2). Only 678 records in DIAS contained information on who was responsible for the introduction; this field was blank in 2192 records.

Biological and social mechanisms operate to influence the impact of an alien species (Table 2). However, DIAS does not allow a very complete examination

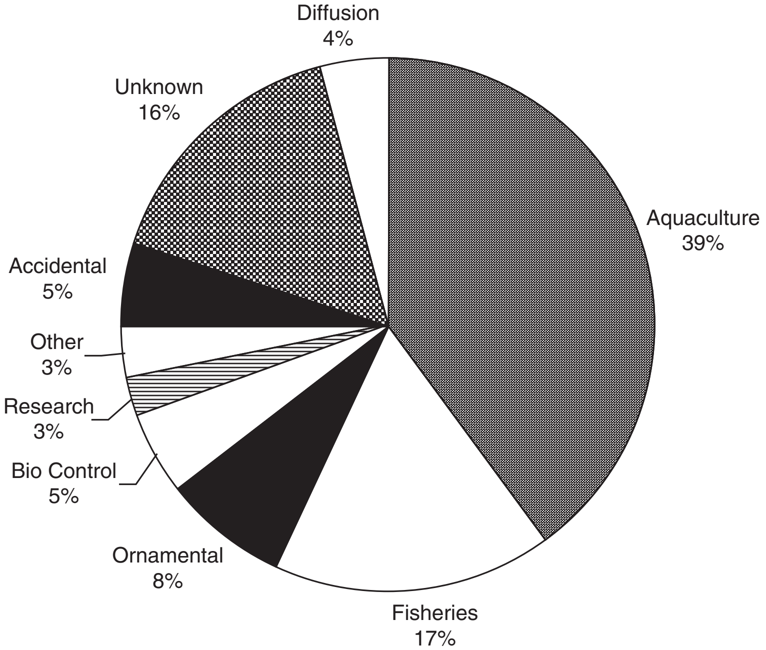

Figure 1. Reasons for the introduction of aquatic species. A total of 3,219 records from the Food and Agriculture Organization of the United Nations Database on Introductions of Aquatic Species (DIAS) were assessed. Fisheries include both sport and commercial fisheries

Table 1. The ten most commonly introduced species, according to the United Nations Food and Agriculture Organization Database on Introductions of Aquatic Species. N = number of records

Species	N	Trophic status[1]
Common carp (*Cyprinus carpio*)	119	3.1
Rainbow trout (*Oncorhynchus mykiss*)	99	4.5
Mozambique tilapia (*Oreochromis mossambicus*)	91	2.0
Silver carp (*Hypophthalmichthys molitrix*)	79	2.0
Grass carp (*Ctenopharyngodon idella*)	79	2.0
Nile tilapia (*Oreochromis niloticus*)	69	2.0
Large-mouth bass (*Micropterus salmoides*)	64	3.8
Mosquito fish (*Gambusia affinis*)	61	3.2
Big head carp (*Aristichthys nobilis*)	51	2.3
Goldfish (*Carassius auratus*)	50	2.0

[1] From FishBase: 2.00–2.19 = herbivores; 2.20–2.79 = omnivores; >2.80 = carnivores (Rainer and Pauly, 1998).

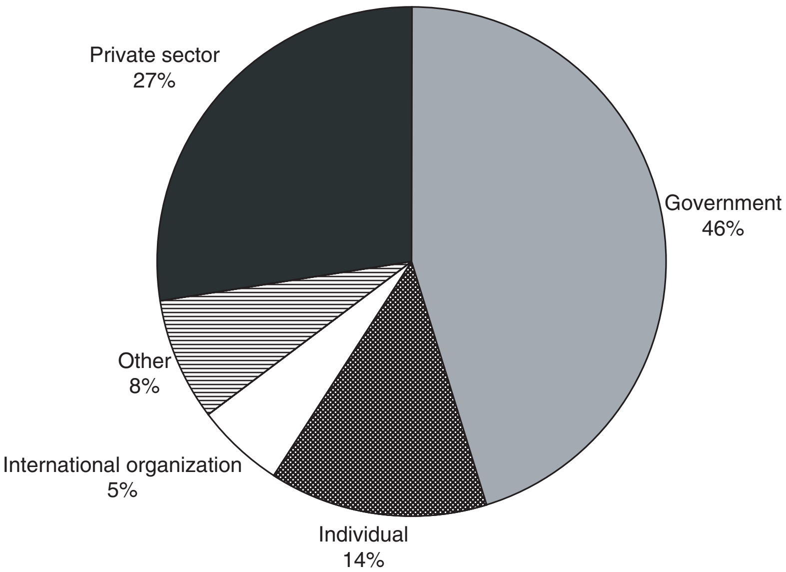

Figure 2. Groups responsible for the introduction of aquatic species. A total of 678 records from DIAS were assessed; the remaining records (see Figure 1) either were blank or the responsible group was identified as ''unknown'' and were not included in the figure

Table 2. Potential adverse effects from alien species introductions (after Bartley and Casal, 1999)

Impact	Mechanism—biological	Mechanism—social
Ecological impact		
Reduction or elimination of aquatic species	Competition, hybridization, predation/herbivory; disease; disruption of gene pool	Change in fishing pressure and access to resources; treatment to enhance alien species, e.g., predator removal
Alteration in habitat	Burrowing, sediment mobilization; removal of vegetation	Change in land use, e.g., creation of more fish farms and access roads
Social/economic impact		
Change in value of fishery resource	Change in species abundance or distribution (leads to lesser or greater value of fish stocks)	Increase in availability in market (usually reduces value of individual fish)
Change in access to resources such as land, water, and fish	Construction of ponds or reservoirs for aquaculture (may disrupt natural distribution and migration of aquatic species, which prevents fishers from harvesting them)	Construction of fences, presence of guards, or legal restrictions (often accompanies the introduction of high-value species into a waterbody, to ensure that benefits of the introduction go to those who financed it or own the resource)

of these mechanisms. More detailed ecological, and social and economic, impact assessments are presented below.

3.1. Ecological Impacts

Four broad categories exist for ecological impacts: basic species interactions such as predation and competition, genetic impacts, disease impacts, and habitat alteration. According to the records in DIAS, there were nearly as many positive ecological impacts from alien species as there were negative impacts. However, the ecological impacts of many of the introductions were undecided (Figure 3).

3.1.1. Predator–prey interactions

Moyle and Light (1996) implied that predation by alien top-carnivores is the most significant threat from introduced species. Although the generality of this statement is not borne out by an analysis of the records in DIAS (Bartley and Casal, 1999), predation directly reduces population size of the prey species, and may cause cascading ecological effects such as increased plant growth when herbivores are removed by top predators. The Nile perch (*Lates niloticus*) was introduced into Lake Victoria in the 1950s and has since directly caused the

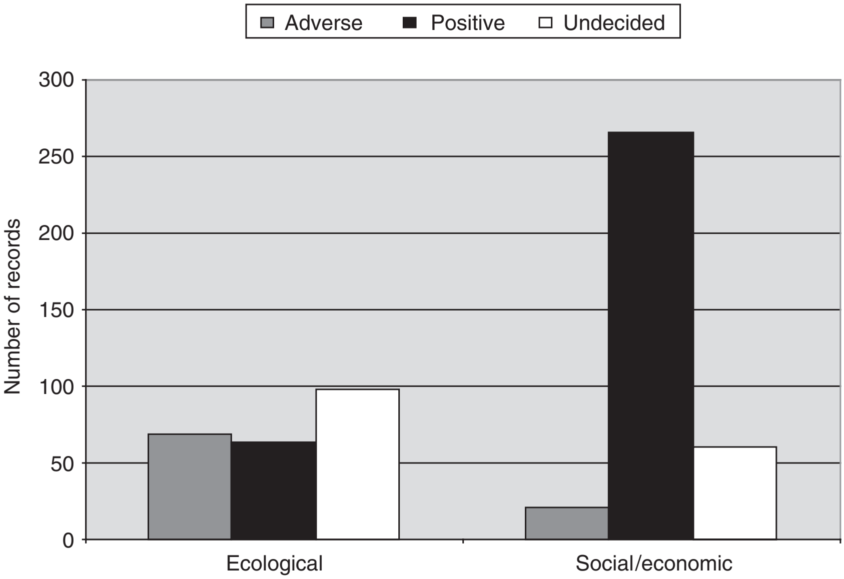

Figure 3. Types of ecological and social/economic impacts resulting from the introduction of aquatic species for aquaculture. Of the 231 ecological impact records reported in DIAS, 28% were positive, 30% were negative, and 42% were undecided. Of the 347 social/economic impact records reported in DIAS, 77% were positive, 6% were negative, and 17% were undecided

extinction of possibly hundreds of species of herbivorous and detritivorous haplichromid cichlid fishes; phytoplankton and other debris normally consumed by the haplichromids now accumulates in the bottom anoxic layer of the lake, further decreasing water quality (Barel et al., 1985). In Australia, Chile, and New Zealand, introduced Pacific salmon (*Oncorhynchus* spp.) and rainbow trout (*Oncorhynchus mykiss*) have displaced galaxid fishes, many of which are anadromous, through predation (McDowell, 1990; Arthington and Bluhdorn, 1996). Striped bass (*Morone saxatilis*) that were introduced from the Atlantic coast (USA) to the Pacific coast (USA) prey on outmigrating juvenile chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento-San Joaquin Delta (California Department of Fish and Game, personal communication). Striped bass may have also displaced juvenile white seabass (*Atractoscion nobilis*) from the northern section of their distribution by predation in coastal lagoon nursery areas (D. Bartley, unpublished report).

3.1.2. Competition

Competition can occur between alien and resident species for food, habitat, mates, or other essential resources. Resident species that have evolved together in communities partition resources; an invader disturbs this partitioning. There is a current moratorium on expansion of salmon farming in British Colombia because of *inter alia* evidence that exotic Atlantic salmon (*Salmo salar*) have escaped from cages and have reproduced in the Tsitika River of British Colombia (Volpe et al., 2000). The fear is that Atlantic salmon will outcompete wild stocks or will contaminate the native gene pool (see genetic impacts below). A similar fear is expressed in Norway, where farmed Atlantic salmon, i.e., alien genotypes, constitute about 30% of all salmon spawning and actually out-number wild Atlantic salmon in many Norwegian river systems (Gausen and Moen, 1991).

The Pacific oyster, *Crassostrea gigas*, was introduced to Australia in the 1940s and since has spread to areas where the native *Crassostrea commercialis* and the Sydney rock oyster, *Saccostrea commercialis*, are farmed. Because of high fecundity and rapid growth rate, the Pacific oyster is crowding out these local species and has been declared a pest in Port Stephens (New South Wales) (Chew, 1990; Ogburn, 2007). The Pacific oyster has been introduced into every continent except Antarctica, but only in Australia does there seem to be the concern for competitive displacement of other mollusks. This may in part be due to the fact that the Pacific oyster was often introduced into areas where the existing oyster fishery was in serious decline and therefore resources were not limiting oyster population densities (but see section on hitch-hiking organisms and habitat impact from introduced Pacific oysters, below).

Tilapia (*Oreochromis* spp.) and especially the Mozambique tilapia, *Oreochromis mossambicus*, are considered to be a threat to native diversity in many areas where they have been introduced (De Silva, 1989; Pullin et al., 1997; but see also De Silva et al., 2004). In the Philippines and Pacific islands, *O. mossambicus*, which can tolerate brackish water, competes for algae and other resources and has displaced the preferred species of mullet (*Mugil cephalus*), brackish-water shrimp (*Fenneropenaeus merguiensis*), and milkfish (*Chanos chanos*) in brackish-water fish ponds (Juliano et al., 1989; see Pullin et al., 1997 for review).

3.1.3. Genetic interactions

Possible genetic impacts from alien species include the following:

1. loss of species integrity from mixing with alien genotypes,
2. reduced reproductive efficiency from hybridizing with alien species, resulting in inviable offspring,
3. decreased fitness from incorporation of alien genes or the loss of co-adapted gene complexes, and
4. indirect genetic impacts resulting from other ecological interactions, e.g., competition or predation, which can reduce a native population to the point where genetic diversity is lost or inbreeding becomes problematic.

Genetic impacts of introduced species have been studied extensively in salmonids. Salmon, which have homing abilities, genetic subpopulation structures, and complicated life histories, provide an ideal model to study the effects of genetic changes.

However, the great majority of studies on fish (and this is mostly on salmonids) merely documents genetic change and not actual change in numbers of individuals or in fitness parameters as a result of that change (Campton, 1995). It is much easier to document a change in gene frequency than to document a change in fitness that will adversely affect a population, or to ascribe a species decline to genetic factors when many other factors such as habitat loss, pollution, and fishing pressure may also be acting on the stock. Hindar et al. (1991), in a review of the salmon literature, list numerous examples of genetic changes in farmed salmon compared to wild salmon and of differences between farmed and wild salmonids in biology and behavior. The differences are fitness-related and under genetic control (at least partially), and therefore would theoretically affect fitness. For example, hybridization between escaped farmed Atlantic salmon and native brown trout (*Salmo trutta*) in Scotland has been shown to reduce the reproductive efficiency of these species (Youngston et al., 1993). Hindar et al. (1991) concluded that the mixing of farmed and wild salmonids is generally detrimental to the wild stock, but they admit that empirical evidence is not abundant.

One reason that it is very difficult to document genetic impacts on fitness traits is that the necessary baseline studies have generally not been done (Campton, 1995). For example, the European sea bass, *Dicentrarchus labrax*, is gaining in popularity in aquaculture. Due to adult migration, extensive larval dispersal, and absence of obvious barriers to gene flow in the Mediterranean, it was expected that wild populations would be homogenous. However, studies revealed genetic structuring in these populations, and almost diagnostic allele differences between farmed and wild stocks (Castilho and McAndrew, 1998; Sola et al., 1998). European sea bass are being widely moved around the Mediterranean with little regard for the natural genetic diversity of the species. Thus, it is prudent to be aware of the issues and potential problems and to try to gain as much knowledge of baseline information as possible.

3.1.4. Disease impacts

One of the main risks with the use of alien species is the spread of pathogens along with species transported or traded in aquaculture (Subasinghe and Arthur, 1997). Of particular concern relating to the introduction of exotic species is that, with new introductions, the level of uncertainty will be higher regarding the pathogens that may also be introduced and the problems that they could cause in the new environment. Disease agents introduced with exotic species or strains may be more pathogenic in their new environment, where they may spread to atypical hosts or encounter a more favorable environment (such as a mariculture facility) (Langdon, 1990).

Numerous examples of the problems that such introductions have caused can be cited:

1. Along with the abalone that the California aquaculture industry imported from South Africa (*Haliotis* spp.) came a sabellid worm parasite that caused no problems in South African culture systems. Thus, screening for the presence of the parasite was not included during the mandatory quarantine and examination of the imported abalone. This worm has become established in California abalone aquaculture facilities and it has devastating effects on cultured abalone there, and the impact on natural populations of abalone and other marine mollusks is unknown. Abalone farmers compounded the problem by transferring stock among farms before they knew the identity or effects of the parasite (Culver et al., 1997).
2. In the western USA, whirling disease in native rainbow trout (*O. mykiss*) is caused by a myxosporean that is non-pathogenic in brown trout (*S. trutta*), which is a non-native species that has escaped within the range of the rainbow trout.
3. Infectious hypodermal and haematopoietic necrosis virus (IHHN) in *Litopenaeus vannamei* can devastate *L. stylirostris*, which is cultured in many tropical countries.
4. Shrimp containing *Penaeus monodon*-type baculovirus, yellow-head virus, and newly discovered viruses caused financial losses of over a billion US dollars in Asia in the early 1990s (Chamberlain, 1994; Subasinghe et al., 1998). For example, the Taiwan, Province of China, shrimp industry collapsed after the introduction of alien diseased animals.
5. In Norway, native Atlantic salmon are highly susceptible to the parasite *Gyrodactylus salar*, to which Baltic strains of Atlantic salmon are resistant (Bakke et al., 1990). In 1975, *Gyrodactylus salaris* was found in wild Atlantic salmon parr; it was probably introduced from infected and resistant Atlantic salmon from Sweden.

6. The causative agent of furunculosis, *Aeromonas salmonicida*, was introduced into Norwegian salmonid farms through infected stocks of rainbow trout that had been imported from Denmark in 1966. The pathogen spread to over 500 fish farms and to 66 salmon streams by 1991 (Heggberget et al., 1993).
7. Furthermore, *A. salmonicida* has been found in seawater over 20 km from infected farms, which indicates its potential for dispersal. The spread of both *Gyrodactylus* and *A. salmonicida* was probably facilitated by stocking programs that inadvertently used infected fish. Authorities in Norway have tried to reverse the impact of *G. salar* infection to their Atlantic salmon stocks by poisoning entire river systems (Walso, 1998).
8. In Ireland, researchers demonstrated that 95% of the production of the stage I nauplius of the sea louse, *Lepeophtheirus salmonis*, originated from farmed Atlantic salmon and that the lice had contributed to the decline in both wild Atlantic salmon and wild brown trout (*S. trutta*) fisheries (Tully and Whelan, 1993; Edwards, 1998).
9. Finally, the European flat oyster, *Ostrea edulis*, once imported into the western USA, became infected with the blood cell parasite *Bonamia* sp. This parasite was subsequently spread back into Europe, where it caused the demise of the majority of the native flat oyster fishery (Chew, 1990).

Pathogens can also impact native species by affecting other interactions between related species. The introduction of crayfish from North America to Europe also introduced the crayfish plaque to European crayfish species. North American crayfish species, such as *Pacifastacus leniusculus*, are resistant carriers that also outcompete native European crayfish due to their higher reproductive rates; the plague gives the invaders an additional competitive advantage by weakening European crayfish (Pöckl, 1999).

Disease agents that hitchhike in and on the shells of mollusks are another important method of disease transmission that has affected the aquaculture industry and coastal environments. A significant environmental impact of the movement of the Pacific oyster has been in the spread of such organisms, not as a result of catastrophic disease outbreaks but because hitchhiking organisms have altered local habitats (Chew, 1990; see below). The Japanese oyster drill *Ceratostoma inornatum*, the oyster flatworm *Pseudostylochus ostreophagus*, and the copepod parasite *Mytilicola orientalis* were all inadvertently introduced with Pacific oysters (Chew, 1990).

3.1.5. Habitat alteration

Many species of freshwater animals greatly modify aquatic habitats when placed into a new area. Notorious in this regard are crayfish (*Procambarus* sp.), common carp (*Cyprinus carpio*), and grass carp (*Ctenopharygodon idella*). Examples of marine species that modify coastal environments are more difficult to find. The Asian clam, *Corbicula fluminea*, was probably introduced into the USA by Chinese immigrants as a food item (though possibly not for intentional farming) in 1938. The clam has since spread widely to inland and coastal areas of 38 states in the USA. Its most significant affect is in biofouling of freshwater systems; the clam can grow in numbers large enough to alter the water flow and substrate in streams and lakes (CRS, 1999) and can remove large amounts of phytoplankton from the water column. In New Zealand, the common river galaxias (*Galaxias vulgaris*) is displaced not only by predation and competition from introduced chinook salmon, but also because stream bottom habitat is disturbed when the salmon build redds (spawning nests) (McDowell, 1990).

As mentioned above, a significant impact of oyster movements has been from epibionts inadvertently introduced along with them. Twenty-nine species, including algae, diatoms, protozoans and invertebrates, were found in the water of oyster shipments. In addition, seaweeds and seagrasses used as packing material for oyster shipments have invaded and transformed thousands of square kilometers of open mudflats along the Pacific coast (Posey, 1988). The altered mudflats now contain a completely different assemblage of species (Posey, 1988).

3.2. Social and Economic Impacts

Social and economic impacts associated with introduced species include changes in income and in access to resources and land. According to the records in DIAS, the overall socio-economic effect of introduced species used for aquaculture has been beneficial (Figure 3). Although 1284 records cited aquaculture as a reason for the introduction, the social and economic impacts of these introductions were listed in only 347 records and the ecological impacts were listed in only 231 records. Thus, 706 records had no information on the impacts. Accurate monitoring and evaluation of the impacts of introduced aquatic species are still needed. Of those records that reported social/economic onomic impacts, the ratio of positive to adverse impacts was approximately 2:1 (Figure 3).

3.2.1. Changes in income

Aquaculture is primarily an economic activity; worldwide production was valued at US$ 53.6 billion in 1999. Over US$ 43 billion of this amount was generated in developing countries or in countries with economies in transition (FAO FISHstat Plus, 1999). Introduced species account for a significant proportion of this production; in 1994, 11.4% of fish production, 0.7% of crustacean production, and 6.6% of mollusk production was derived from introduced species (Garibaldi, 1996). For example, the introduction of salmon to Chile provides employment for 30,000 people (Fundacion Chile, Santiago Chile, personal communication) who previously had few employment opportunities. The value of the Chilean salmonid aquaculture production has increased tremendously, from a value of slightly greater than US$ 3 million in 1984 to over US$ 803 million in 1999.

However, in many cases, the economic impact of aquaculture can have negative components. For example, on the Pacific coast of Canada, farmed Pacific and Atlantic salmon represent alien genotypes that have escaped and reproduce in local rivers (Volpe et al., 2000). Therefore, Canadian salmon farmers were asked to raise triploid salmon to reduce the chance of breeding with wild populations. The Canadian aquaculture industry asked for real evidence that diploid farmed salmon present a significant danger to native stocks (Stuart, 1996) because the industry is required in many places to undertake additional financial burdens to produce these non-reproductive salmonids.

Feral populations of animals with alien genotypes can impact aquaculture operations more than they impact wild populations; some of the most economically significant genetic impacts from exotic species have been on farmed stocks of commercially important species (Pullin et al., 1997). They have led to loss of revenue, disease, and reduced production efficiency. For example, feral populations of *O. mossambicus* invaded a breeding program in which *O. mossambicus* and *O. honorum* were hybridized. The *O. mossambicus* and *O. honorum* cross should have produced all male offspring (Ang et al., 1989), but because of the influence of genes from feral *O. mossambicus*, the aquaculture facility produced mixed-sex progeny and the commercial viability of the all-male line failed.

Sometimes an exotic species is proposed for aquaculture when its financial value has not been well considered. A proposal was drafted to increase the use of introduced tilapia in the Tonle Sap area of Cambodia, a forest flood plain off of the Mekong River (FAO, unpublished report). However, this increase could threaten extremely productive capture fisheries in the flooded forest and may not provide the anticipated economic benefits. Tilapia are not as highly valued as the local species and therefore do not fetch a high market price (P. Evans, FAO, personal communication; personal observation). However, the market price of tilapia would decline as supply increases; consumers and the rural poor may benefit from the reduced price of tilapia if they learn to like the fish and if farmers can produce it economically.

In Lake Victoria, the Nile perch also was not well liked initially by the local people because its flesh is oily; the consumers around the lake have since adjusted to the fish (Reynolds and Greboval, 1989). Although the Nile perch was not introduced into Lake Victoria for aquaculture, the social and economic impacts associated with the changed fishery may be similar to those expected from introductions for aquaculture. The changes included increased fish consumption, increased foreign exchange, change in local employment, and a move from small fisheries to larger-scale fisheries (Reynolds and Greboval, 1989).

Aquatic introductions can also economically impact other sectors. The golden apple snail (*Pomacea* sp.) was introduced to the Philippines to provide additional animal protein and income. The long-term result of this introduction has been disastrous in that the snail consumes large areas of rice (a staple and main export commodity), is extremely difficult to control, is not well liked by Philippinos, and has no real market value (Acosta and Pullin, 1991).

3.2.2. Changes in access to resources and land

Exotic species are usually introduced to increase the value of the catch from a water body or the value of an aquaculture venture. As a result of this increased value, some of the traditional resource users, usually subsistence fishers or farmers, may be denied access to land and water. The introduction of exotic carp in Bangladesh changed access rights to land and inland fishery resources because of the increased value of carp over native species (see papers in Petr, 1998). Oxbow lakes, reservoirs, and small water bodies provided diverse and highly nutritious native species (Thilsted et al., 1997) to local people in Bangladesh, but these fish were usually bartered or consumed locally and were never accurately recorded in fishery statistics (personal observation). Inland fishery enhancements, including the stocking of exotic carp and construction of aquaculture ponds, reduced the number of native species and restricted access to many of these water bodies (personal observation).

4. SUMMARY AND CONCLUSIONS

It is important to consider that the decision to introduce a species will be a matter of societal choice and that environmental and economic conditions will change as a result of that choice. An ecosystems approach to risk assessment is one means to help make informed choices by incorporating ecological, social, and economic factors. The early codes of practice and guidelines on introduced species focused on ecological impact only (Turner, 1988; ICES, 1995), but now socio-economic impacts have been added to the codes and impact assessments of alien species (Bartley et al., 1996; Garibaldi and Bartley, 1998; Bartley and Casal, 1999; INGA, 2001).

However, risk assessment and the proper application of many codes of practice are dependent on accurate information concerning the animal to be introduced, the habitat it will be introduced into, and the associated skakeholders. Information sources such as DIAS, FishBase, and the statistics compiled by FAO from Member States, will be valuable in developing sound policy on the use of alien species and genotypes, but more information is needed. Unfortunately, many of the records in DIAS had incomplete information on the impacts of introductions. FAO Member States submit fishery production information to FAO, but many records are incomplete and data on who benefits from the production and the environmental impact are not compiled.

In developing areas or where food security is lacking, introduced species may appear to provide immediate solutions to malnutrition, poor fishery management, or unemployment. Policy makers and fish farmers generally assume that it is more expedient to import a species with proven performance in another environment rather than to domesticate and farm local species. This short-term emphasis may lead to longer-term problems and missed opportunities.

In times of economic hardships and efforts to provide more food to a growing human population, aquaculturists should still balance short-term priorities with concern for the ecological impacts of species introductions. Although the overall benefits of alien fish introductions in aquaculture appear substantial, international treaties and conventions such as the CBD (1994) require countries to protect their biodiversity. Therefore, aquaculturists will be forced by national regulatory bodies to comply with environmental safeguards. In addition, there are more practical reasons to comply.

Many of the adverse ecological impacts of introduced species that have affected the aquaculture industry include loss of production through introduced diseases, such as the example of the shrimp farming collapse in Taiwan, Province of China; failure of breeding programs through contamination of broodstock with introduced species, such as the example of the failure of the all-male tilapia line; and loss of time and money through developing and promoting inappropriate species, such as the introduction of the golden apple snail into the Philippines. All are negative impacts that directly affect food producers. Aquaculturists may be better served by taking advantage of opportunities to develop local species. For example the Mekong River Commission initiated a program to domesticate native species from the Mekong Basin, *inter alia,* to replace the alien species currently under culture (Mekong River Commission, unpublished document written in 2000). Using local fish, this program would develop and refine culture techniques to reduce the risk of disease introduction, to reduce other environmental impacts, and to take advantage of established markets for local species. However, all risk would not be eliminated because, as this program and other similar programs increased production through artificial selection for these desirable culture characteristics, domesticated genotypes would become more "alien." If these domesticated fish escaped, they could impact native gene pools unless the level of domestication reached a point where they were unable to live in the wild. Resource managers and policy makers have a lot to learn about the real impacts of alien species and genotypes, and the aquaculture industry has a lot to gain from the responsible use of alien species. Information sources such as DIAS, FishBase, and FAO statistics will be able to provide data relevant to some aspects of the problem. However, information must be improved regularly.

Although DIAS provided summary information on the kinds and impacts of alien species, there are potential biases in the database. Often introductions that are unsuccessful are forgotten or not reported; often those introductions that are reported are poorly monitored. Thus, there may be more instances of the failure of alien species to become established than are reported in DIAS. Many published reviews on aquatic introductions report on numerous failures in the establishment of marine and brackish-water species (see papers in Pollard, 1989; Rosenfield and Mann, 1992). Additionally, many aspects of the ecological impact of introductions are poorly known because only cursory, or no, initial assessments were made prior to the introductions and follow-up monitoring of the coastal environment is poor or non-existent. Finally, simply counting the number of positive versus negative impacts does not give the complete picture of the situation. For example, although many introductions may have little adverse ecological impact, a few may have disastrous consequences, such as the introduction of diseased penaeid shrimp into Taiwan, Providence of China, which led to the collapse of the country's marine shrimp industry or the re-introduction of diseased European flat oysters, which led to the decimation of European flat oyster populations.

Accurate risk assessment will be necessary and is dependent on information concerning the animal to be introduced, the habitat into which it will be introduced, and the associated stakeholders. This is the essence of an ecosystems approach. Increased communication and dissemination of advances in aquaculture, fish health, and genetic technologies will enable fish farmers to produce better and safer products; improved understanding of the social and cultural context of aquaculture development will help ensure that costs and benefits are evaluated accurately; and national and international agreements will provide the moral authority for parties to act responsibly. An ecosystems approach is seen as the best means to bring these components together for the conservation and sustainable use of aquatic resources and for the betterment of the people that depend on them.

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AUTHOR NOTE

Since the original analysis of DIAS we have updated the database to include over 4000 records of international introductions of alien species. The new database and other information on alien species in fisheries and aquaculture is available on CD-ROM: Bartley, D.M. (ed/comp) 2006. Introduced species in fisheries and aquaculture: information for responsible use and control [CD-ROM]. FAO, Rome.

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CHAPTER 3

INDICATORS FOR THE SUSTAINABILITY OF AQUACULTURE

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Abstract: Global demand for fish will probably double in the next 30–50 years. To what extent can aquaculture increase and sustain its contributions to world fish supply without unacceptable environmental impacts? Indicators towards answering this question are suggested here. These are as follows: (1) biological indicators—potential for domestication, with genetic enhancement; trophic level; feed and energy conversion efficiency; (2) ecological indicators—ecological footprint; emissions; escapees and feral populations; (3) intersectoral indicators—sharing water (e.g., with agriculture, fisheries, forestry, water supply, waste treatment); diversity; cycling; stability; and capacity. Back-calculation of FAO fisheries statistics yielded a dataset for aquaculture production from 1950 to 1997. This dataset, and reviews of literature on the sustainability of world food production, suggest that expansion of aquaculture will not result in sustainable and environmentally acceptable systems unless such indicators are used by policymakers and developers.

Key words: aquaculture, biology, ecology, environment, indicators, sustainability

1. INTRODUCTION

World food supply will probably have to double in quantity and to increase in quality over the next 30–50 years, as populations and incomes rise. The demand for fish as food will probably double or increase even more. We use the term “fish” here to mean all aquatic animals.

Would it be a wise investment to attempt to increase the contribution of aquaculture (currently about 20%) to world fish supply? What would be the

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environmental implications of such expansion? The extensive literature on aquaculture and the environment (e.g., Pullin et al., 1993; FAO 1997a; New, 1998a, b) does not provide ready answers. Naylor et al. (2000) concluded that aquaculture must reduce its dependency on wild fish for feeding farmed fish and must also adopt "ecologically sound management practices" in order to contribute sustainably to world fish supply. Substantial efforts are indeed being made towards lessening the adverse environmental impacts of aquaculture; for example, through the work of FAO (Barg, 1992, 1997; FAO, 1995, 1997b) and through the aquatic work programs of Parties to the Convention on Biological Diversity (CBD).

We consider here three categories of broad indicators for the sustainability of aquaculture: biological, ecological, and intersectoral. We consider that the economic sustainability of aquaculture is ultimately a product of all of these categories. Moral and ethical aspects and the sharing of benefits from expansion of aquaculture are beyond the scope of this paper.

2. SUSTAINABILITY

Much has been written about the environmental aspects of sustainability (e.g., Becker, 1997) and about its application to aquaculture (e.g., Folke and Kautsky, 1992; Pillay, 1997; Naylor et al., 2000). We follow here the definition of sustainability adopted by the Technical Advisory Committee of the Consultative Group on International Agriculture Research (TAC/CGIAR, 1989): "Successful management of natural resources . . . to satisfy human needs while maintaining or enhancing the quality of the environment and conserving natural resources."

There is general agreement that sound management of natural resources is the key to sustainability. However, short-term needs and objectives (addressing food and employment deficits and providing quick returns to investment) usually dictate policies and events. Overall, macro-economic factors (e.g., trade and consumption patterns) have been the main controllers of aquaculture production trends (Born et al., 1994). The environmental and social costs of aquaculture development have been inadequately addressed.

Poverty alleviation, sustainability, and the environment are common watchwords in aquaculture research and development, but planning horizons and assessments of impact and success usually relate to only the present generation of humans. Moreover, developers sometimes appropriate lands and water for aquaculture as a temporary front for other developments (e.g., housing, industry, recreation). Consequently, the history of aquaculture, like that of agriculture, has many examples of adverse environmental impacts and unsustainability (e.g., see Pullin et al., 1993).

Such a history cannot continue indefinitely. Non-negotiable, natural laws are already forcing changes against a background of resource depletion, environmental degradation, and increasing conflict, as is happening for many capture fisheries. The productive capacity of the Earth's lands and waters is finite, as is the capacity of the ecological services upon which biological productivity and waste processing depend.

We suggest that aquaculture needs a fundamental transition (as indeed do agriculture, capture fisheries, and forestry) from management that is based solely on maximizing the exploitable biomass of target species (and on "mining" natural resources towards that end) to integrated management of natural resources and ecosystems. This applies at the farm level and also to entire watersheds, the coastal zone, and open waters. The following indicators are suggested as a framework for assessing progress towards such a transition.

3. BIOLOGICAL INDICATORS

3.1. Farmed Fish

Most farmed fish are far less domesticated than terrestrial livestock and there is enormous scope for their domestication, with genetic enhancement and improved husbandry. Genetic enhancement can greatly improve the growth performance, feed conversion ratio (FCR) and disease resistance of farmed fish (Gjedrem, 1998). For comparison, in 1935, it took 16 weeks to raise a broiler chicken to market size with an FCR of 4.4:1, but by 1994 it took only 6.5 weeks at FCR 1.9:1 (Forster, 1999). About 80% of the FCR improvement was attributed to genetics and 20% to better nutrition. Forster (1999) concluded that farmed salmon and other fish can become "more feed cost-efficient" than chickens and other terrestrial livestock, and maintained that an FCR of 1:1 could be approached for salmonids. Following patterns established for plants and livestock, such genetic enhancement contributes to the progressive domestication of fish. This is already occurring, purposefully and coincidentally, on a wide front.

As an example, we compared growth data for farmed and wild Nile tilapia (*Oreochromis niloticus*) (Figure 1). Nile tilapia clearly show different growth patterns in captivity, where on the average they take about half a year to reach a maximum size of 22 cm. Their wild relatives need about 7 years to reach a maximum size of 37 cm. Fast growth, however, correlates with early maturity at about 2 months and 14 cm in captivity, compared to about 20 months and 21 cm in the wild.

There remains the question, to what extent should genetic enhancement research concentrate on developing very high performance fish for use in intensive feedlot systems (which might themselves be unsustainable) or on fish that can perform well in less intensive systems, thereby maximizing use of the natural aquatic productivity on site? Whatever the answer, all fish breeders face some unavoidable fish design constraints.

3.2. Design Constraints

One design constraint affecting finfish is that their scope for growth depends strongly on oxygen uptake through gills, the surface of which, for reasons of

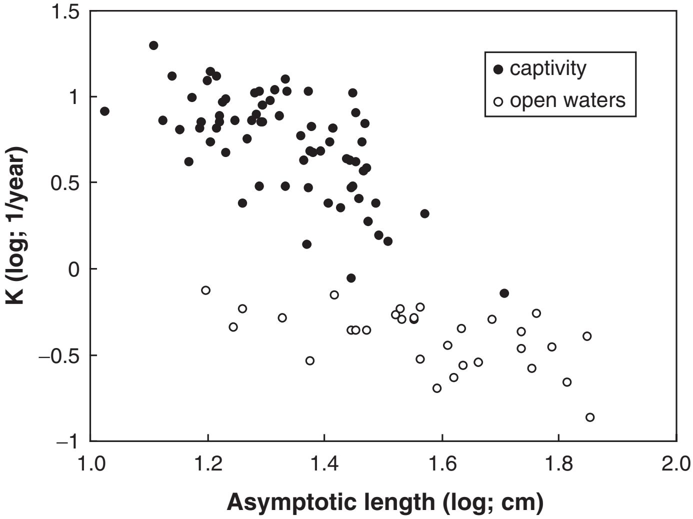

Figure 1. Growth performance of Nile tilapia (*Oreochromis niloticus*) in captivity and in open waters as expressed by two parameters (Asymptotic length and K) of the von Bertalanffy growth function; K is a constant. Data from independent growth studies as compiled in FishBase (Froese and Pauly, 1999)

geometry, cannot grow as fast as their body mass. Thus, as fish grow, their gill area per unit body weight declines, thereby reducing growth and precipitating a number of related processes, including maturation (Pauly, 1994). This mechanism explains the stunting of tilapias crowded in small waterbodies (Noakes and Balon, 1982). Moreover, it explains why domestication, which leads to calmer fish that waste less of their scarce oxygen on aggressive encounters, also leads to faster-growing fish (Bozynski, 1998; see also Figure 1).

3.3. Feeds, Trophic Levels, and Energy

The future availability and costs of fish feeds and their ingredients (especially proteins), fertilizers that enhance aquatic productivity, and energy are major topics for forecasters of the future of aquaculture (e.g., Chamberlain, 1993; Tacon, 1995, 1997). Concerning "fed" aquaculture, a comparison with feedlot livestock is useful. Goodland (1997) regarded current livestock production methods as unsustainable, pointed out that livestock eat about half of the global production of grain, and considered aquaculture as potentially "more productive and at much less environmental cost than livestock if grain inputs only are counted." However, he found (intensive) aquaculture to be economically uncompetitive "if fossil energy and water costs are included."

The fossil fuel energy requirements of intensive aquaculture can indeed be high. For example, cage farming of salmon was found to require 50 kcal of fossil energy/kcal protein output, compared to 22 for raising broiler poultry and 35 for raising pigs, in the USA (Folke and Kautsky, 1992). Analyses of change in agriculture have indicated the importance of energy; for example, Dazhong and Pimentel (1990) showed that from 1957 to 1978, fossil fuel use in Chinese agriculture increased about 100-fold, whereas grain production increased only 3-fold. Simultaneously, most traditional, organic farming systems disappeared.

Goodland (1997) suggested that humans should eat more sustainably (lower in the food chain) and be differentially taxed on consumption of food items produced by inefficient conversion processes: for example, grains—no tax; poultry, eggs, dairy—moderate tax; pork, beef—high tax. He also suggested that "ocean fish" be taxed the lowest among the animals consumed (Goodland, 1997). Note, however, that most of the ocean fish consumed by humans have trophic levels ranging between 3.0 and 4.5 (Pauly et al., 1998)—up to 1.5 levels above that of lions. Moreover, the energy costs of catching these fish are high, especially for large commercial fishing vessels.

Kinne (1986) has also drawn attention to the necessity to "develop new, long-term concepts for combating hunger and for harmonizing large-scale food production with ecological dynamics and principles . . . the solution is recycling and large-scale food production from *low-trophic-level* (present authors' emphasis) organisms."

Aquaculture statistics on levels of production over time of species in different trophic levels can be compared to determine whether aquaculture production of low-trophic-level species is increasing relative to that of higher-trophic-level species. We looked at aquaculture statistics to see if there are any discernible trends in this direction.

3.4. Trends in Aquaculture

Unfortunately, the time series for aquaculture production statistics available from FAO (1998) is rather short (1984–1997). Before 1984, values for aquaculture production were contained in the FAO fisheries *catch* statistics.

We used the following approach to extract pre-1984 values for aquaculture production from the FAO fisheries catch statistics.

1. We linked the FAO "Catch" and "Aquaculture" databases so that species, country, and FAO area were identical.
2. For every record, we calculated the average ratio of aquaculture production in the reported total production in the Catch database for the years 1984–1987.
3. If no catch and no aquaculture production were reported by a country in these years, we assumed that no aquaculture had been conducted with the species in question in the past.
4. We used the obtained ratios to calculate aquaculture production for the years 1950–1983. This approach worked well for most records—over 1600 cases. However, in 286 cases, there were no pre-1984 records in the Catch

table, although substantial and continuous production was reported after 1984, suggesting that production data for these species had not been reported to FAO before 1984. This caused an increase in total aquaculture production from 1983 to 1984. Therefore, we used the following approach to estimate previous aquaculture production for these cases.

5. We looked at cases where no production was reported in 1981, 1982, and 1983, but some production was reported in 1984.
6. We ignored cases where the production in 1984 was 10 metric tons (t) or less, or where the aquaculture part of the production + catch (see above) was less than 10% of the total.
7. We calculated the average year-to-year production difference between the years 1984 and 1987 as ratio of the later year (ignoring cases where this value was negative or zero).
8. We used the average of the ratio derived in (7) to project the production backwards for the pre-1984 years as a continuous exponential decline in this ratio from year to year, to approach gradually the "no production reported" status.
9. In cases where the ratio in (7) had been negative or zero, we replaced it with the arbitrary ratio of 0.05, so as to avoid projecting steady or increasing production when actually none had been reported.
10. When the back-calculated production value reached a value less than 10 t, we set it to zero.
11. For introduced species, where the year of their introduction to the respective country was known from the FishBase Introductions Table, (www.fishbase.org; Froese and Pauly, 1999), we set projected values before that year to zero.

Our dataset (Figure 2) has, undoubtedly, some entries that do not match the real history of aquaculture development in some countries. Further country-specific studies, by experts, would be needed to check this.

We looked at the trends in trophic levels of farmed fish using the trophic levels of their wild populations as reported in FishBase 99 (Froese and Pauly, 1999). Note, however, that fish trophic levels on farms can differ from those in the wild. They can be lower when carnivores such as salmonids are fed pellets rich in plant material like soya protein or higher when herbivores such as grass carp (*Ctenopharyngodon idella*) are fed pellets containing fish or animal protein. We did not attempt to check actual species-specific components.

Based on the assumption that many fish on farms feed as they do in the wild, Figure 3 (upper graph) suggests little overall change, or perhaps a slight decrease, in the mean trophic level of farmed fish in Africa, Asia, the former USSR, and, on average, globally. This result derives mainly from herbivorous carp, tilapia, shrimp, and bivalve mollusk farming in Asian, especially Chinese, aquaculture. The irregular nature of the curve for Africa likely reflects year-to-year uncertainties in the status of aquaculture there, with frequent externally funded, project-dependent starts and stops and the difficulties of an unpredictable

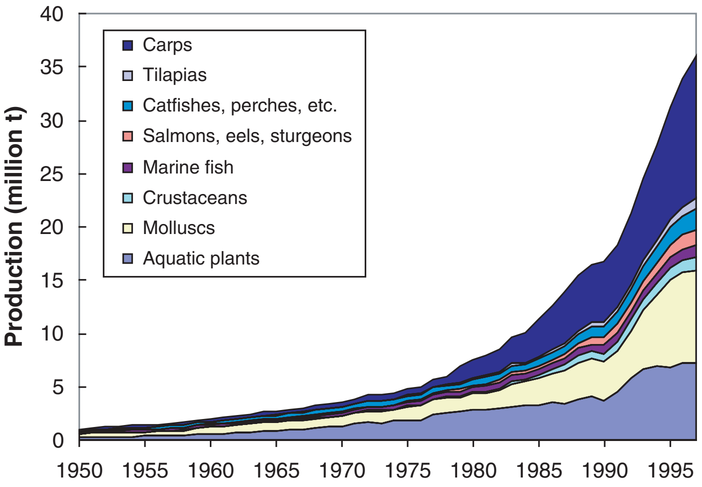

Figure 2. Contribution of major groups to aquaculture production, based on FAO (1998) statistics. For methods of estimating pre-1984 values, see text

climate, especially rainfall. Figure 3, lower graph indicates that the Americas and Europe are farming fish (e.g., catfishes, salmon) at progressively higher trophic levels. These trends are particularly evident since 1984, when aquaculture statistics became more accessible.

3.5. Indicators

From the evidence presented above, it is clear that further domestication and genetic enhancement of farmed fish are needed to raise production. Moreover, understanding the feed and energy requirements of farmed fish is paramount for assessing the environmental implications of these interventions. We therefore suggest the following biological indicators for the sustainability of aquaculture:

1. potential for domestication, with genetic enhancement;
2. trophic level;
3. feed and energy conversion efficiency.

4. ECOLOGICAL INDICATORS

4.1. Footprint

The concept of the ecological footprint—the ecosystem area that is functionally required to support human activities—has been applied extensively in analyses of aquatic food production (e.g., Folke et al., 1998). We note the current criticisms of this method (e.g., see discussions in van der Bergh and Verbruggen, 1999a, b; Ferguson, 1999; Wackernagel, 1999). We conclude that these

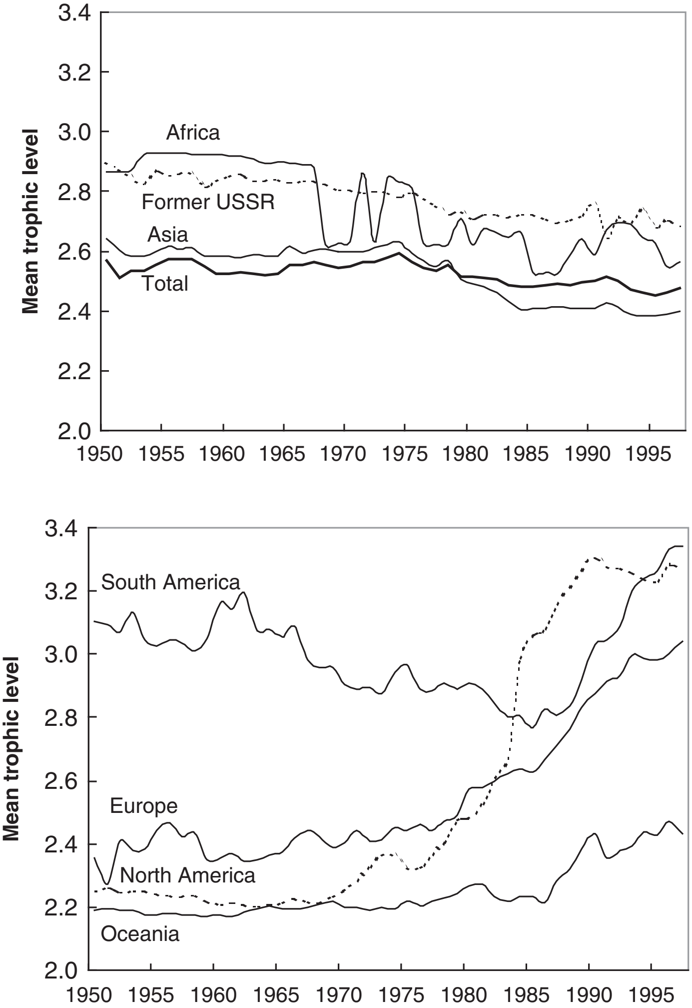

Figure 3. Mean trophic levels (from Froese and Pauly, 1999) of aquaculture production (1950–1997), including mariculture, by region. For methods used, see text

criticisms do not lessen the utility of the method that remains, to quote Wackernagel (1999), "one of the few ecological measures that compares human demand to ecological supply."

For total food and energy, Wackernagel et al. (1999) found that only 12 out of 52 countries had ecological footprints smaller than the bioproductive areas required for their human populations. This was based on an estimated average requirement of 2.0 ha of land/sea space per global citizen plus an allowance of another 0.3 ha (12%) per caput for sustaining biodiversity. In total, the 52 countries studied were found to use 35% more "biocapacity" than exists within their own land/water space. These authors also suggested that average bioproductive space worldwide will decline to 1.2 ha per caput in just over 30 years. They assumed no further ecological degradation (which is unlikely) and a world population of 10 billion. Their analyses did not mention aquaculture *per se* but for Italy's annual consumption of "marine fish" at 30 kg per caput they estimated a footprint of about 1.05 ha of sea, compared to only 0.32 ha per caput available to that nation. Pauly and Christensen (1995), and others cited by Wackernagel et al. (1999), have pointed out that of the 6 ha of sea space per caput on the planet only about 0.5 ha are bioproductive and that these generate only about 12 kg per caput per year of actual fish on the table.

Aquaculture has, inevitably, an ecological footprint and draws upon the world's ecosystem services and natural capital, the total value of which has been estimated to average US $33 trillion annually, mostly outside of the market and balance sheets (Costanza et al., 1997). What spare capacity is there for human food production in the world's bioproductive water space, if any? Pauly and Christensen (1995) found that about one third of the primary production over marine shelves—the productive areas down to 200 m around continents—is required to maintain the marine fish catches extracted from these shelves, i.e., about 90% of global fish catches. Channeling more of this production into aquaculture might be a wise investment because some farms might generate more product for less footprint. This needs to be further investigated, through modeling and case studies.

Concerning land-based food and feed production, Wackernagel et al. (1999) concluded that there is currently less than 0.25 ha of highly productive arable land and about 0.6 ha of grazing pasture per caput. No doubt more of the produce and by-products of agriculture from these lands could be used to feed farmed fish. Ultimately, however, the ecological footprint of feeding humans will be minimized if humans eat plants and maximized if we eat carnivorous animals, including carnivorous fish.

4.2. Emissions

Aquaculture systems, except closed recirculating systems, have emissions (effluents, diffusion and settlement around cages, drainage products, etc.). The nutrients (principally nitrogen and phosphorus) and suspended solids in such emissions, together with associated microorganisms, create oxygen demands and sediment accumulation in the surrounding environment. These nutrients and suspended solids are derived from excreta and the proportions of feeds and fertilizers that are not either incorporated into the fish or retained by the system. Moreover, the residues of anthropogenic chemicals used in the production process (e.g., antibiotics, disinfectants, heavy metals in feeds, etc.) are also present in emissions. The environmental impacts can be serious; for example, see papers in Pullin et al. (1993), Rosenthal et al. (1993), Ackefors and Enell

(1994) and Páez-Osuna et al. (1998). The safety for human consumption of aquaculture produce from such systems must, of course, be assured. Forecasting the composition and minimizing the impacts of emissions from aquaculture has become a major research field (see, e.g., Kaushik, 1998; Young Cho and Bureau, 1998).

Clearly it is advantageous, both for farmers and for the environment, that feed conversion efficiency (see Biological Indicators, above) and the efficiency of fertilizers used to produce natural foods for farmed fish are maximized and that emissions from aquaculture are as low as possible in oxygen demand, nutrient content, and suspended solids and residues from anthropogenic chemicals. The same applies to agriculture (see, e.g., Pan and Hodge, 1993; Oláh and Pékar, 1995). Note in this context that aquaculture can sometimes act as a waste-processing and clean-up system, for example, in wastewater-fed aquaculture (see below, Intersectoral Indicators).

4.3. Escapees and Feral Populations

Farmed fish (whether native or alien species and whether genetically distinct from wild types or not) can escape and establish feral populations. Escapees and feral populations of domestic animals (e.g., cats, camels, cattle, dogs, goats, pigs) have caused adverse environmental impacts. Feral fish (e.g., some tilapias [Pullin et al., 1997]) have done likewise and are usually impossible to eradicate. Hence, the development of aquaculture must proceed in parallel with effective environmental safeguards, including biosafety procedures, for *all* farmed fish—and especially for alien species and "alien genotypes." We looked at the proportions of native and alien finfish species used in aquaculture from 1950 through 1997 (Figure 4).

Most aquaculture production that is reported by countries to FAO derives from species that are native to these countries. The proportion of farmed fish production from native species increased from about 75% in the 1950s to about 85% in the 1990s. However, this result is again highly biased by the predominance in aquaculture production statistics of Chinese carps farmed in China. The percentages for the actual numbers of native fish species that contributed to aquaculture production decreased from about 60% in the 1950s to about 55% in the 1990s. Although over 80% of aquaculture production still comes from native species, the number of alien fish species used in aquaculture is now high (over 40%) and is tending to increase.

4.4. Indicators

From these ecological considerations, we conclude that if the farming and ranching of fish are to expand and be sustainable, they must contribute to *reducing* the ecological footprints of food production. The effects of emissions and escapes from fish farms will have to be kept within acceptable limits.

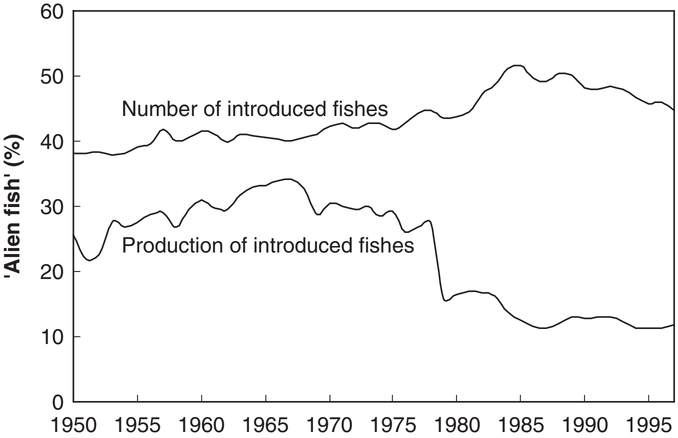

Figure 4. Aquaculture production (%) derived from introduced (i.e., alien) species, 1950–1997, and numbers of species contributing to that production. Data were derived from back-calculations of FAO statistics and from FishBase 99 (Froese and Pauly, 1999)

We therefore suggest the following ecological indicators for assessing the environmental relations of aquatic farms:

1. ecological footprint of the aquaculture enterprise as a whole, and per metric ton of product;
2. composition and environmental impacts of aquaculture emissions;
3. impacts of escapees and feral populations.

5. INTERSECTORAL INDICATORS

5.1. Sectoral Boundaries

Land can be used for growing crops, pasturing livestock, forestry, etc. Waters also have many options for use; e.g., irrigation, waste processing, recreation, navigation, aquaculture and fisheries, etc. These uses are often competitive rather than cooperative. Moreover, institutional structures and governance mechanisms have established and tend to maintain boundaries among sectors rather than fostering intersectoral partnerships. This can reduce resource-use efficiency and prevent synergism among sectors. The limited reuse of organic wastes and wastewater worldwide, despite a wealth of knowledge and skills that would facilitate greater recycling (e.g., Strauss and Blumenthal, 1990; Bartone, 1991; Edwards, 1992; Prein, 1996; Yan et al., 1998), is an example.

5.2. Water

The water resources sector has greatly underutilized the *aquatic* productivity of waters that are managed for domestic and industrial supply, irrigation, hydropower, etc. Even the more farsighted advocates of an ecological approach to water resources management (e.g., see Zalewski et al., 1997) have underemphasized the potential for producing food *in water itself*, before and/or after its use for other purposes. For water resources managers, the resource of interest has been usually only the water. They have tended to see aquatic biota only as agents that influence its supply and quality. In irrigation science and management, the very term "aquatic productivity" has usually meant the harvests of *terrestrial* plants grown through the use of irrigation waters. These attitudes are now changing. For example, the "Global Water Partnership", hosted by the Stockholm International Water Institute, is emphasizing *multiple* use/reuse of water (for information, see http:/ www.gwp.sida.se).

For inland aquaculture, the growing scarcity of freshwater (e.g., Gleick, 1993; Abramovitz, 1996; McAllister et al., 1997) poses both constraints and opportunities. The constraints apply particularly to aquaculture for which freshwater is used exclusively, without recovery or multipurpose use or reuse. The same applies to crops and livestock. According to Pimentel (cited by Pearce, 1997), producing 1 kg of beef requires 100,000 l of water, compared to 3,500 l for 1 kg of chicken. Obviously, there are huge variations in freshwater requirements among aquaculture systems and species. These would have to be thoroughly compared with those for other food production systems in order to make policy decisions. Boyd (2000) compared the water requirements for soybean, rice, and pond-raised channel catfish (*Ictalurus punctatus*) in the USA and estimated production values (US $ per m^3) of water used as follows: rice, 0.12; soybean, 0.13; catfish, with annual pond draining, 0.31; and without annual pond draining, 0.78. Moreover, some of the freshwaters used for aquaculture can probably be used or reused for other enterprises prior to, simultaneously with, or after their use in aquaculture.

We compared, for 1997, the intensity of freshwater aquaculture (FAO, 1998) with human population density (Figure 5). This plot suggests a log-linear relationship between the intensity of freshwater aquaculture and human population density; i.e., more people results in more demand and higher productivity per unit area for local or national supplies of freshwater aquaculture produce. Inland aquaculture is heavily dependent upon the availability and cost of freshwater. Figure 6 shows inland aquaculture production by region, (excluding Asia), based on the methods that are described above for back-calculating production (from FAO statistics) to 1950.

5.3. Integrated Aquaculture

Aquaculture frequently competes with other sectors rather than seeking partnerships. Tacon (1998) stated, "... if finfish and crustacean aquaculture is to maintain its current high growth rate then it will have to compete with other users (i.e., human and animal livestock) for ... nutrient or feed resources." The same author concluded, however, that long-term expansion of aquaculture will

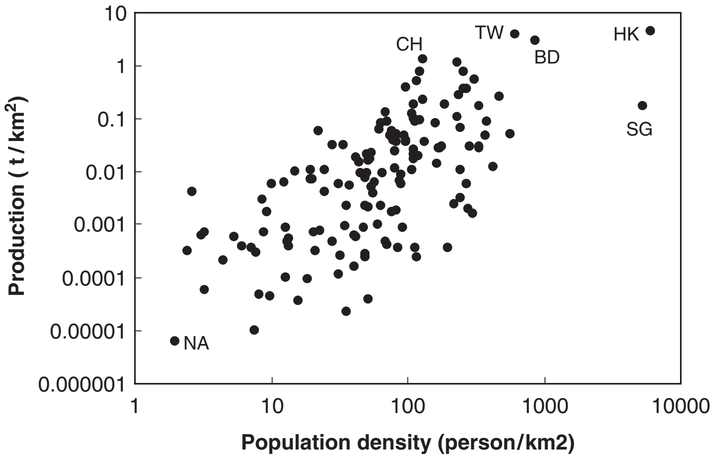

Figure 5. Freshwater aquaculture production in 1997 per square kilometer for various countries and territories, plotted against population density. BD = Bangladesh, CH = People's Republic of China, HK = Hong Kong, NA = Namibia, SG = Singapore, TW = Taiwan, Province of China (data from FAO, 1998)

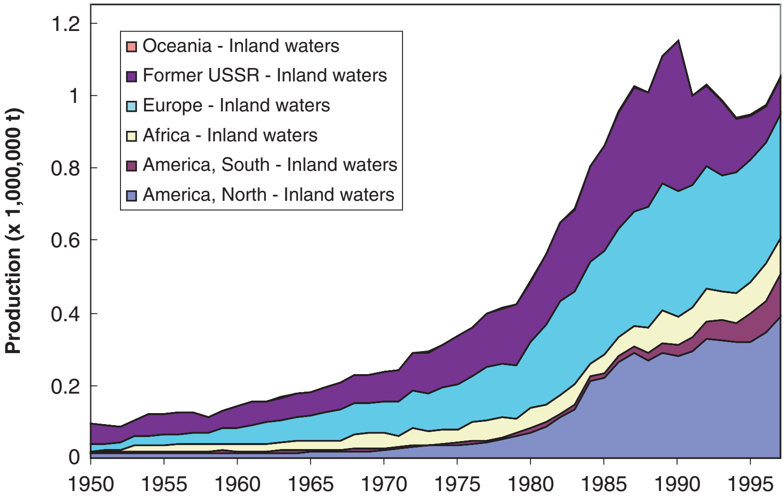

Figure 6. Inland aquaculture production by FAO area, aquatic plants excluded; estimated from FAO (1998). For methods of estimation of pre-1984 values, see text

depend upon improved efficiency of resource use and on systems that use "primary renewable resources." This implies intersectoral integration.

Edwards (1998) published "narrow" and "broad" definitions of "integrated aquaculture," the former meaning synergistic linkages among subsystems on mixed enterprise farms and the latter covering integration with agriculture, agroforestry, fisheries, industry, power supply, sanitation, and water supply. In addition to those tabulated by Edwards (1998), sectors such as forestry, nature conservation, sport, and tourism can be integrated with aquaculture. For example, the historic sewage-fed fishponds near Munich are an important bird sanctuary (Prein, 1996). Folke and Kautsky (1992) made the case for aquaculture as a subsystem of overall ecosystems and pointed out the advantages of integrating agriculture, vegetable production, mangrove forestry, polyculture ponds, and small-scale fisheries in the coastal zone, rather than maintaining them as "industrial monocultures", whether aquatic or terrestrial.

The problem is how to put into practice the environmentally desirable concepts called for by these and many other authors while increased productivity is pursued largely through monosectoral intensification (and often monocultures) and integrated systems are in decline; (e.g., in China [Dazhong and Pimentel, 1990; Boyd, 1999]). Edwards (1998) has "small-scale farms" in mind for integrated aquaculture but, despite their productivity and efficiency, their survival is threatened by current policies and trends. Agriculture faces similar problems of resource limitations and sectoral isolation. Lightfoot et al. (1993) have illustrated the role that integrated aquaculture can play in improving this situation.

We suggest that the "narrow" and "broad" categories of integrated systems, as defined by Edwards (1998), are really the same things at different scales. The problems of achieving partnerships and integration among enterprises on farms and among sectors at watershed, coastal zone, waterbody, and even national levels, are similar. For example, Pauly and Lightfoot (1992) adapted concepts and tools from farming systems research for analyzing resource systems in the coastal zone. Similarly, some established ecological indicators could be adapted for analyzing intersectoral relationships in large ecosystems.

We looked at four such indicators—diversity, cycling, stability, and capacity (Dalsgaard et al., 1995). These indicators, well-proven in ecological research, were applied by Dalsgaard et al. (1995) for assessment of the ecological sustainability of integrated versus non-integrated farms. We propose that these indicators be further investigated for assessing intersectoral integration in coastal zones, islands, river basins, entire countries, and seas. In Table 1, we compare the use of these indicators at the farm level (Dalsgaard et al., 1995) with our suggestions for their application at intersectoral level.

5.4. Indicators

Aquaculture must become more integrated with other sectors that use natural resources. We suggest the following intersectoral indicators for assessing the intersectoral integration of aquaculture:

1. sharing water with other sectors;
2. diversity of produce, services and livelihood opportunities;
3. cycling of by-products among sectors;

Table 1. Suggested indicators for assessing the degree of integration of aquaculture with other sectors. Entries in brackets are those adopted by Dalsgaard et al. (1995) for using these indicators at the farm level

Indicators (system attributes)	Goals (desirable properties)	Methods of assessment (measures/selected method of quantification)
Diversity	High diversity of produce and of livelihood opportunities (high diversity of farm enterprises, functional diversity)	Quantify the diversity of produce on farms and in markets, and of livelihood opportunities (species diversity/Shannon index)
Cycling	Extensive recycling of by-products; positive interaction and feedlack loops within system (as above)	Develop cycling indices and flow diversity indices (internal ascendancy)
Stability	High reliance on sharing resources; mutual benefits of integration to cope with changes in climate, markets, etc. (high reliance on internal dynamics and ability to recover from perturbations)	Quantify the degree to which natural resources and ecosystem services are conserved (buffer capacity; system overhead; resilience; development—capacity; ascendancy)
Capacity	High quantity and quality of produce, with a healthy environment (high resource quality)	Quantify production levels and quality, with corresponding water, soil, and air quality (soil depth, organic content, pH; water color, pH, biomass/throughput; average standing biomass/sum of all flows)

4. stability to cope with change;
5. capacity—quality of produce, services, and the environment.

And for all of these, the higher the level that a given aquaculture enterprise can achieve the more acceptable and sustainable it is likely to be.

6. PROSPECTS FOR USE

In Table 2, we summarize our proposed indicators and give broad indications of their desired levels (high or low) for the sustainability of aquaculture. There are, of course, interactions within and between categories. Are these indicators likely to be of any practical use? The complexity of ecosystem-based management and sustainable food production systems (e.g., see Slocombe, 1993; Parris, 1995; Bertollo, 1998) means that some of the codes of conduct and tools that have been developed for the pursuit of these goals are difficult to apply. For example, codes of practice on fish introductions and transfers (Turner, 1988) and a schema that was devised for assessing environmental impacts of aquaculture (Pullin, 1993) have seen little use. The FAO Code of Conduct for Responsible Fisheries (FAO, 1995) includes criteria, indicators, and obligations for responsible aquaculture development, and it has been expressed as a questionnaire (Sproul, 1997). Barg et al. (1997) suggested that this voluntary code be

Table 2. Summary of biological, ecological, and intersectoral indicators with broad levels (F = few, H = high, L = low, S = small) that are appropriate for sustainability in aquaculture

Indicators	Desirable levels
Biological	Potential for Domestication (H), with Genetic Enhancement (H); Trophic Level (L, 2.5 to 3.0; see Froese and Pauly, 1999); Feed and Energy Conversion Efficiency (H)
Ecological	Ecological Footprint (S); Emissions (L in contents harmful to the environment and to humans); Escapees (F) and Feral Populations (S and/or harmless to other biota and ecosystems)
Intersectoral	Water Sharing (H); Diversity (H); Cycling (H); Stability (H); Capacity (H)

viewed as a "framework" for dialogue. It contains the key recommendation that, "States should produce and regularly update aquaculture development strategies and plans, as required, to ensure that aquaculture development is ecologically sustainable and to allow the rationale use of resources shared by aquaculture and other activities" (FAO, 1995).

We believe that the main actors in aquaculture—policymakers, regulators, the private sector, communities, development donors, and individuals involved as producers and consumers of farmed fish—will have to strive more for its sustainability. Its net contributions to world fish supply and their ecological consequences (Naylor et al., 2000) will also have to be examined more thoroughly. Otherwise aquaculture will decline, as many capture fisheries are doing. The general public is beginning to ask questions about the sustainability of fish supply and to find some guidance for what they can do to improve it. For example, Lee (2000), for the National Audubon Society, has a color-coded "Audubon Fish Scale" for what are, in effect, the implications of choosing to eat a particular species farmed or fished by a particular method.

The Second International Symposium on Sustainable Aquaculture, held in Oslo in 1997, issued a revised set of what are termed the "Holmenkollen Guidelines for Sustainable Aquaculture" (NATS, 1998). This document is a consensus statement from that symposium and has, as an appendix, aquaculture-related sections of the FAO Code of Conduct for Responsible Fisheries (FAO, 1995). The Holmenkollen Guidelines set out principles and practices which are entirely compatible with the indicators that we suggest here, although they give less emphasis to intersectoral issues and do not mention explicitly the concept of ecological footprints.

For some of our proposed indicators, quantitative information is already available. For example, information on the trophic levels of fish available in FishBase (Froese and Pauly, 1999) and information on feed conversion is available through the aquaculture trade and scientific journals. Therefore, it should be relatively easy for a proposed development or research initiative to be checked against these indicators for its implications with respect to sustainability.

For the remainder, (domestication with genetic enhancement, footprints, escapes, emissions) information is less accessible and needs to be supplemented through research and collated for cross-comparisons, preferably via the internet. In the case of water sharing and our suggested intersectoral "analogues" of ecosystem parameters, quantification has either barely started or is not yet readily accessible. Therefore, the use of these indicators will require a marked improvement in the availability of quantitative information—locally, nationally, and internationally.

Ultimately, the use of any or all of these indicators will depend on the *will* of potential users to actually use them. Those responsible for aquaculture development within sovereign States, as well as other actors who are involved directly or indirectly with aquaculture development, will need to become more proactive in the quest for sustainability. History suggests, however, that serious environmental degradation must be experienced before countermeasures are sought. During such degradation and (where possible) recoveries, the "baselines" for what is regarded as acceptable will shift (Pauly, 1995) as will the modes of governance that are chosen by or imposed on resource users (Kooiman et al., 1999).

Kiley-Worthington (1998) cited evidence that "Current developments in high-input agriculture, which were predicted to be able to feed the exponentially growing world population . . . are not solving the world's food problems; rather, in some cases, they have been responsible for creating them . . . " A similar path for aquaculture development would further damage the environment and lessen food security. Aquaculture must rather seek to avoid or to minimize environmental degradation. It cannot rely indefinitely on "mining" resources from elsewhere. The "elsewheres" will run out—like switching from one overfished species to another in capture fisheries (Pauly et al., 1998). We hope that use of broad biological, ecological, and intersectoral indicators will contribute to progress towards the sustainability of aquaculture.

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CHAPTER 4

SUSTAINABLE APPROACHES FOR AQUACULTURE DEVELOPMENT: LOOKING AHEAD THROUGH LESSONS IN THE PAST

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Abstract: Aquaculture has significantly progressed in recent years. Thirty percent of the total world fishery production now comes from aquaculture. Because capture fisheries production is leveling off and unlikely to increase, aquaculture is considered to be the production mechanism that will provide fishing products that capture fisheries can no longer provide. Unfortunately, the rapid expansion of aquaculture has brought negative effects on the environment, primarily in nearshore areas, and has prompted some people to wonder whether it is necessary to sacrifice the environment for the sake of food production. Inadequate understanding of aquatic environments has led to the perception that the oceans have an inexhaustible supply of resources and an unlimited capacity to receive wastes from all of mankind's activities, including those from aquaculture. In marine aquaculture, problems such as deposition and dispersal of wastes in bays and coastal areas cause the destruction of mangrove habitats, which serve as important larval nursery grounds. In freshwater aquaculture systems, environmental impacts include exhaustive use of groundwater, resulting in land subsidence and intrusion of saltwater into the water table. Nevertheless, there remains enough room and opportunity to gain the benefits that aquaculture can provide. In this paper, two approaches are proposed. One is a non-technical approach, which includes the implementation and strict enforcement of policies as well as a massive educational program on the need of a rational and environmentally sound basis in the practice of aquaculture. This would minimize or prevent environmental impacts and resolve conflicts among different users of particular resources. The second approach is technical in nature. This includes the development and application of technologies that are in harmony with the environment, such as constructing super-intensive recirculating culture systems, properly placing sea-cage aquaculture systems, replenishing seeds in the wild through stock enhancement, and practicing sea ranching. Aquaculture plays a vital role in food production. However, caution should be taken

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in aquaculture development in the future. Although there is probably no ultimate technology that will prevent impacts of aquaculture on the environment, continued surveillance and monitoring are highly desirable. Scientists and aquaculturists must work together to transfer to future generations the high-quality environments inherited from previous generations.

Key words: aquaculture, environment, impacts, non-technical approach, Taiwan, technical approach

1. INTRODUCTION

World fishery production, including both capture fisheries and aquaculture, increased from 117 million tons in 1995 to 121 million tons in 1996 and to 122 million tons in 1998 (FAO, 1999). This continued increase is attributed to better fishery management and regulations and to the expansion of the aquaculture industry worldwide. However, the demand for seafood is still increasing; thus, pressure to produce aquaculture products remains. Producing an adequate quantity of aquaculture products and improving their quality to meet the nutritional requirements of an increasing world population have become important issues. In this century, the importance of aquaculture will become even more apparent as the world population, and thus the demand for food, continues to increase.

The dynamic aquatic environment covers over 71% of the earth's surface. The nearshore marine environment, which was principally utilized during the rapid expansion of aquaculture, comprises only 6% of the world's aquatic surface area but provides 43% of the world's aquatic products. The three-dimensional, open-ocean environment could be utilized more for aquaculture development in the future.

World freshwater environments are also limited; only 3% of the world's water resources are freshwater. Of those, 2.3% is frozen as glaciers and permafrost and is not available for consumption. Only about 0.7% is available in rivers, lakes, soil, swamps, groundwater, and vegetation. In addition, freshwater is poorly distributed among countries and regions. Many developing countries, even those with adequate water, suffer from regional and seasonal shortages that are disadvantageous for aquaculture development.

Following are important components of aquaculture. All of these factors are associated with their respective listed environmental stresses (in parentheses), to varying degrees:

1. larval culture (the discharge of used water containing insecticide, algaecide, antibiotics, or diseased larvae);
2. live food-organism culture (discharge of high-density phytoplankton or zooplankton species, some of which may be exotic to the area);
3. formulated feed production (discharge of feed-manufacturing pollutants);
4. grow-out (destruction of coastal land or mangrove areas for construction of grow-out ponds, over-pumping of groundwater);

5. cage culture (modification of original fauna in open waters, loss of excess feed and nutrients to the environment);
6. post-harvest handling (discharge of industry pollutants from seafood processing);
7. genetic biotechnology (accidental release of genetically modified aquatic organisms).

Research and development of aquaculture technologies today means food for the future. Therefore, it is important for the aquaculture industry's researchers, practitioners, and regulators to adopt appropriate perspectives for the sustainable utilization of both marine and freshwater resources for aquaculture. Aquaculture appears to have more potential as a future source of food than other currently developed technologies because the marine biosphere could potentially support a much higher level of culture than the terrestrial biosphere.

Lessons from the past indicate that inadequate understanding of aquatic environments has led to the misconception that bays, nearshore areas, and inland aquatic systems have an inexhaustible supply of resources and an unlimited capacity to receive wastes from many sources, including aquaculture (Chua and Garces, 1994). However, there is now, and will be in the near future, a rapidly increasing consumer demand for fish and other aquaculture products. The principal products from the ocean are not currently well utilized. We know that several of the most important food resources for protein production can be utilized much more efficiently if used in fish farming. From an ecological perspective, many ingredients in fish feeds have their origins in the sea and should ultimately be returned to the sea for improved recycling in the marine ecosystem. With future progress in areas such as systematic breeding, feed development, and culture management, aquaculture can be made to be in harmony with the environment.

2. PAST EXPERIENCES AND LESSONS TO LEARN

Aquaculture depends on the right quantity, quality, and management of water resources from rivers, oceans, or land–ocean interfaces. Waste products from aquaculture and other sources are usually discharged into water masses and transported to coastal areas, causing pollution problems. The effect of neglecting sustainability in aquaculture development can be devastating to the aquaculture industry itself, as illustrated by the dramatic collapse of the prawn culture industry after it reached an annual production of 450,000 metric tons (t) in Asia and Latin America. In that industry, the absence of aquaculture regulations and lack of good management concepts led to tremendous expansions of culture areas and increases in stocking densities beyond the carrying capacities of the aquaculture facilities and local environments. The spread of contagious diseases, provoked by the deteriorated environments, the lack of quarantine systems, and the practice of maintaining very high stocking densities, led to the collapse of the industry (Liao, 1991). This enabled aquafarmers to realize the importance of maintaining an ecological balance within aquaculture systems and in the neighboring environments.

Other problems associated with coastal aquaculture are land subsidence and the large-scale harvest of commercial wild larvae from coastal wetlands in some countries where artificial propagation is not available. Prawns are produced mainly from land-based ponds built along the seashore or in mangrove areas. This alteration results in land subsidence, intrusion of saltwater into the water table, and destruction of nursery areas and habitat for aquatic animals, particularly in mangrove areas. Many species ideal as aquaculture candidates have some life-history stages associated with coastal wetlands. The excessive harvest of these species when they are concentrated in mangrove swamps can endanger the abundance of these species. Coastal wetlands are characterized by high rates of biological activity. Rates of both primary production and, correspondingly, rates of degradation of organic matter, in wetlands are relatively high. This high rate of production and decay and the rapid exchange of water due to tidal fluxes create the potential for active transport of organic matter and nutrients into and out of coastal wetlands, thus benefiting broad areas of the nearshore environment. If these ecologically important wetlands are destroyed, it may take years for them to recover, and this may be possible only under vigilant protection.

The interactions between aquaculture and the environment have been the subject of several reviews (Phillips, 1998). The following categories of interactions are generally considered:

1. Impacts of aquaculture on aquaculture. The rapid expansion of aquaculture in some areas with limited natural resources has sometimes led to overexploitation of these resources beyond the capacity of the aquaculture environment to sustain itself. When this occurs, it may be followed by an eventual local collapse of aquaculture as an enterprise. In addition, within the aquaculture system, self-pollution may lead to disease and water quality problems that can undermine the sustainability of the aquaculture endeavor.
2. Impacts of aquaculture on the environment. These include the positive and negative effects that aquaculture operations may have on water, land, and other resources required by other aquafarmers or other user groups. Impacts may include the degradation or loss of natural habitats and resources such as water, land, and wild seed. Introduction of exotic species into environments and competition between different sectors for resources may also cause problems.
3. Impacts of the environment on aquaculture. These include the positive and negative effects that environmental change may have on water, land, and other resources required for aquaculture development. The effect may be negative or positive for aquaculture sustainability. Aquaculture is highly sensitive to adverse changes in the natural resources upon which it depends. Therefore, it is in the long-term interest of aquafarmers to work toward protecting and enhancing environmental quality. Traditionally, aquaculture

has been considered as an environmentally friendly activity. However, some forms of industrial aquaculture require closer examination of this philosophy. This perception principally resulted from a scarcity of sound information on the adverse effects of aquatic farming activities on natural resources and the environment. Aquaculture can be intensified only up to a limit; otherwise adverse ecological effects will follow with negative feedbacks on the aquaculture operation itself.

3. APPROACHES TOWARD A BETTER ECO-BALANCE BETWEEN AQUACULTURE AND THE ENVIRONMENT

The future needs more than the abilities of today's professionals to draw up new ideas and to provide relief for both the environment and aquaculture. Decisive action is required to minimize or prevent the problems of aquaculture–aquaculture, aquaculture–environment, and environment–aquaculture impacts and conflicts among different users of aquatic resources. This can be done if people shift their understanding toward the necessity of sustainable management of natural resources as a global responsibility. Then, long-term policies can be developed and enforced. The following approaches are recommendations for the practice of environmentally compatible aquaculture.

3.1. Non-Technical Approaches

These approaches generally involve increasing communication and public and industry-personnel awareness about the importance of the environmentally conscious pursuit of aquaculture and about developing and adhering to environmentally sound regulations.

1. Promote public awareness through education. Incorporating environmentally conscious thinking into everyday industry practices is largely the product of exposure to the problems and to their solutions and of education about the importance of practicing environmentally friendly aquaculture. Some types of activities that will increase awareness follow:
    a. strengthen worldwide the concept of environmental conservation of the earth;
    b. increase awareness among the public and aquaculture-related industry personnel on issues regarding the sustainable development of aquaculture;
    c. ensure that people involved in the aquaculture industry are aware of new and existing rules and that the rules are continuously implemented;
    d. encourage the private sector to play an active role in protecting the environment while operating aquaculture sustainably and profitably (Holthus, 1999);
    e. conduct functions that promote environmentally compatible aquaculture, such as conferences, seminars, dialogues, poster exhibitions, and photo contests;

   f. establish international websites that allow people to access updated aquaculture information and regulations and to interact with other people of the same interest.
2. Implement and enforce regulations. To protect the environment for both humans and aquaculture, the following regulations and measures are suggested:
   a. impose penalty fees on those who cause pollution;
   b. regulate ocean pollution as strictly as land pollution;
   c. legislate regulations against all types of coastal pollution on an international basis;
   d. increase dialogue, interactions, and partnerships to ensure that environmental funds are used for the benefit of the public and industries at multi-sectorial levels;
   e. set up an internationally recognized monitoring method to protect the coastal and ocean environments from aquaculture-associated problems that occur on a worldwide basis, such as feed pollution from open-water cage culture and seabed recovery after marine farming;
   f. when the need arises, amend regulations and legislation to suit particular situations that may arise within communities, regions, or nations, or globally.

3.2. Technical Approaches

3.2.1. Further development of technologies that are in harmony with the environment

These approaches include the development and continuation of all types of technical advances associated with aquaculture. These should be developed in an environmentally conscious manner.

1. Conduct scientifically based stock enhancement and sea ranching. If approached from a scientifically based background, stock enhancement and sea ranching may be beneficial for rebuilding wild stocks of native species to original population levels with the hope of causing little risk to natural wild-population dynamics. For the sustainability of aquaculture based on sea ranching, basic knowledge of the diet, physiology, and behavior of the cultured species is necessary, as well as knowledge of their ecology in the natural habitat (Masuda, 1998; Liao, 1999).
2. Increase use of super-intensive recirculating culture systems. Recirculating systems that completely clean and reuse rearing water have been proven to use much less manpower and fewer natural resources (e.g., land and water) than non-recirculating systems. For example, a super-intensive eel culture system in Taiwan, saves land and water by 30- and 100-fold, respectively, over non-recirculating systems, thus causing fewer adverse impacts on the environment.

3. Employ sea-cage aquaculture. Sea-cage aquaculture reduces competition with land or coastal users. Since it is a newly emerging technology in many countries, lessons should be taken from countries where sea-cage aquaculture is an established technology and environmental concerns such as the escape of culture species are addressed (Asgard et al., 1999).
4. Impose mandatory fallowing. Fallowing is advantageous for reducing the impacts of aquaculture because stocking levels in the following crop can be increased without exceeding the capacity of the environment. Fallowing is also an ideal method for seabed recovery after intensive marine farming. Studies are needed to provide estimates of the contribution of farmed and fallow sites to the nitrogen budget and to identify and compare the relative rates of accumulation, decay, and natural removal of waste.

3.2.2. Monitoring the environment

Regular monitoring of degradation both of the surrounding natural environments by aquaculture facilities and, in some systems, of the aquaculture facilities by the environments is important to prevent unexpected and potentially irreversible damage. Following are some suggested methods for environmental monitoring:

1. Use shellfish as pollution bioindicators. Shellfish can filter many liters of water per day and thus accumulate trace contaminants. Measurement of contaminant concentrations such as polychlorinated biphenyls and polycyclic aromatic hydrocarbons in shellfish can provide environmental managers with a powerful monitoring tool.
2. Use electronic proximity sensors. Chemical analyses can be used to check water quality but using shellfish and electronic proximity sensors is a simpler and more effective way of checking for water quality problems. Electronic proximity sensors can precisely measure from the gaping shells of bivalves (e.g., mussels). Such instruments are sensitive to any deterioration in the quality of the surrounding water. Real-time monitoring based on a mean value of multiple sensors can be used to trigger alarms, shut off pumps, or operate automatic samplers. This can be of particularly importance when monitoring the quality of water incoming to shellfish farms, which could be affected by accidental spillages from land or shipping and by dangers associated with floods.
3. Perform routine taxonomic analysis of aquatic organisms. Periodic sampling and identification of benthic and planktonic organisms in aquaculture zones can serve to announce impending pollution. Changes in faunal or floral species composition or biodiversity levels are indicators of pollution; thus, systematic taxonomic surveys can give early warning before a crisis.

3.2.3. Application of gene-based technology and other biotechnologies

Aquatic-organism genetic resources represent a source for the production of new strains, either through traditional crossbreeding or through biotechnology (e.g., gene infusion or transplantation). The use of modern biotechnological tools, such as one of the methods used to survey DNA (e.g., Randomly Amplified Polymorphic DNA or Restriction Fragment Length Polymorphism analysis, DNA sequencing, microsatellite DNA analysis) can facilitate fast and reliable screening of the available germplasm. As in plants (El Bassam, 1999), the genetic resources of aquatic organisms constitute the reservoir of genetic adaptability that can act against potentially harmful environmental changes. The erosion of these resources poses a severe threat to the world's aquatic-resource food security in the long term. Although often undervalued, the need to conserve and utilize genetic resources as a safeguard against an unpredictable future is evident (FAO, 1996). However, caution should also be taken when applying gene-based technology to aquaculture because of the possible risks that genetically modified organisms can impose on native populations. For example, genetically altered organisms can have superior intraspecific and interspecific competitive capabilities; or, genetically altered individuals can interbreed with conspecifics or closely related species, with unknown consequences.

In some cases, biotechnology has provided a new range of tools for rapidly improving the environmental tolerance and disease resistance of farmed stocks. Prevention and control of viral infection also may be possible through broodstock selection that utilizes DNA diagnostic techniques such as the polymerase chain reaction (PCR).

3.2.4. Other environmentally sustainable monitoring methods

If an unexpected fish-kill or other problem occurs in an aquaculture facility, the cause of the poor environmental situation should be identified as quickly as possible. Through designation of safe or refuge zones, cages for culture could be relocated. Alternatively, research could be done to determine or evaluate the technologies available to minimize possible damage to cultured organisms that could be caused by existing pollutants such as oil spills or leakage, chemical runoff, or polluted water discharge.

Despite the apparent conflicts between the practice of aquaculture and the preservation of natural environmental components, there is optimism that, in the future, protection of the environment will occur through the practice of sustainable aquaculture. The significance of research designed to provide the basic information needed for the implementation of long-term management policies must be recognized. To facilitate the sustainability of aquaculture in the new millennium, the following principles should be strictly implemented:

1. The relevant media should be periodically used to educate those in the aquaculture industry and to encourage them to access information sources relevant to sustainable aquaculture.
2. Problematic environmental parameters should be routinely and systematically monitored in all aquaculture operations.
3. Environmentally friendly aquaculture strategies should be continuously performed and encouraged.

4. Both appropriate and significant penalties and rewards should be used to encourage adherence to regulations and the practice of environmentally friendly aquaculture.

4. CONCLUSIONS

How can we reduce existing and future concerns about environmental degradation resulting from aquaculture and its infrastructure business? According to the definition set by the FAO (1995), sustainable development is "the management and conservation of the natural resource base, and the orientation of technological and institutional change in such a manner as to ensure the attainment and continued satisfaction of human needs for present and future generations. Such sustainable development (in agriculture, forestry, and fisheries sectors) conserves land, water, plant, and animal resources and is environmentally non-degrading, technically appropriate, economically viable, and socially acceptable."

To achieve environmental management for sustainable aquaculture, policies that meet both the presence status of aquaculture and its future potential must be adopted. If properly executed, aquaculture has enormous potential for further expansion and intensification with minimal increases in pollution effects. Meanwhile, there are solid reasons for promoting all types of less pollutive aquaculture enterprises. Aquaculturists should follow technologies and procedures that do not degrade the environment at present and do not cause excessive damage in the future. The sustainability of aquaculture itself is linked to that of the environment.

A separate but related issue is that conflicts with many other users of the environment must be solved. Such complicated conflict resolution may require proper legislation based on the results of adequate investigations and research, and should be formulated, implemented, and amended to suit varying conditions and needs. The cost of superficial material gains from improperly managed aquaculture can be tremendous: the corruption of natural beauty and the disruption of ecosystems and of the goods and services they provide. Looking ahead through lessons learned from past experiences is a reasonable approach for attaining sustainable aquaculture development in the new millennium. Scientists, aquaculturists, politicians, and the public all agree that aquaculture plays a vital role in food production, now and in the future. But they also must agree that there is probably no single technology that can prevent the impacts of aquaculture on the environment. Therefore, continued efforts in terms of public education, developmental planning, environmental surveillance and monitoring, mitigation of adverse impacts, and regulatory improvement are highly desirable.

People around the world should work together to preserve the high-quality environments that were inherited from previous generations and that will be handed down to future generations. It should be clearly understood that we are on "one earth, one community and one future." Our way of thinking should be changed from "I, here, and now" to "we, everywhere, for today and tomorrow." We agree with the Declaration of Braunschweig (Anonymous, 1998) that, unless we become the responsible stewards of current and future generations, we will face more unprecedented and severe regional and global changes and environmental inequities.

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SECTION TWO

POPULATION GENETIC CONSIDERATIONS

CHAPTER 5

GENETIC RISKS OF MARINE HATCHERY ENHANCEMENT: THE GOOD, THE BAD, AND THE UNKNOWN

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Abstract: As global capture fisheries level off or decline, hatchery enhancement of marine species is being undertaken on a large, though poorly documented, worldwide scale. Hatchery enhancement can potentially reduce the genetic diversity of natural stocks because the enormous fecundity of many marine fish and shellfish species enables the swamping of populations with the progeny of a very few adults. Much of the impact of hatchery supplementation on genetic diversity can be predicted from its effects on the effective size of the natural population. A simple mixing model (Ryman and Laikre, 1991) allows calculation of the effective population size of an enhanced population, if the effective sizes of the hatchery and prestocked natural populations and the fraction that each contributes to the mix are known. This model has been applied to a hatchery supplementation program for the endangered Sacramento River winter chinook salmon (*Oncorhynchus tshawytscha*). This example shows that a reduction in effective population size is not inevitable and that supplementation can increase the effective sizes of small populations. For highly fecund marine species, on the other hand, a severe reduction in effective population size appears to be a more likely result because hatchery populations are generally small and contributions to populations are large. Unfortunately, a paucity of data prevents application of the model to any of the major marine supplementation programs. The precautionary approach to fisheries management suggests slowing the development and implementation of marine enhancement programs until and unless sufficient data are available to evaluate their potential impact on effective population size and genetic diversity.

Key words: aquaculture, effective population size, environment, genetic diversity, hatchery enhancement, stock enhancement

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1. INTRODUCTION

Demand for seafood on a global scale is projected to increase by 70% in the next 30 years, yet most fisheries are at or beyond sustainable yields and many are in decline (Botsford et al., 1997). Traditional methods of managing fisheries are clearly failing and new strategies for protecting and enhancing marine resources are emerging. "No-take" marine reserves, for example, are being discussed widely and intensively as an alternative method for protecting species and habitats (Allison et al., 1998; Hastings and Botsford, 1999).

Other strategies for meeting the challenge of growing global demand for seafood involve aquaculture. Farming of aquatic species is supplying an increasing portion of seafood demand, albeit with growing concerns about ecological impacts (FAO, 1997; Naylor et al., 2000). Another use of aquaculture is to enhance natural stocks through artificial hatchery propagation of seed or juvenile stages for release into the wild. Fish and shellfish hatcheries have been around for more than 100 years, and they can successfully produce very large numbers of fish fry or shellfish seed for release. Although hatchery enhancement has become controversial as a ready technological solution to the decline in natural fish stocks (Meffe, 1992), large-scale hatchery supplementation programs are already in place in anadromous and marine fisheries (Travis et al., 1998). Moreover, the global extent of hatchery enhancement of wild fisheries is poorly documented, especially for marine species (A.F. Born, A.J. Immink, and D.M. Bartley, FAO Fisheries, personal communication).

The benefits and risks posed by hatchery supplementation with respect to conservation of genetic diversity have been widely discussed (Waples and Do, 1994; National Research Council, 1996; Waples, 1999). We focus here on only one aspect of this wider problem, the risk that natural genetic diversity might be lost from within populations as a consequence of hatchery enhancement. This risk appears particularly acute for marine fish and shellfish, whose enormous fecundities enable releases of large numbers of individuals representing very few adults (Ryman et al., 1995). We illustrate our points primarily with data from two hatchery enhancement projects that have brought these issues to our attention.

Concern is often expressed about genetic changes in supplemented populations resulting from artificial or domestication selection for survival in the hatchery environment or from shielding of adults or hatchery-reared progeny from natural selection (e.g., Waples, 1999). While this is certainly true for hatchery stocks propagated generation after generation, many enhancement hatcheries get broodstock continually from the wild and do not typically use hatchery-reared progeny to propagate the next generation. In this case, the efficiency of selection on a single pass through a hatchery is likely to be low, especially if differential survival among families is minimized. Data on the relative survival of hatchery and wild fish for one of our examples indeed suggests that artificial selection is very weak. At least in this case, the risk to diversity from over-propagating a few adults appears to us to far outweigh the

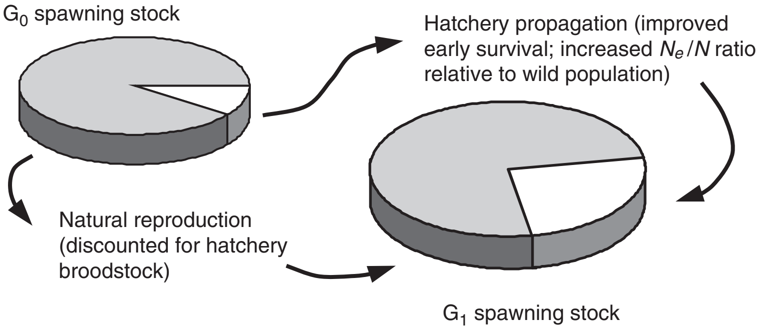

Figure 1. Schematic diagram of the effects of hatchery supplementation on a natural population. A small segment of the spawning stock is removed from the wild at generation G_0. The offspring of this segment of the adult population enjoy higher survival than their wild counterparts, causing an increase in the population size in generation G_1, represented by the larger pie. Genetic diversity of the G_1 will be less than that of the G_0, however, unless the hatchery component has a higher ratio of effective (N_e) to actual (N) population size than does the naturally spawning component of the population

risk from artificial selection. Whether or not this is true in all cases, the population genetic context must be known to evaluate the magnitude of risk from domestication selection.

A simplistic view of hatchery supplementation (Figure 1) makes a negative impact on effective population size appear almost certain, because a small segment of the natural population contributes disproportionately to the next generation. We shall show, however, that this need not be the case, either in principle or in practice. Hatcheries can sometimes be managed to enhance effective population size and may thus have potential for conserving endangered populations or species, provided that other risks not discussed here (e.g., disease transmission, artificial or domestication selection, or breakdown of stock structure) can be minimized.

Much of the impact of hatchery supplementation on genetic diversity can be predicted through its effects on the *effective size* (N_e) of the natural population. N_e is defined as the size of a mathematically ideal population that has the same rate of random genetic drift (predicted by the variance effective size) or inbreeding (predicted by the inbreeding effective size) as the actual population under study (see Crow and Denniston, 1988). At demographic equilibrium, variance and inbreeding effective sizes are the same, but they can differ when a population experiences a rapid change in size (Ryman et al., 1995). Here, we are concerned primarily with the variance effective size, which determines the rate at which genetic variants are lost or fixed by chance (random genetic drift). In the mathematically ideal population, there are equal numbers of both sexes, adults mate at random, and variance in number of offspring per adult is binomial or Poisson. The number of adults in the ideal population (N) is, by definition, equal to the effective size, and the ratio of $N_e/N = 1.0$ in the ideal case. In actual populations, the sexes may not be in equal numbers, mating may not be at random, or the variance in offspring number may be larger than binomial or Poisson. Consequently, the N_e/N ratio for most terrestrial vertebrate populations is thought to lie between 0.25 and 0.75 (Nunney, 1996).

Conservation guidelines on minimum N_e have changed with advances in the genetical theory of small populations. To protect against inbreeding, which increases at a rate of $1/2N_e$ per generation, inbreeding effective sizes of 50 and above would appear to be sufficient (Franklin, 1980). To avoid long-term loss of variation or to conserve rare alleles that might be the basis of future adaptation, however, variance effective sizes above a minimum 500 or even 5000 may be needed (Franklin, 1980; Lande and Barrowclough, 1987). Finally, to reduce the chance fixation of mildly deleterious mutations (Lande, 1995) and the resulting increased risk of extinction from a "mutational meltdown" (Gabriel et al., 1993), N_e should be at least 5000. Whether mutational meltdowns inevitably draw small populations into extinction vortices from which they cannot escape remains controversial (Kondrashov, 1995; Gilligan et al., 1997). Still, a precautionary approach should embrace the higher threshold of N_e for conserving viable populations. Traditionally, N_e has been difficult to estimate for natural populations, though a variety of methods for estimating N_e has emerged in the past decade (Waples, 1991; Pudovkin et al., 1996; Luikart and Cornuet, 1999).

2. GENETICS OF A HATCHERY-SUPPLEMENTED POPULATION

For a hatchery-supplemented population, the variance effective size, N_e, depends on the effective sizes of the hatchery (N_{eh}) and wild (N_{ew}) components of the population and on the relative proportion of hatchery-origin fish (x; $x + y = 1.0$; after Ryman and Laikre, 1991):

$$N_e = \frac{N_{eh} \times N_{ew}}{x^2 N_{ew} + y^2 N_{eh}}$$

In this model, only three independent parameters are necessary and sufficient to describe the impact of hatchery enhancement on variance effective population size. Thus, the "good" part of hatchery enhancement is that a simple theory is available for evaluating this major genetic impact of hatchery supplementation. At least, we know what we need to know.

The equation above models the impact of a single generation of supplementation on the effective size of a population with discrete generations. The model must be evaluated in each year of a continuing supplementation program. If the N_e of the supplemented population varies over time, the long-term size will be given by the harmonic mean of the per-generation sizes, which is closer to the minimum than to the arithmetic mean effective population size. In addition, if there are overlapping generations, the drift variance in the natural population should be adjusted for age-specific survival and reproductive contributions (Waples and Do, 1994; Jorde and Ryman, 1995; Turner et al., 1999). Finally, it is not yet clear how to quantify and model lifetime reproductive success for iteroparous marine species. Still, the simple Ryman–Laikre model illustrates the basic genetic principles of supplementation and is of heuristic value in revealing risks that have until recently been largely ignored.

3. HATCHERY SUPPLEMENTATION OF WINTER CHINOOK SALMON

Hedrick et al. (1995, 2000a, b) have used the Ryman–Laikre model to evaluate the potential genetic impact of a hatchery supplementation program for the endangered Sacramento River winter chinook salmon (*Oncorhynchus tshawytscha*). Having plummeted from annual runs of nearly 100,000 fish in the late 1960s to less than 200 fish in 1991 and 1994, the winter chinook was protected under both state and federal endangered species laws in the early 1990s. In 1991, the U.S. Fish and Wildlife Service (USFWS) initiated a hatchery supplementation program, under permits from the National Marine Fisheries Service and the California Department of Fish and Game. From 1991 to 1995, the USFWS captured up to 20% of the spawning run or a maximum of 120 adults from the Sacramento River. Broodstock were then taken to the Coleman National Fish Hatchery on Battle Creek for maturation and spawning. Progeny were reared to a size of about 75-mm fork length, tagged internally with coded-wire tags, marked externally by clipping of adipose fins, and released into the Sacramento River. As noted by Hedrick et al. (2000a, b), the actual genetic impact of this program is difficult to assess because the hatchery fish imprinted on Battle Creek water. Some, but not all returning adults were trapped at the hatchery weir and were re-located to the proper spawning grounds on the Sacramento River. Nevertheless, the example is instructive, and the model is being applied to a revised supplementation program that rears progeny at a new facility on the Sacramento River.

For each year, from 1991 through 1995, we calculated N_{eh} from data on the number of progeny contributed by each male and female brood fish to the released juveniles (smolts). The N_e/N ratio for the naturally spawning population is assumed to have a lower bound of 0.1 (Bartley et al., 1992) and an upper bound of 0.333 (R.S. Waples, personal communication). These ratios are multiplied by the run-size estimate in any year to obtain N_{ew} before capture of adults (i.e., what the effective size would have been without supplementation). The N_{ew} after capture of adults for supplementation is obtained by multiplying the upper and lower N_e/N ratios by run size minus the number of adults taken to the hatchery. Estimates of N_{eh}, N_{ew}, x, and N_e, with and without supplementation, for 1994 and 1995 illustrate the impact of hatchery supplementation in years with different natural run sizes (189 vs. 1361, respectively; Table 1).

Table 1. Summaries of estimates of Ryman–Laikre model parameters for the Sacramento River winter chinook salmon (*Oncorhynchus tshawytscha*) for 1994 and 1995 (after Hedrick et al., 2000a)

Parameter	1994	1995
Number of wild adults returning	189	1,361
Number taken captive (N_h)	29	47
Number of adults left in the wild	160	1,314
Number of hatchery breeders ($N_f + N_m$)	26	42
N_{eh} (95% confidence interval)	23.2 (15.9, 30.8)	29.2 (21.3, 37.8)
N_{eh}/N_h ratio	0.80	0.62
Proportion of smolts from hatchery (x)	0.407	0.083
N_{ew} range without supplementation	18.9–63.0	136.1–453.7
N_{ew} range after adult capture	16.0–53.3	131.4–438.0
N_e range with supplementation	34.3–72.8	150.7–463.6

Three important points to note are as follows:

1. The supplementation program would likely have had little, or perhaps a slightly positive, impact on winter-run effective population size in both years, i.e., ranges for N_e were lower without than with supplementation (bottom line, Table 1).
2. The proportion of fish contributed by the hatchery, x, was high (0.41) in 1994, when the run size was low, and low (0.08) in 1995, when the run size was higher. Estimates of x are based on numbers of females, their egg production, and the survival of their progeny from egg to smolt stages. For hatchery stocks, the egg-to-smolt survival is estimated to be 28.5%, about twice as high as an estimate of 14.7% for egg-to-smolt survival in the wild (Hedrick et al., 2000a). Of course, this boost in early survival is precisely what makes hatchery supplementation such an attractive idea in the first place.
3. Ratios of effective to actual numbers of captive broodstock, N_{eh}/N_h, were 0.80 and 0.62 in 1994 and 1995, respectively, much higher than the N_e/N ratio assumed for the naturally spawning population (0.10 to 0.33). This boost in N_e/N ratio of the hatchery component can counterbalance the dilution of natural genetic diversity that ought always to occur in the simple view of supplementation (Figure 1).

Since N_{eh} is based on adult contributions at release rather than at return and spawning, the above calculations are predictions of N_e. By typing microsatellite DNA markers (Banks et al., 1999, 2000) on all returning, adipose fin-clipped adults during 1996–1998, we were able to assign 116 fish to year class and family (Hedrick et al., 2000b). We found that the contributions of each brood fish at release remained approximately the same at return and that the N_{eh} calculated for spawning adults was within the predicted 95% confidence intervals given in Table 1.

The equivalence in the relative proportions of families at spawning, release, and return suggests little genetic variation for survival in the hatchery or at sea. Moreover, data on the relative numbers of naturally spawned and hatchery fish returning to the Sacramento River, though subject to large uncertainty (Botsford and Brittnacher, 1998), suggest that x is not consistently less at return than at release. For 1995 through 1997, the proportions of hatchery-origin winter chinook salmon at return compared to release (three years prior) are 6.1% vs. 6.1%, 20.1% vs. 16.1%, and 25.0% vs. 41.7% (addendum to the USFWS Endangered Species Act, Section 10, Permit Supplement; dated February 20, 1998). These data suggest that the relative survival of hatchery and wild fish in the wild is not grossly different, given the large uncertainty in the escapement estimates. In this one example, at least, we see little evidence for selection as the result of a single pass through a supplementation hatchery. This may not be the finding when more data are available and need not be true of other programs. The important point is that data on family proportions at spawning, release, and adult stages allow evaluation of the relative strengths of selection and random drift and should be required for supplementation programs.

As illustrated in this example, higher survival and higher N_e/N ratios of hatchery offspring, combined with contributions that are inversely proportional to the wild stock size, can increase variance effective size and conserve more of the natural biodiversity than would have been conserved in the absence of supplementation. Hatchery enhancement does not necessarily constitute a threat to genetic resources; indeed, hatchery supplementation can help to retain biodiversity that would otherwise be lost from threatened and endangered populations without intervention. However, we agree with Waples and Do (1994) that supplementation programs are likely to succeed only when the initial environmental causes of population decline are ameliorated.

The impact of hatchery enhancement on genetic diversity can be visualized as the proportional change in effective size that results from hatchery supplementation relative to what N_e would have been had there been no supplementation program. This proportional change in effective size is shown in Figures 2 and 3 as a response surface plotted over the x and N_{ew} dimensions, holding hatchery effective size (N_{eh}) constant. Note, again, that N_{ew} is the effective size of the natural population discounted for the removal of hatchery broodstock.

Response surfaces for the Sacramento River winter chinook supplementation program in 1994 and 1995 are shown in Figure 2. Note the much narrower range of conditions that yields a positive impact in 1995, when the spawning population was large, compared to 1994, when the spawning population was small. This comparison suggests that hatchery supplementation is more likely to have a positive impact on genetic diversity when the natural population is small, suggesting a role for enhancement in the management of threatened species. Conversely, hatchery supplementation has a greater scope for negative impacts when the natural population is moderately large. A small increase in x

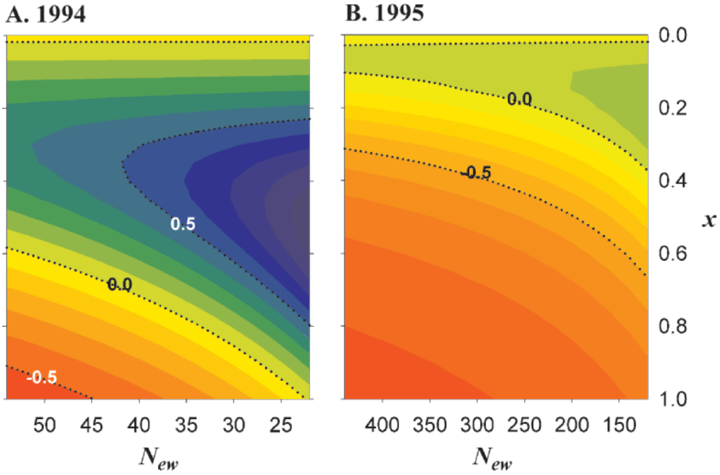

Figure 2. The impact of hatchery enhancement on the effective population size, N_e, of the Sacramento River winter chinook salmon in (A) 1994 and (B) 1995. Impact is visualized as the proportional difference between N_e with and without hatchery supplementation. The difference is plotted on a two-dimensional response surface, contoured in increments of 0.2; cool colors indicate positive impacts, warm colors, negative impacts of supplementation on N_e. Effective size of the hatchery component, N_{eh}, is a constant in each panel (23.2 in 1994 and 29.2 in 1995). N_{ew}, the effective size of the naturally spawning population discounted for the removal of hatchery broodstock, and x, the proportion of the population contributed by the hatchery, vary as shown. Hatchery contribution, x, was 0.41 in 1994 and 0.08 in 1995

would have resulted in a large decrease in N_e, suggesting cautious application to fisheries that are depressed but still of moderate effective size.

4. ENHANCING MARINE FISHERIES

With highly fecund marine species, a very large number of juveniles can be artificially propagated from very few adults. This makes likely an unfavorable balance between N_{eh} and x, which constitutes the ‘‘bad’’ part of marine hatchery enhancement. Hatcheries contribute substantially to certain marine or estuarine fisheries (Table 2). In Japan, large-scale sea farming for 68 native species is practiced, with annual releases of approximately 20 million red sea bream (*Pagrus major*) and Japanese flounder (*Paralichthys olivaceus*), 300 million kuruma shrimp (*Marsupenaeus japonicus*), 30 million swimming crabs, 25 million abalone, and 60 million sea urchins. Consequently, hatchery contribution (x) reportedly reaches 20–50% of harvest in extreme cases (see references in Table 3). Such large releases could easily be achieved using only tens of broodstock because fecundities are so high. Furthermore, effective sizes of most hatchery-propagated marine aquaculture stocks are generally much smaller

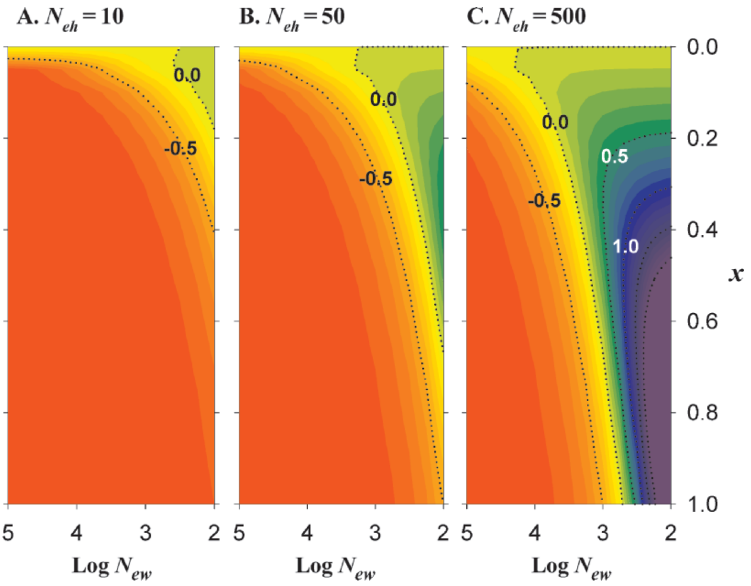

Figure 3. Hypothetical response surfaces, showing the impact of hatchery supplementation on effective sizes of highly fecund marine species, as in Figure 2. Effective sizes of hatchery components are fixed for each panel at the size indicated. Effective sizes of the wild population, discounted for removal of hatchery broodstock, are shown on a log scale. Cool colors indicate positive impacts, warm colors, negative impacts of supplementation on N_e. Contours show the proportional difference between N_e with and without hatchery supplementation in increments of 0.1

Table 2. Large-scale releases of hatchery-produced marine and estuarine species (from A.F. Born, A.J. Immink, and D.M. Bartley, FAO Fisheries, personal communication)

Top 10 hatchery-enhanced marine or estuarine species	Number released (in millions)	Years reported	Primary country
yesso scallop *(Patinopecten yessoensis)*	5,656	1994–96	Japan
fleshy prawn *(Fenneropenaeus chinensis)*	1,370	1985	China
Kuruma shrimp *(Marsupenaeus japonicus)*	366	1986–92, 1994–97	Japan; Republic of Korea; Taiwan
Scallop sp.	166	1986–88	Russia
Pacific oyster *(Crassostrea gigas)*	160	1994–96	Japan
fleshy prawn *(Fenneropenaeus chinensis kishimouye)*	106	1987–92, 94, 95	Korea
red sea bream *(Pagrus major)*	105	1994, 95	Japan
Japanese flounder *(Paralichthys olivaceus)*	56	1995, 96	Japan
tiger prawn *(Penaeus monodon)*	26	1994–95	Brunei; Taiwan
giant clam (*Tridacna maxima*)	25	1996–97	Tonga

Table 3. Ryman–Laikre model parameters for hatchery-enhanced marine species. N_{ew} is the effective size of the wild population; N_{eh} is the effective size of the hatchery population; x is the proportion of the enhanced population that is contributed by the hatchery.

Species	N_{ew}	N_{eh}	X	Source[a]
Red drum (*Sciaenops ocellatus*)	14,000	5–50	14–30%	1, 2, 3
	10^5–10^6		2%	3
White sea bass (*Atractoscion nobilis*)	—	20	3–5%	11
Red sea bream (*Pagrus major*)	—	63.7	50%	4
Japanese flounder (*Paralichthys olivaceus*)	—	—	38.5%	5
Black rockfish (*Sebastes schlegeli*)	—	—	35.5%	6
			73.1%	
Spotted seatrout (*Cynoscion nebulosus*)	75,000	—	—	7
Striped mullet (*Mugil cephalus*)	—	—	14%	8
Turbot (*Scophthalmus maximus*)	—	—	9.5%	9
Gulf sturgeon (*Acipenser oxyrinchus desotoi*)	2,500	50–100	75%	3
Abalone (*Haliotis discus hannai*)	—	—	10–30%	10
Bay scallop (*Argopecten irradians*)	—	—	20%	12

[a] Sources are as follows: (1) Turner et al. (1999); (2) McEachron et al. (1998); (3) Tringali and Bert (1998); (4) Perez-Enriquez et al. (1999); (5) Fujio et al. (1985); (6) Fujio and Nakajima (1989); (7) in Richardson and Gold (1993); (8) Leber and Arce (1996); (9) Iglesias and Rodriguez-Ojea (1994); (10) Masuda and Tsukamoto (1998); (11) K. Jones and M. Drawbridge, personal communication; and (12) Munro and Bell (1997). Estimates of x for red drum and red sea bream are per generation. The first estimate of x for black rockfish is for the Sea of Japan population, while the second is for the Pacific Ocean population

than numbers of breeders, so that N_{eh} is often less than 50 (Hedgecock et al., 1992; *cf.* Perez-Enriquez et al., 1999).

Indeed, if one plots hypothetical impacts of hatchery enhancement on effective size of marine populations (Figure 3), the picture is much gloomier than for the Sacramento River winter chinook salmon (Figure 2). The three plots in Figure 3 assume N_{eh} values of 10, 50, and 500, respectively. The vertical axis gives x, as in Figure 2, and the horizontal axis gives $\log_{10} N_{ew}$. All three panels show large areas of negative proportional changes in N_e, suggesting that enhancement of marine populations may often be detrimental to genetic diversity. If hatchery contributions do constitute 20–50% of the adult population, as reported for some Japanese fisheries, genetic diversity will be lost unless N_{eh} is in the hundreds and N_{ew} is less than a few thousand.

To illustrate further the potential risk, let us assume $N_{eh} = 50$, $N_{ew} = 50{,}000$, and $x = 0.1$. Then, according to the Ryman–Laikre model, the effective size of our hypothetical "enhanced" stock would be reduced to 4,625, less than 10% of the non-enhanced natural population of 50,000. Indeed, even for $N_{ew} = 500{,}000$, which is off the scale of Figure 3, $N_{eh} = 50$, and $x = 0.1$, the effective size would be 4960, only 1% of the non-enhanced population and just at the threshold number of 5000 for mutational meltdown (Lande, 1995). These calculations suggest that N_{eh} is more critical than N_{ew}, but x is also important.

With $N_{eh} = 500$, $N_{ew} = 500{,}000$, and $x = 0.1$, N_e is 46,000; however, at $x = 0.5$, N_e drops to 2000. Clearly, large-scale marine enhancement programs *can* have detrimental impacts on the conservation of marine fisheries, but we need much better estimates of effective population sizes and of hatchery contributions to natural spawning populations to evaluate this risk.

In California, a large enhancement program for white seabass (*Atractoscion nobilis*) was initiated in 1994 under a memorandum of agreement between the California Department of Fish and Game, California Coastal Commission, Ocean Resources Enhancement Advisory Panel, and Southern California Edison (Bartley et al., 1995; Drawbridge et al., 1995; Kent et al., 1995). The genetic risk of this program is unknown. In the hatchery, white seabass spawn en masse at night, making parentage difficult to know. Preliminary genetic analyses on the parentage of fry in single spawns suggest, however, that a single female and one or two males contribute offspring on a given night (K. Jones and M. Drawbridge, personal communication). Of course, several spawns may be released, so that N_{eh} may be larger, perhaps 20. At the same time, coded-wire tag recoveries suggest that hatchery-reared fish comprise up to 5% of white seabass sampled in southern California. Under these conditions, the hatchery program will reduce effective population size and genetic diversity if the effective size of the natural population is greater than about 800.

The extent of hatchery enhancement worldwide has been difficult to ascertain (A.F. Born, A.J. Immink, and D.M. Bartley, FAO, personal communication); the genetic impacts of even the largest programs are not yet understood. A review of the limited literature on marine enhancement suggests that the three Ryman–Laikre parameters are rarely known for species being supported by artificial propagation worldwide (Table 3). In most cases, only one parameter has been estimated, which makes it impossible to estimate the effect of hatchery programs on the natural populations. This lack of understanding could have dire consequences for species such as Japanese flounder or rockfish (*Sebastes* spp.), for which hatchery progeny may constitute 35% to 75% of the entire population. Yet, the effective sizes of neither the hatchery nor the wild components of the enhanced populations are known. Thus, the long-term genetic consequences of marine fisheries supplementation on a global scale are unknown.

An important consideration in reviewing the literature on marine enhancement is discrepancy in methods for estimating parameters of the Ryman–Laikre model. Often, authors (e.g., Richardson and Gold, 1993; Tringali and Bert, 1998) use an equilibrium estimate of effective size described by Avise et al. (1988). Tringali and Bert's (1998) equilibrium estimate of N_e for wild red drum (*Sciaenops ocellatus*) population, 10^5–10^6, is consistent with fisheries estimates that place the actual number at 7 million fish. However, by measuring temporal change in mitochondrial haplotypes among year classes of red drum in the Gulf of Mexico, Turner et al. (1999) estimate that female effective size in that region may be only 14,000, though the upper 95% confidence limit on this estimate is infinite. Such discrepancies may be resolved by more data and new methods for estimating effective population sizes.

Along with estimation methods, definitions of populations can vary among studies. Many supplemented marine populations, such as red drum or Japanese rockfish, can be subdivided into two components. For example, Tringali and Bert (1998) use the Atlantic Ocean population of red drum in defining wild N_e, because the enhancement effort was directed at an Atlantic embayment. McEachron et al. (1998) and Turner et al. (1999) both focus on the Gulf of Mexico population of red drum and the hatchery in Texas that releases fingerlings into the Gulf. A similar situation is found in Fujio and Nakajima (1989), concerning the black rockfish (*Sebastes schlegeli*; regional common name; official common name is kurosoi or Korean rockfish). For their study, the contribution of hatchery progeny to the overall population can be calculated differently, depending on whether the natural population is defined as extending throughout the entire Pacific Ocean or only the Japan Sea. Even in cases for which all three parameters of the Ryman–Laikre model appear to be known, it may be necessary to verify that the estimates apply to the actual population being supplemented. The inconsistencies found in the literature emphasize the uncertainty of the risk that large hatchery programs will reduce viability of the populations they are designed to aid.

5. COMMENTS ON THE EFFECTIVE SIZE OF MARINE POPULATIONS

The effective size of natural marine populations is obviously a critical parameter in assessing the risk of enhancing marine fisheries. Marine populations, even those that are overfished, are often assumed to have large effective population sizes because of their abundance and dispersal of pelagic larvae. If true, marine enhancement will usually have a negative effect on genetic diversity (Figure 3). However, effective sizes of natural marine populations may be much smaller than previously appreciated, owing to large variances in the numbers of offspring that individuals contribute to the next generation of reproducing adults (Hedgecock, 1994; Li and Hedgecock, 1998). One individual, for example, might leave an enormous number of offspring if it happens to match its reproductive effort with environmental conditions conducive to reproduction, larval survival, and settlement. A nearby individual might fail to leave offspring if it happens not to match its reproductive activity with permissive environmental conditions.

Successful reproduction by marine organisms with planktonic larvae comprises a long, biologically and physically complex chain of events, from sexual maturation to spawning, fertilization, larval development, metamorphosis, and transport to and settlement into the adult habitat. Although marine species are evidently well adapted for completing their biphasic life cycles (Parrish et al., 1981; Morgan, 1995), boom or bust recruitment may still result from stochastic physical perturbations in this complex chain of causation. Consequently, the individual reproductive success of marine organisms might resemble a sweepstakes in which there are a few big winners and many losers. Owing to sweepstakes reproductive success, the N_e/N ratios for highly fecund marine species may range from 10^{-5} to 10^{-2} (Hedgecock et al., 1992; Hedgecock, 1994), far below the range of 0.25 to 0.75 for terrestrial vertebrates and invertebrates (Nunney, 1996).

Nunney (1996) criticizes the low N_e/N ratio reported by Hedgecock et al. (1992) for the Dabob Bay (Washington, USA) population of Pacific oysters (*Crassostrea gigas*) and argues that fecundity variation is relatively ineffective in lowering the N_e/N ratio. Nunney speculates that observed temporal genetic change in this population was caused by mixing of hatchery or imported Japanese seed. However, diploid hatchery seed are not routinely planted in Dabob Bay and the importation of oyster seed from Japan ceased in the late 1970s. Nunney also relies heavily on terrestrial studies that frequently exclude adults producing zero offspring from calculations of standardized variance in reproductive success (Clutton-Brock, 1988). This category of zero success is likely to be large for highly fecund marine species, although there are no demographic studies to verify this, owing primarily to the inaccessibility of planktonic larvae.

As already noted, variation in fecundity is only one of several factors that could contribute to variance in reproductive success. Spawning behavior, fertilization success, larval survival, and larval transport all determine “larval supply” in marine ecosystems, so that failure at any one of these critical stages can affect the supply of settlers and the dynamics of marine populations. For example, differences between sites of heavy and poor settlement can reflect differences in adult maturation and spawning, not larval ecology or oceanography (Park et al., 1999). Gametes of highly fecund marine species can vary widely in quantity, quality, and competence (Lannan, 1980; Gaffney et al., 1993) and may fail to fertilize, owing simply to dilution or to low densities of spawning adults (Denny and Shibata, 1989; Levitan et al., 1992; Levitan and Young, 1995). Variance in reproductive success, which can arise before fertilization, has many opportunities to increase during the larval phase, with its high mortality. For example, on average, 95% of the annual production of northern anchovy (*Engraulis mordax*) larvae dies before recruiting to juvenile schools, (Peterman and Bradford, 1987). An assemblage of long-lived rockfish (*Sebastes*) produces significant recruits only once or twice per decade in central California (S.V. Ralston, National Marine Fisheries Service, Tiburon/Santa Cruz laboratory, personal communication). For the larviparous European flat oyster, it is estimated that 1 million larvae may yield only 250 attached spat, of which 95% perish before the onset of winter (Clark, 1964; Galtsoff, 1964).

To resolve whether Nunney (1996) or Hedgecock (1994) is correct, we need more data on N_e/N ratio in highly fecund marine species. To the extent that Nunney may be correct, however, hatchery enhancement is likely to have a strong, negative impact on biodiversity. To the extent that natural effective population sizes are in the hundreds or low thousands, well-managed hatchery programs could have positive effects on biodiversity, particularly in areas where the natural population has already been severely depleted.

6. CONCLUSIONS

Use of hatchery technology to reverse the decline of marine fisheries is likely to erode genetic diversity. The likelihood of a negative impact can be calculated, using a genetic model of population mixture (Ryman and Laikre, 1991), provided adequate estimates of the three parameters of the model are available. Large hatchery enhancement programs should undertake evaluation of these parameters to assess their likely impact on the effective size and genetic diversity of the natural population to be supplemented. Reductions of genetic diversity are not easily or quickly reversed, unfortunately. The prospect of increasing the risk of extinction for already depleted resources is unwelcome. On the other hand, hatchery programs can retard loss of genetic diversity in small populations, if they can elevate the N_e/N ratio by reducing variance in reproductive contributions and release numbers of individuals appropriate to local effective population sizes. The precautionary approach to fisheries management suggests slowing the development and implementation of marine enhancement until and unless sufficient data are available to evaluate the potential impact on effective population size and genetic diversity.

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CHAPTER 6

PREVENTING GENETIC POLLUTION AND THE ESTABLISHMENT OF FERAL POPULATIONS: A MOLECULAR SOLUTION

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Abstract: Aquaculture animals that escape from farms have the potential to create major environmental problems. These include establishment of potentially destructive feral populations (e.g., Pacific oysters [*Crassostrea gigas*] in Australia, Atlantic salmon [*Salmo salar*] in British Columbia) and genetic contamination of wild stocks. The latter includes introgression of foreign genes into natural populations from both hatchery-reared fish and genetically modified fish and invertebrates. Concern about these environmental and genetic effects has already led to restrictions on aquaculture industry development and is likely to grow as demand for genetically improved stocks escalates to fulfill production objectives. To circumvent these problems, we have developed a genetic construct that, when properly integrated into production-line fish or invertebrates, should render individuals functionally sterile outside of hatchery conditions. In the hatchery, however, provision of a simple repressor compound at a particular life-history stage allows the animals to be bred and reared as normal. We

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are developing this "Sterile Feral" technology for both invertebrate and fish species, and we anticipate practical commercial application within a few years.

Key words: aquaculture, Australia, environment, feral populations, genetic damage, molecular genetics, stock enhancement

1. INTRODUCTION

The increasing gap between supply and demand for high-quality seafood has resulted in a growing reliance on aquaculture as wild stocks are fished to full capacity (Pauly et al., 1998). Efforts to take advantage of this opportunity for growth expansion and to maximize investment returns by the aquaculture industry have included attempts to increase production through use of more cost-effective stock (i.e., faster growing and higher yield) and diversification into more profitable species that, in many instances, are not native to farm locations. Despite the aquaculture industry's ability to take advantage of such market potential, expansion of the industry is hampered by community and scientific concern over escapees from aquaculture facilities and their impacts on aquatic ecosystems (Naylor et al., 2000). Debate over the costs versus benefits of these issues has divided communities and resulted in the development of strict environmental policies and legislation that often preclude growers from producing the seafood product of choice. Satisfying market demands by developing new grow-out areas, particularly for exotic species, has become unacceptable for many government and stakeholder groups, who perceive that there is high risk that escapees will establish feral populations and negatively impact local ecosystems.

2. EXAMPLES OF ORGANISMS REQUIRING CONTAINMENT

2.1. Feral Pacific Oysters in Australia

In Australia, the Pacific oyster (*Crassostrea gigas*) industry is a prime example of an industry where expansion has been retarded predominantly over public concern regarding feral populations. In a joint initiative of the Australian Commonwealth Scientific and Industrial Research Organization and several state governments, the Pacific oyster was deliberately brought to Australia as a market product (Thomson, 1952; Sumner, 1974) in the 1940s as a means of supplementing and essentially replacing vastly overfished native oysters. Despite the promise of a new industry, the planned aquaculture activity was far from universally welcome. Even in the 1940s, introduction of this species into Australia was already of concern to New South Wales Sydney rock oyster (*Saccostrea glomerata*) industry personnel. These people and other concerned individuals went so far as to destroy the first shipment of Pacific oysters as it passed through Sydney (Holliday and Nell, 1987). Nonetheless, between 1947 and 1970, a series of aquaculture operations that utilized three different

Japanese strains of *C. gigas* were initiated at sites in Western Australia, Victoria, South Australia, and Tasmania. Only the aquaculture operation in Tasmania was successful. The oysters produced at that facility have since formed the source stock for the development of aquaculture operations in other areas of Australia (Thomson, 1959). Pacific oyster aquaculture is considered one of the major industry success stories for Tasmania.

Despite its success however, the negative effects of the industry have been significant. Farmed stocks constitute a spawning reservoir that has resulted in the widespread distribution of feral Pacific oysters in intertidal and shallow subtidal areas in estuaries around Tasmania. Local community concern about the alteration of native ecosystems has been substantial (e.g., van Gelder, 1998) and has slowed expansion of farms into new areas. Expansion is usually curtailed following very public and often acrimonious debate between industry and "green elements" of the community (e.g., environmental and conservation organizations, concerned local groups). These discussions inevitably deteriorate into arguments about whether beaches degraded by feral oysters are an acceptable price to pay for a new industry and jobs. For example, despite the promise of hundreds of new jobs in coastal communities and an estimated annual net value of up to US $50 million, the state of Victoria has indefinitely postponed the establishment of a Pacific oyster industry until the problem of feral oysters can be overcome (Davis, 1996). In South Australia, production of Pacific oysters is increasing, but they are declared noxious pests in both Victoria and New South Wales (with the exception of a single site, Port Stephens, NSW). In Victoria, this declaration was made due to environmental impact concerns. In New South Wales, the principal reason was due to overgrowth of Pacific oysters on the more valuable stocks of Sydney rock oysters, which results in significant increases in production costs of the Sydney rock oysters (Medcof and Wolf, 1975). Pacific oysters are also on the target pest list of the Australian Ballast Water Management Advisory Committee, and an objective of ballast-water regulations for commercial shipping is to stop the further spread of feral Pacific oysters.

2.2. Farmed Salmonids

Salmonids constitute major recreational and commercial fisheries and form the basis of extensive aquaculture operations worldwide. In many instances, nonnative species and stocks have been used to establish or enhance aquaculture ventures. The number of feral stocks (aquaculture escapees) has increased substantially in the last decade. In Norway, for example, 20% to 30% of the Atlantic salmon spawning in local rivers have escaped from aquaculture operations (Saegrov et al., 1997).

Hindar et al. (1991) and Hindar (1999) review the genetic effects of sea-ranched and feral salmonids on local stocks. Three broadly overlapping effects have been identified: interbreeding between wild and feral cultured fish; competition between wild and feral cultured fish, which may be enhanced due to interbreeding; and contamination of wild fish by feral cultured fish (e.g., through the introduction of parasites and diseases), the impacts of which may be higher on genetically naïve local strains. Total impacts on native salmonid species and strains range from no discernible effect to complete eradication. Hindar (1999) concludes that genetic effects on native populations (e.g., reduced population size and lower survival rates) are typically negative; he attributes this to the effects of genetic pollution on locally adapted stocks. As a result of the widespread introduction of sea-ranched fish, high-profile attempts to preserve native strains are underway in North America for both Pacific salmonid stocks on the west coast and Atlantic salmon on the east coast.

2.3. Genetically Selected or Altered Organisms

Areas of the Mediterranean Sea are now under threat of invasion by a genetically superior strain of what is normally considered to be harmless tropical marine alga, *Caulerpa taxifolia*. This strain of *Caulerpa* was developed by European aquarists, who used conventional selection techniques to produce a particularly hardy variety that tolerated a wide range of environmental conditions, had fast growth rates, and was easy to propagate (Jousson et al., 1998). In the mid-1980s, a few fronds of this variety escaped into the Mediterranean Sea from an aquarium in the south of France (Meinez et al., 1998). Since then, it has spread aggressively and has overgrown seagrass beds, mud flats, rocky reefs, and other coastal or nearshore habitats. There, it outcompetes native species and forms extensive single-species beds. Coastal fisheries in these invaded areas have declined massively, to the extent that the plant is referred to locally as the "death weed". This invasive strain, which is toxic and distasteful to fish and most browsing invertebrates, is now projected to eventually spread over most of the Mediterranean. Numerous attempts to physically eradicate the species have failed, and contentious discussion is now underway about possible biological control (Meinez, 1999).

The invasion of the Mediterranean by a strain of *C. taxifolia* selected for increased growth and environmental tolerances may be only the first in a series of invasions of a large number of such optimized strains. For example, genetically selected Pacific oysters, bred specifically for enhanced growth performance, may be introduced into Australian aquaculture. The high probability that genetically altered or selected strains of Pacific oysters will escape into natural environments has already been demonstrated by the previous spread of this species in Australian waters. Conventional approaches of genetic selection to produce strains of algae, fish, and a range of invertebrates particularly well suited for aquaculture is underway worldwide.

Thus, the spread into the wild of organisms selected for performance in aquaculture environments will likely be exacerbated in the future.

Now, modification of organisms by means of genetic engineering is used to improve characteristics of production lines. Salmon containing additional genes that enhance levels of growth hormones have been produced in Europe, New Zealand, and North America (Reichhardt, 2000). In North America, the marketing of these fish may be near. A/F Protein (also known as Aqua Bounty Farms, Waltham, Massachusetts, USA) submitted an application to the U.S. Food and Drug Administration (Rockville, Maryland, USA) to gain approval for their ‘‘GM super salmon’’, which contain genetically modified growth hormone genes (Niiler, 2000). Whether or not this product enters the market will be largely determined by the company's ability to alleviate concerns about the impact of these fish as ‘‘super-competitors,’’ should they escape and form feral populations or pass on the growth genes to wild stocks (Reichhardt, 2000). Stocks of growth-enhanced salmon in New Zealand and Scotland have been destroyed because these concerns could not be allayed.

3. BIOLOGICAL APPROACHES FOR CONTAINMENT

A large part of community concerns over the farming of exotic species and genetically modified stocks would be alleviated if aquaculturists could utilize the species and strains of choice with no possibility that escaped animals could establish feral populations or transfer genes into wild stocks. This concern is particularly heightened for those species that are allowed to mature in aquaculture facilities located in areas where they could escape into environments conducive to both their survival and reproduction. Physical containment of aquaculture species has typically demonstrated a high failure rate and many barriers have no effect on dispersive larvae. Biological containment thus represents an attractive option to prevent both gene transfer and establishment of feral populations.

No reliable and cost-effective means yet exists to deliver effective biological containment. Various methods such as sterile hybrids and ploidy manipulation have been tried but these have proven to be unreliable and not cost effective. Because interspecific congeneric hybrids can be fertile, creating hybrids that are sterile often requires the interbreeding of taxa from different genera. This usually causes a dramatic change to the phenotypes associated with the parental species. Thus, production of such hybrids may have a decidedly negative impact on consumer acceptance in the marketplace. Triploid salmon appear to be effectively sterile, but may have subtle flesh-quality differences when compared to diploid fish. Furthermore, variation among cultured broods does not guarantee that all individuals produced are in fact triploid (Reichhardt, 2000). Triploidy via chromosome manipulation has proven to be an unsuccessful biological containment mechanism to prevent the establishment of feral Pacific oyster populations. Triploid oysters were principally developed to provide an autumn crop to compensate for the loss of condition in diploids following the spawning season. The oyster industry is now moving toward more routine use of tetraploid oysters that should, in theory, produce 100% triploids when crossed to normal diploids (Guo and Allen, 1994a; Guo et al., 1996). Industry personnel are interested in the tetraploid–diploid mating strategy because they can avoid the use of carcinogens such as DMSO and cytocholasin-B, which were historically used for routine production of triploids. However, investigations into the genetics of oysters spawned from crosses between tetraploid and diploid oysters indicated that, although the fecundity of triploid females combined with survival of their progeny compared to that of diploids was very low (0.0008% of the normal diploid-fecundity + offspring-survival percentage), the chance that matings between triploids will produce diploid progeny is not zero (Guo and Allen, 1994b, 1997). Thus, in any "zero tolerance" environment, triploids are not a containment solution because they only reduce the rate at which feral populations can become established; they do not completely prevent their establishment.

A mechanism for biological containment that has been proposed for genetically modified plants is the so-called "terminator gene" or Technology Protection System. This approach was developed by Delta and Pine Land Company (Oliver et al., 1998). Essentially, the method utilizes the following to stop the seeds of certain plants from germinating:

1. a transiently active promoter gene operably linked to a toxic gene but separated from it by a blocking sequence that prevents the lethal gene's expression;
2. a second gene, encoding a recombinase which, upon expression, excises the blocker sequence;
3. a third gene, encoding a tetracycline-controllable repressor of the recombinase.

Plants transformed with all three genes grow normally and produce viable seeds. However, seeds sold to farmers are treated with tetracycline (Tc) to activate expression of the recombinase, which excises the blocker sequence. These seeds germinate, but since the blocker sequence is removed, expression of the toxin gene occurs and causes these plants to produce seeds that are sterile. Whether this technology has been developed to an operational level is not clear, but even if so, it remains untested in animals. Furthermore, few recombinases have been identified that will function in animals (vertebrates in particular) and those that have been identified (e.g., Cre and Flp recombinase) function in only a limited number of species. Moreover, terminator gene technology has a substantial problem that has severely affected its market acceptability. Once the blocker sequence has been excised, it is virtually impossible to reverse the sterility process. This forces a farmer to return to the seed vendor for his next crop. This forced dependence on a vendor has embroiled the use of the technology in so much controversy that it has been temporarily abandoned (Service, 1998; Niiler, 1999). Other strategies, such as "Trait-specific Genetic Use Restriction Technology", have also been suggested to address intellectual property protection issues, but these do not prevent gene transfer to wild stocks (Masood, 1999).

To solve the biological containment problem, we have developed an alternative strategy in which we use molecular engineering to produce broodstocks that are fertile in captivity but functionally sterile outside of hatchery conditions (Figure 1). Over the last four years, we have been developing to a

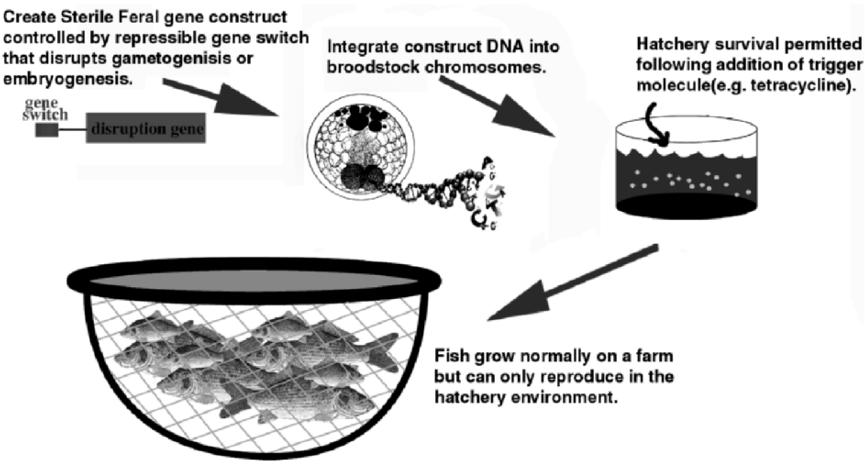

Figure 1. Schematic of "Sterile Feral" concept. Gene switch refers to any spatially and temporally restricted species-specific promoter

functional level the promoters, blockers, and repressors for three target species—the zebrafish (*Danio rerio*), the Pacific oyster, and mouse (*Mus musculus*). The basic approach, which is covered by a provisional patent, is similar for all three species, though we used different, usually native, promoters and blocking sequences for each. Specifically, we have developed a "Sterile Feral" plasmid gene construct that prevents production of functional gametes or causes mortality in offspring produced by escapees that mate outside of a controlled hatchery environment.

Components of the Sterile Feral construct consist of a temporally defined, species-specific promoter gene (genetic switch) coupled to a repressible gene element (tTA) that in turn drives the expression of a blocker gene (here defined as a sequence that disrupts function of a critical gene, causing lethal effects; e.g., an antisense or dsRNA-knockout sequence). This construct is inserted into the broodstock of a desired species. If repression is not initiated in the hatchery system, the blocker gene causes mortality by disrupting function of a critical gene. This condition, which we have defined as functional sterility, renders broodstock gametes or embryos unviable by preventing fertilization or larval growth. The minimal promoter that drives expression of the blocker gene has a narrow spatial and temporal window of activity. Thus, addition of a specific repressor molecule (e.g., zinc or Tc) to the food or water in the hatchery broodstock tanks is required only for a brief period to repress transcription and subsequent gene-function disruption, or knockout, in the resulting offspring. Outside of this temporal window, even in the absence of the repressor molecule, the promoter is inactive and the blocker gene is not transcribed. This permits hatchery-reared offspring to survive and remain free of any exogenous protein produced by the introduced genes after the offspring are placed into the farm environment for grow-out. However, the promoter expresses in any offspring that are produced outside of the hatchery conditions (i.e., in the absence of the repressor molecule). The active promoter transcribes the blocker sequence, which leads to disruption of critical gene function and eventual mortality. The blocker gene functions as a dominant allele and thus escapees cannot produce viable offspring even if they interbreed with wild fish.

Disruption of normal cellular activity to cause embryonic mortality can be achieved through production of a cytotoxic protein. However, production of animals carrying a toxic gene is not an acceptable approach to use in animals destined for human consumption. An alternative approach to achieve knockout is to use mRNA specifically targeted for interference of gene function. Mechanisms used to achieve mRNA knockout include expression of ribozymes, antisense mRNA, and double stranded mRNA. These have been shown to work in a wide variety of plants and animals (Izant and Weintraub, 1984; Xie et al., 1997; Fire et al., 1998; Waterhouse et al., 1998; Bosher and Labouesse, 2000; Yin-Xiong et al., 2000). Because of the high specificity of mRNA targeting, the targets in aquaculture species are unlikely to have any close homologies in humans, which eliminates this as an issue should it ever become of concern.

For the zebrafish, on which we have done the most work, repression of the knockout function is achieved by coupling a stage-specific promoter (VP16) to components derived from the commercially available Tet-Off controllable expression system (P_{CMV} + *tetR*; Figure 2), marketed by CLONTECH (further information available from http://clontech.com/, Protocol # PT3001-1, version # PR95962). We have demonstrated the functionality of the Tet-Off system in oyster primary cell cultures and it has also proven effective at repressing action of a transgene system in *Drosophila* (Thomas et al., 2000). Tc or doxycycline (Dox; a Tc derivative) can be used as the repressor molecule and both are ideally suited for use in an aquatic system, in part because of the ease in administering. Tc is a routinely used antibiotic in fish and shellfish culture (see Stoffregen et al., 1996), it readily traverses cutaneous membranes while retaining its biological activity, and can be delivered by immersion of the whole organism.

In the Sterile Feral construct, Tc or Dox achieve repression of the blocker gene by acting upon the regulatory protein tTA, which is a fusion of TetR and VP16 products, as derived from the pTet-Off regulatory plasmid. A zebrafish promoter (P_{CMV}) is used to drive expression of the tTA. The tTA in turn regulates the Tet-responsive $P_{\mathrm{hCMV^{*}-1}}$ promoter that controls expression of the blocker gene (Gene X). $P_{\mathrm{hCMV^{*}-1}}$ contains the Tet-responsive element (TRE). This consists of seven copies of the tet operator sequence (*tetO*) located just upstream of the minimal CMV promoter (P_{minCMV}). $P_{\mathrm{hCMV^{*}-1}}$ is silent in the absence of binding of transactivator protein (tTA) to the *tetO*. The tetracycline-sensitive element is described by Gossen and Bujard (Tet-off; 1992),

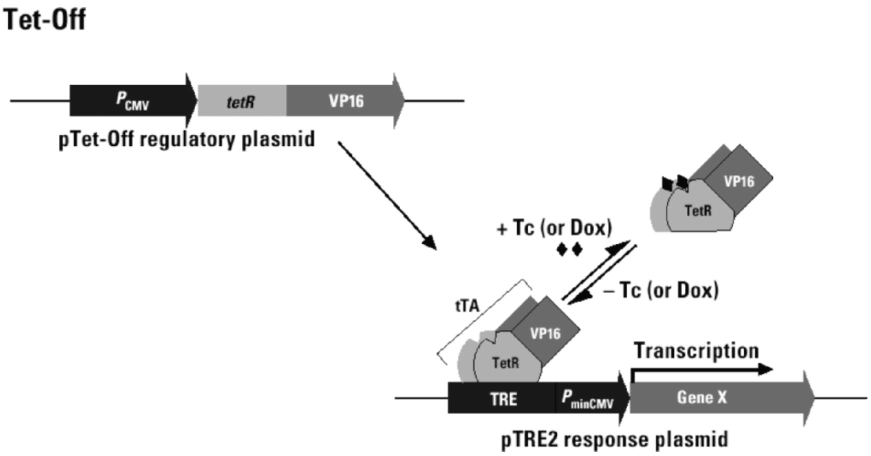

Figure 2. Schematic of gene regulation in the Tet-Off system. Gene X = blocker gene of interest. The TRE (tetracycline responsive element) is located upstream of the minimal immediate early promoter of cytomegalovirus (P_{minCMV}), which is silent in the absence of activation. tTA (the tetR/VP16 regulatory fusion protein) binds the TRE—and thereby activates transcription of Gene X—in the absence of Tc (tetracycline) or Dox (doxycycline). (This figure is reproduced from the Tet-Off$^{\text{TM}}$ and Tet-On$^{\text{TM}}$ Gene Expression Systems User Manual, PT3001-1.)

Gossen et al. (Tet-on; 1995), and Kistner et al. (1996). In the Tet-Off system, addition of Tc or Dox prevents the binding of tTA to the *tetO*. Expression of the blocker gene, which is controlled by the TRE, is thereby repressed until Tc is removed from the system. However, in the absence of Tet or Dox, the blocker gene is transcribed as long as the zebrafish promoter continues to actively express tTA.

4. FUTURE DIRECTIONS

Development of Sterile Feral technology could produce opportunities as diverse as farming of tilapia in the freshwaters of inland Australia to culturing Pacific oysters along the Atlantic coast of the USA, at no risk to the native environment. More specifically, developed to a commercial scale, the technology fills four industry needs:

1. It provides a safe system for preventing the establishment of feral populations of exotic species used for production purposes. Multiple Sterile Feral constructs should provide redundant sterility, and virtually ensure no escapement. This should fundamentally change the risk assessment for importing exotic species and reduce public antagonism to importation and farming of potentially environmentally damaging species.
2. The same technology can be used to protect investments in breeding stock developed by, for example, selective breeding. Currently, the commercial

advantages from improved stock can be lost when the product (e.g., oysters, prawns, fish) is marketed alive and is capable of reproducing. The repressible sterility approach we have developed can be used as a lock-and-key process that permits improved stocks to be bred only when they contain the correct combination of repressors in exactly the right sequence.

3. Repressible-sterile animals could be used to slow the expansion or reduce the extent of existing feral populations because these reproductively active but infertile animals could be released and potentially interbreed unsuccessfully with feral fertile individuals. This could allow more general application of pest management strategies similar in concept to the sterile male approach used in the biological control of insects.
4. Repressible sterility provides a security system for the application of genetic engineering to animal production. Linking a genetically engineered process (faster growth, longer spawning seasons, etc.) to a Sterile Feral construct would ensure that the genetic enhancements do not enter wild populations, and that escaped, genetically superior animals could not produce environmentally threatening feral populations.

Our Sterile Feral technology is ready to be taken to the pilot project stage, to bridge the gap between laboratory results and commercial-scale production. However, there are obvious sensitivities surrounding the use of genetically modified organisms (GMOs) in food production. Continued development of this technology will require further improvements in its use in the species of interest. Parallel studies should also examine the costs, benefits, and risks surrounding the potential use of GMOs as solutions to problems caused by exotic and genetically enhanced species. The use of a real biological and technological case study is crucial to the success of this risk evaluation because hypothetical studies of the technology and its alternatives are difficult to substantiate.

The science behind most food health issues, and particularly level of risk, is not well understood in communities. Risks need to be assayed not only at the physical level but also at socio-political levels. Explaining issues as clearly as possible requires a thorough and objective (versus media-fueled) risk assessment appropriate to the food that has been genetically modified. A key element to be developed in concert with the genetic aspects of this technology is a formal analysis of the risks to both the environment and to the consumer associated with development of a species that is incapable of producing viable offspring outside of hatchery conditions.

More broadly, this assessment would be needed to provide clear and accurate information on the basis of which informed debate on GMOs can progress. The issues of GMOs in aquaculture needs to be brought into such an arena so that, at both State and Federal levels, guidelines can be developed and legislative frameworks established that specify unambiguous criteria for use, if any, of GMOs in the marine environment.

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CHAPTER 7

BEHAVIORAL AND GENETIC INTERACTIONS BETWEEN ESCAPED FARM SALMON AND WILD ATLANTIC SALMON

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Abstract: The production of Atlantic salmon (*Salmo salar*) dwarfs the wild salmon fishery by two orders of magnitude. Throughout the North Atlantic region, large numbers of aquacultured (farm) fish escape and invade rivers that contain native salmon. This causes considerable concern, because interactions between escaped farm fish and native fish can cause a decline in the fitness and productivity of the native stock. Norwegian farm salmon originate from salmon collections taken from wild populations in the early 1970s. They have been under artificial selection for growth rate, age at maturity, disease resistance, and flesh quality. Farm strains have changed genetically relative to the original populations from which they were taken and they have lost allelic variation compared to wild populations. Escaped farm salmon can spawn successfully in the wild, but their breeding performance can be inferior to that of wild salmon. Farm offspring outgrow those of wild origin, both under artificial and natural conditions. Farm juveniles also differ in aggressive behavior and dominance relative to wild juveniles, and they appear to suffer higher mortality during early life stages, possibly due to their lower response to predation risk. Farm-X-wild offspring are behaviorally intermediate between farm and wild juveniles, and show superior growth compared to wild juveniles. In a whole-river experiment, we showed that the lifetime reproductive success of farm salmon was 16% that of the native salmon. Differential selection against farm-salmon genotypes occurred during breeding and early survival but was similar to that of wild salmon thereafter, despite significant ecological differences between the two groups. The overall productivity of the population, however, appeared depressed. Our findings suggest that gene flow from escaped farm fish to native fish will lead to genetic and behavioral changes in wild populations in the direction of domesticated salmon. Moreover, wild populations may suffer depressed productivity caused by ecological interactions with escaped farm salmon and their offspring. These findings call into question the long-term viability of many salmon populations.

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Key words: *Salmo salar*, aquaculture, domestication, competition, environment, gene flow, lifetime reproductive success, Norway

1. BACKGROUND

The farming of Atlantic salmon (*Salmo salar*) has expanded exponentially from its beginnings in the 1960s. Today, the production from salmon farming exceeds that from wild salmon populations by two orders of magnitude. One consequence is that, throughout the North Atlantic, large numbers of aquacultured (farm) fish escape and enter rivers that have native salmon. The impact of such invasions is the subject of mounting concern, especially because native salmon populations are declining globally. Interbreeding between escaped farm salmon and native wild salmon can have a number of undesirable consequences, such as loss of adapted genes or gene complexes through interbreeding, loss of entire populations as a result of competition or disease introduction, homogenization of previously structured populations through swamping by a common gene pool, and blockage of re-adaptation to local conditions if the introductions continue (Ryman et al., 1995).

Salmonid fishes have been artificially reared and released into the wild for more than a century (Hindar and Jonsson, 1995). In a review of the genetic effects on native populations following releases of nonnative salmonid populations, Hindar et al. (1991) provided two broad conclusions:

1. The genetic effects of (intentionally or accidentally) released salmonids on natural populations are typically unpredictable; they vary from no detectable effect to complete introgression or displacement of native genotypes by released genotypes.
2. Where genetic effects on performance traits have been detected following releases of cultured salmonids into natural settings, they appear always to be negative compared with the unaffected native populations.

However, only a few fully controlled experiments addressing the genetic and ecological effects of releases have been carried out. Here we review the current knowledge about escaped farm salmon and wild Atlantic salmon and present a whole-river experiment in which we quantify the lifetime success of farm salmon released into a native population (Fleming et al., 2000).

2. GENETIC AND BEHAVIORAL CHARACTERISTICS

Atlantic salmon have a high level of population genetic structuring. Differences have been demonstrated among populations in protein-coding genes (Ståhl, 1987), nuclear and mitochondrial DNA markers (Nielsen et al., 1996, 1999), and genetically based performance traits (reviewed in Taylor, 1991). A major genetic dichotomy exists between Atlantic salmon populations from either side of the North Atlantic Ocean, with further sub-structuring within each continent (Ståhl, 1987; Verspoor, 1997; Nilsson et al., 2001).

Farm Atlantic salmon represent a mixture of wild populations that have been selected (intentionally and unintentionally) for the captive environment since the early 1970s (Gjedrem et al., 1991). Farm salmon now differ genetically from the wild populations from which they were derived (Mjølnerød et al., 1997). This difference includes change in allele frequencies at protein-coding loci and the loss of alleles and total genetic variability in DNA minisatellite loci (Mjølnerød et al., 1997). Similar results have been obtained using DNA microsatellite analysis on farm and wild strains (Norris et al., 1999).

Farm salmon also differ genetically from wild salmon in morphological, behavioral, and ecological traits that are affected by domestication. Fleming and Einum (1997) compared a seventh-generation strain of farm salmon in Norway with its principal founder population from the wild—the River Namsen population. The fish were reared in a common environment and compared for several fitness-related traits. Farm salmon showed more robust bodies and smaller fins. Farm juveniles were more aggressive in a tank environment, but wild juveniles dominated in a stream-like environment. Farm juveniles were also more risk-prone, reappearing from cover soon after a simulated predator attack (see also Johnsson et al., 2001). Growth performance in farm juveniles was higher than in wild juveniles. This appeared to reflect changes in endocrine regulation; farm individuals with more active endocrine growth regulatory components are apparently selected indirectly during culture (Fleming et al., 2002). Similar results were obtained in comparisons between another strain of farm salmon and two wild populations (Einum and Fleming, 1997). These results suggest that farming generates rapid genetic change due to genetic drift and intentional and unintentional selection in culture, and that some changes involve important fitness-related traits.

3. FULL-SCALE EXPERIMENT IN THE RIVER IMSA, NORWAY

In November 1993, Fleming et al. (2000) released 22 farm and 17 native Atlantic salmon above a fish trap in River Imsa, a small, 1-km-long river in southwestern Norway (58°5′N, 5°58′E) that supports a small native population of Atlantic salmon (Jonsson et al., 1998). The farm salmon (fifth generation) were derived from Norway's national breeding programme (Gjedrem et al., 1991). The released fish had been selected so that all farm salmon were homozygous for the protein-electrophoresis detectable muscle enzyme locus *MEP-2*(*125/*125)*, whereas all native fish were homozygous for the **100* allele (Cross and Ward, 1980).

In parallel with the river release, an experiment was conducted involving the release of 12 farm and 9 native salmon into an experimental spawning arena (for description, see Fleming et al., 1996). During March 1994, the arena was excavated and the number of live and dead Atlantic salmon eggs was recorded in all nests present. Nests were assigned to females using spawning records and egg-size data.

In the river, farm and native adults had similar migration patterns and nesting locations; however, farm females spawned before native females. Courting of females by both farm and native males began shortly after release of the fish into the river. Native males, however, courted females more often and retained less of their initial testes unspawned than did farm males. In the experimental spawning arenas, farm males attained just 24% of the breeding success of native males, and farm females achieved 32% of the success of native females.

Offspring (age-0 parr) from the spawnings in the river were sampled by electrofishing the River Imsa in September–October 1994. The proportion of native to farm genotypes among the offspring (age-0 parr) from spawnings in the river had shifted significantly from the proportion of native to farm spawners ($P < 0.001$). Most of the fish were now of native origin (65%); farm genetic representation occurred mainly through hybridization with native fish. The maternal origin, identified using restriction fragment analysis of the mitochondrial ND-1 region (Nielsen et al., 1996), revealed that, of the 31 hybrid offspring, 25 had a unique farm-female haplotype (found in eight farm females), five had a common haplotype (found in three farm and six native females), and none had a unique native-female haplotype (found in two native females; one offspring could not be analyzed). Thus most, if not all hybrids had farm mothers.

In total, farm adults had only 19% of the reproductive success of the native fish to this stage (i.e., breeding and early offspring survival). Furthermore, based on breeding success in the experimental spawning arena, where the success of farm fish was 28% of the success of native fish, survival of farm genotypes in the early-stage offspring was estimated to be 70% of that of native genotypes. Thereafter, there was little evidence of differential freshwater survival between the offspring of the farm fish and offspring of the native fish (parr 1994 to smolt descending 1995–96, $P = 0.397$).

Production of downstream migrants relative to the estimated total potential egg deposition was compared to the population's stock–recruitment relationship (Jonsson et al., 1998). The total potential egg deposition by native and farm females was estimated from their respective fecundity–weight relationships. The total production of smolts (i.e., migrants to the ocean) from the spawnings was 28% below that expected based on the estimated potential egg deposition (48,831) and the stock–recruitment relationship for River Imsa (Jonsson et al., 1998). Moreover, smolt production by native females was 31–32% below that expected from their estimated potential egg deposition (19,443) in the absence of farm females.

Most fish descended as smolts in the spring. There were distinct behavioral and life history differences among the smolts. Smolts produced by farm fish (farm smolts) descended earlier and at a younger age than did wild smolts, and hybrids descended at a time that was intermediate to that of the farm smolts and native smolts (all pairwise comparisons: $P < 0.05$, Bonferroni adjustment). Hybrid smolts were also longer and heavier ($P < 0.001$) than native smolts, whereas farm smolts weighed less for a given length than did their wild counterparts.

There was no significant difference among the offspring types in survival from seaward migration to return as sexually mature individuals ($P = 0.840$). The lifetime reproductive success, adult-to-adult, of the farm salmon was 16% that of the native salmon. All adult recaptures occurred in either the coastal fishery or the River Imsa; no fish were reported as straying into other rivers. The mean age-at-maturity of hybrid fish (3.4 years, S.D. = 0.5) was less than that of native fish (4.2 years, S.D. = 0.4; $P = 0.002$).

4. GENETIC AND ECOLOGICAL EFFECTS IN THE RIVER IMSA

One-way gene flow is a potent evolutionary force (Hedrick, 1983; Barton, 1992). The native population may eventually be composed of individuals that all have genes descended from the migrants, and this situation may be approached rapidly for selectively neutral loci/traits.

We calculated the effect of t generations of one-way gene flow from farm salmon on the allele frequency (q_t) of the recipient (River Imsa) population as

$$q_t = (1 - m)^t q_0 + [1 - (1 - m)^t] q_m$$

where q_0 is the allele frequency of the recipient population before migration, m is the proportion of migrants entering the population in each generation, and q_m is the allele frequency of the migrants (Hedrick, 1983). The equation applies also to weakly selected quantitative genetic traits that have an additive genetic basis (Bulmer, 1980). Half of the genetic difference between donor and recipient populations remains after $t_{0.5} = \ln(0.5)/\ln(1 - m)$ generations. The calculations assume that the effects of genetic drift and selection in the recipients are small relative to migration, and that allele frequencies of the migrants remain stable.

The proportion of 55% of the farm spawners in our experiment participated in gene flow from farm to native salmon during one generation of $m = 0.19$; that is, the farm spawners contributed 19% of the genes to the adults returning one generation later. Based on the equations above, the genetic difference between the donor (farm) and recipient (native) population is halved every 3.3 generations for $m = 0.19$. The lower age-at-maturity, and thereby shorter generation time, of hybrid compared with native fish observed in the present study would also tend to increase the rate of introgression; however, this may not be a general pattern (McGinnity et al., 1997).

This genetic impact comes on top of the potential effects on smolt productivity. The production of seaward migrants was depressed, particularly that of native females, which was 31–32% below that expected from the population's stock–recruitment relationship. This depression was the second largest in 16 years (Jonsson et al., 1998) and occurred despite the absence of competition from older salmon cohorts, a condition that should have been favorable for smolt production (Gibson, 1993). Moreover, abiotic environmental conditions did not appear unfavorable.

The depression in smolt production may reflect the presence of different types of selection specific to offspring type. Competition from farm and hybrid offspring may depress wild offspring survival during one or more life history episodes and maladaptation may depress farm and hybrid offspring survival at other times. Although the definitive cause of the depression in production is unknown, it appears likely that interactions of native salmon with farm and hybrid salmon played a role.

5. CONSEQUENCES

The experiment in the River Imsa (Fleming et al., 2000) demonstrated a high rate of gene flow from farm to native salmon, which eventually will cause the native population to lose its genetic integrity. More importantly, at rates of gene flow which we believe are realistic for the present situation over large areas in the North Atlantic, the genetic difference between escaped farm and recipient native populations will be reduced at an unprecedented speed. Average proportions of escaped farm salmon in the North Atlantic have been reported at 20–40% (Fiske and Lund, 1999). Assuming that the reproductive success calculated from our experiment applied generally, this corresponds to a gene flow of $m \sim 0.06$. In that case, the half-life of the overall genetic difference between farm and wild salmon would be on the order of 10 generations.

Because farm salmon have been shown to differ genetically from the wild population of their origin in allele frequencies, allelic diversity, and quantitative traits (Fleming and Einum, 1997; Mjølnerød et al., 1997; Norris et al., 1999), it is clear that escaped farm salmon may have wide-ranging genetic impacts on native salmon populations. The long-term genetic effects are yet to be seen, but substantial evidence from releases of salmonid fishes suggests that they are negative (Hindar et al., 1991).

We also documented a potentially negative short-term ecological effect on smolt productivity in the River Imsa. The mixed cohort of native, farm, and hybrid offspring produced 28% fewer smolts than expected from the estimated potential egg deposition and the stock–recruitment relationship for River Imsa. Because survival of Atlantic salmon in the sea appears to be largely density-independent (Jonsson et al., 1998), a smaller smolt production would be expected to translate into fewer returning adults. Our observation, therefore, invites the suggestion that the current depression of Atlantic salmon population sizes (Kellogg, 1999) may in part be related to invasion of farm salmon genes into wild populations. In addition, wild populations may be depressed by increased transmission of diseases and parasites related to aquaculture and by environmental and man-made changes unrelated to aquaculture. This further calls into question the long-term viability of many Atlantic salmon populations.

6. POSSIBLE SOLUTIONS

To protect wild populations alongside the development of aquaculture, salmon aquaculture in Norway and elsewhere should be based on closed culture, where the possibility for escape is eliminated and where inflowing and outflowing water is controlled. Another important measure for reducing gene flow is to base aquaculture on sterile fish, which can be produced at a large scale through simple, inexpensive technology (O'Flynn et al., 1997). Other measures include coastal protection zones that secure localization of fish farms away from important river populations, selective harvesting of farm escapees, restrictions on transport of cultured fish, and gene banks to protect threatened wild populations.

Some of the measures that provide opportunities for coexistence between cultured and wild fish are initially costly to the industry. But maintenance of genetic diversity in wild populations may be crucial in the long run, both for wild populations and for cultured strains. Thus, it remains to be seen what the final costs will be if effective measures to protect native populations continue to be ignored.

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CHAPTER 8

GENETIC MANAGEMENT OF HATCHERY-BASED STOCK ENHANCEMENT

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Abstract: Including genetic considerations in stock enhancement can reduce the probability that enhanced (admixed) populations will undergo damaging genetic alteration through the stock enhancement effort. Avoiding alterations in genetic diversity, decreases in fitness, and reductions in effective population size (N_e) of admixed populations and their wild-population components is important for the long-term sustainability of those populations. Maintaining the genetic diversity of admixed populations and their wild-population components first requires managing both the genetic variability (e.g., numbers of alleles) and the genetic composition (frequencies of alleles) in the broodstocks and the broods. These genetic diversity components should be maintained at levels appropriate for each stock enhancement program throughout all aspects of stock enhancement—from broodstock selection through the rearing and releasing the broods and then, after release of the broods, in the admixed populations and their wild-population components until the admixed populations attain genetic equilibrium. Using small numbers of broodstock individuals, unequal contributions of broodstock individuals to broods, and inbreeding in broodstocks are common causes of alterations in genetic diversity. These pitfalls should be avoided because they can reduce genetic variability, change genetic composition, and increase genetic load (accumulation of deleterious alleles), which decreases the fitness hatchery broods. In an admixed population, reduction in the fitness of any population component (hatchery, wild, or their progeny) decreases the overall fitness of the admixed population. Hatchery brood fitness can also be reduced through outbreeding, which also ultimately decreases the fitness of the admixed population. Decreases in fitness of admixed populations or of any population components can extend over generations, particularly if stocking is repeated over multiple generations. The N_e of a population is directly related to losses in fitness due to inbreeding and reductions in genetic diversity. The smaller the N_e value of a population, the greater the chance that relatives will mate and that alleles (particularly rare alleles) will be lost over generations. Genetic monitoring programs for specific stock enhancement efforts

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should contain sufficient procedures to address all potential genetic concerns. Two types of genetics are used in stock enhancement genetic monitoring programs: population genetics (possibly with some phylogenetics) and diagnostic genetics. Numerous genetic markers are available for use in these programs, including allozyme loci, microsatellite DNA loci, single-nucleotide DNA polymorphisms, and mitochondrial DNA. Genetic tags can be constructed using these markers. The most informative genetic tags enable individuals with alleles derived from hatchery broodstocks to be distinguished in admixed population and also allow the parentage and family relationships of hatchery brood individuals to be identified. A comprehensive genetic monitoring program for stock enhancement should include a baseline population genetics study of the recipient species throughout much or all of its range; genetic identification of all broodstocks at sufficient resolution to distinguish their offspring from wild individuals; genetic monitoring of the broods to compare their genetic diversity components, fitnesses, and N_es with those values for the population into which they will be introduced; and monitoring of the admixed population and its wild-population component during the period of time over which releases occur and after they have occurred. A principal objective of stock enhancement is to improve the probability that wild populations will sustain and be viable over ecological or evolutionary time frames. Managing the genetics of stock enhancement endeavor can increase the probability that this goal will be achieved, as well as improve hatchery production.

Key words: allozymes, aquaculture, DNA, effective population size, environment, fitness, genetics, monitoring, stock enhancement, stock supplementation

1. INTRODUCTION

Stock enhancement is the use of artificial propagation to generate animals for conserving or supplementing natural populations (Waples and Drake, 2004). Most animal propagation for stock enhancement occurs in aquaculture hatcheries, but animals can also be transported from other areas and released at enhancement locations (e.g., see Youngson et al., 1998). The wild populations to be supplemented are usually locally or regionally depleted due to anthropogenic influences. The stocked animals are expected to participate in reproduction and, thereby to improve the viability of the enhanced populations. In hatchery-based stock enhancement, individuals are spawned and reared to a specified life stage (size, age, or developmental phase) in a hatchery and then released into an area where the native population has a reduced number of individuals compared with some defined standard usually associated with the potential for long-term viability of the population. The released hatchery broods are sometimes expected to contribute not only to the reproductive output of the enhanced population but also directly to the fishery harvest. This type of hatchery-based stock enhancement is becoming increasingly popular as a management tool for restoring or maintaining the viability of depleted fishery populations and directly replenishing depleted fisheries (e.g., Bell et al., 2005). In this chapter, we discuss only hatchery-based stock enhancement as described in this context.

It has long been claimed that stock enhancement activities have adverse effects on gene pools of native aquatic populations and species (e.g., Cross and King, 1983; Allendorf and Ryman, 1987; Utter et al., 1993; Busack and Currens, 1995; Campton, 1995; Jørstad et al., 1999; Bert et al., 2001; Jørstad, 2004). However, defining, categorizing, and describing the genetic effects associated with stock enhancement can be difficult. Because stock enhancement involves complicated processes, the genetic consequences of poor stock enhancement practices can be complicated. Numerous types of effects and their causes are interrelated and many groups of organisms are involved. Actions taken or protocols used on one group can affect other groups as well. Moreover, terminology can become confusing. Some words or terms have multiple meanings in the language of researchers who deal with genetics at the levels of populations and species (e.g.,, the word "population" or the terms "genetic diversity" and "genetic variability"). In this chapter, we use the following population-level and genetic terms as defined below.

In this chapter, we use "stock enhancement" or "enhancement" as the time period over which individuals are being introduced into wild populations. This time period extends for the duration of all releases conducted in a stock enhancement program, for example, weeks to years. These terms are used in the context of time (e.g., "prior to stock enhancement" or "after enhancement"). "Stock enhancement programs," "...efforts," or "...endeavors" include all activities related to stock enhancement, including planning, hatchery-based activities from broodstock collection to brood releases, and any post-release monitoring efforts of the stocked populations. In stock enhancement, many groups of individuals form "populations": broodstocks; hatchery broods; wild populations targeted for enhancement; groups of released hatchery animals; mixed wild-individual + hatchery-individual populations after enhancement, together with their offspring and filial descendents; and after enhancement, each group within enhanced populations. In this chapter, we use the following population-level and genetic terms as defined below:

1. Natural conspecific interbreeding groups are "wild populations," or "native populations"; those that will receive hatchery broods for stock enhancement purposes are "recipient wild populations" or "recipient populations".
2. Unless otherwise noted, all individuals in a group designated for breeding and producing offspring in a hatchery constitute a "broodstock," which may be subdivided into "breeding groups," composed of "breeders".
3. All broodstock offspring from a breeding event constitute a "brood" or "hatchery brood." In the hatchery, the animals that constitute a brood are "brood animals" or "brood individuals"; in the wild, these animals are "hatchery animals" or "hatchery individuals".
4. The broodstocks plus their broods, considered together in the hatchery, constitute a "hatchery population".

5. After enhancement, released broods plus their recipient wild populations plus the products of their breeding and interbreeding, including all filial generations, constitute "admixed" or "enhanced" populations.
6. The wild individuals in an admixed population constitute the "wild-population component," or "wild component" of the admixed population (prior to enhancement, this component was the recipient population). Other components of an admixed population are the "hatchery (population) component," comprised of all hatchery-bred individuals and their offspring, and the hatchery/wild "hybrid (population) component," composed of F1 hybrids, produced by mating between hatchery individuals and wild individuals, together with the filial hybrid and backcross progeny, produced by subsequent generations of mating between individuals with alleles inherited from hatchery broodstocks and individuals with alleles inherited from the recipient population.
7. "Interbreeding" refers to any matings that result in the production of individuals that have both alleles derived from hatchery broodstocks and alleles derived from recipient populations. All of these individuals are "hybrids," regardless of the proportional contributions of hatchery alleles and wild alleles in an individual.

Throughout this chapter, we use the word "population" rather than "stock" because "stock" can have specific fishery management connotations that may be distinct from managing interbreeding units such as wild populations.

In stock enhancement (which equals stock supplementation [Bartley, 1999]) genetic diversity and its components, genetic variability and genetic composition, are considered at the level of the organismal group(s) being discussed (e.g., broodstock, brood, population, species). "Genetic diversity" constitutes all of the genetic differences and qualities in the type of genetic material being discussed (e.g., single-nucleotide substitutions, genetic alleles, DNA fragment lengths, chromosomal banding patterns) as contained within the organismal group(s) being considered. "Genetic variability" comprises the number, variety, and combinations of alleles or other genetic elements in the category of genetic material being considered (e.g., gene products, DNA sequences, genes, chromosomes). "Genetic composition" is the frequencies of those genetic elements.

2. WHY CONSIDER GENETICS WHEN STOCKING

The genetic requirements for closed-system aquaculture, which has the objective of containing the broods throughout their lives, are different than those for stock enhancement, which has the objective of releasing the broods for integration into recipient wild populations and interbreeding with individuals in those populations (Utter, 1998). In stock enhancement, genetic considerations associated with recipient wild populations are important because those populations (and potentially, the species) could undergo damaging genetic alteration through the stock enhancement efforts (see e.g., Meffe, 1992; Moran, 2002). The discrete genetic make-up of both wild populations and species is a function of their genetic history, historical and present census sizes, adaptations to local ecological conditions, and changes (including genetic mutations) over ecological and evolutionary time. If lost, this genetic make-up may not be easily recovered, if it can be recovered at all. Therefore, in stock enhancement activities, care should be taken to preserve both the hidden and the expressed genetic variation of recipient populations and the species to which they belong because the principal genetic resource needed to produce viable hatchery broods is all of the genetic diversity residing in the species' natural gene pools. Adhering to a few genetic principals when selecting and breeding broodstocks and when rearing and releasing hatchery broods can improve the genetic diversity of the broods that will be released into wild populations which, in turn, will increase the likelihood that the stock enhancement effort will be successful.

Conserving genetic diversity, particularly genetic variability, is also important for long-term survival of enhanced species because sufficient genetic variability within and among gene pools (e.g., populations) must be maintained to enable species to adapt to changing environments (Lande, 1995; Levin, 1995; Thorpe et al., 1995; Ayala, 1997; Meffe and Carroll, 1997). This adaptive stability directly or indirectly influences all populations and species in the ecosystems inhabited by the enhanced species and increases the likelihood of long-term sustainability of those ecosystems, which provide goods (such as broodstock animals), basic life-support systems, and enjoyment for humans (Burger and Lynch, 1995; Currens and Busack, 1995; Lande and Shannon, 1996).

Species' populations with unusually high natural genetic variability can be of particular evolutionary and aquacultural importance because they are essentially genetic "banks." The high genetic variability they harbor can be important for maintaining the species and their populations over ecological or evolutionary time periods as well as important for all types of aquaculture, including stock enhancement. For example, the source of the genetic bank that aquaculturists use to select for traits beneficial in the culture environment and characteristics advantageous for selling aquaculture products (e.g., the coloration of red sea bream [*Pagrus major*] [Hershberger, 2002]) is the genetic diversity residing in the aquacultured species' wild populations.

Decreases in population genetic variability can render populations less genetically fit in many ways, including those important for both perpetuation of the populations and aquaculture production (e.g., reproductive capability or survival rate). Significantly reducing the genetic variability of populations or species through poor stock enhancement practices would reduce the variety of genetic "tools" that could be used by aquaculturists for stock enhancement and other types of aquaculture. For analogous reasons, populations with any level of genetic variability are also particularly important if they harbor ancestral genotypes or genotypes adapted to unusual environmental conditions.

3. THE GENETIC EFFECTS OF STOCK ENHANCEMENT

The genetic effects of stock enhancement are not easily categorized because any effect can lead to almost any other; no effect is completely dependent upon another or independent of another; multiple effects are usually involved in any problematic situation; and no effect's pattern, magnitude, or outcome can be fully predicted. Based on genetic problems in hatchery populations and in recipient wild populations resulting from stock enhancement activities, Waples (1991) and Campton (1995) classified stock enhancement genetic concerns into three types:

1. direct effects on wild-population components of admixed populations, which are caused by interbreeding between hatchery animals and wild animals and, in Campton's classification, by genetic swamping of wild components by hatchery animals (i.e., outnumbering of wild genotypes by enough hatchery-derived genotypes to significantly change the genetic composition of the admixed population, even without interbreeding);
2. indirect effects due to reductions in numbers of individuals in wild-population components through ecological interactions such as predation, competition, or disease transmission; through altered selection regimes resulting from the presence of hatchery animals in admixed populations; and, in Campton's classification, also through poor fisheries management (e.g., unregulated fishing of the admixed population);
3. genetic changes to the hatchery broods through selection, drift, or stock transfers associated with artificial propagation.

Busack and Currens (1995) based their classification of stock enhancement genetic concerns on reduction of the long-term adaptive potential in wild-population components. Their categories included the following:

1. extinction of genetic integrity, caused by demographically based or random variation in reproductive success among genotypes (including inbreeding);
2. loss of genetic variability within and among populations in species undergoing stock enhancement;
3. domestication—i.e., changes in the genetic variability of alleles due to selection for the hatchery environment by hatchery broods, which then leads to differentiation of the broods from their recipient wild populations; and, after enhancement, results in negative effects on the genetic diversity of admixed populations.

Wild populations are the original repositories of the adaptive and neutral genetic diversity contained in their species and, after enhancement, the admixed populations are the new repositories of that genetic diversity. Therefore, of all populations involved in stock enhancement, the genetic effects on admixed populations and their wild-population components are the most important.

Those genetic effects are likely to influence the long-term sustainability of the species, at least in the region of enhancement. Situations that lead to those genetic effects can originate either in the hatchery or after release of the hatchery broods. The magnitude of the effects usually depends on the levels of ecological (e.g., competition, predation, displacement) and biological (e.g., interbreeding) interactions between the hatchery component and wild-population component after the broods are released, but it may simply be due to the proportions of hatchery animals in the admixed populations. Three types of effects on admixed populations and their wild-population components are frequently discussed:

1. alterations in genetic diversity;
2. decreases in fitness;
3. reductions in effective population size (N_e; after Ryman and Laikre, 1991).

3.1. Alterations in Genetic Diversity

In most stock enhancement, an objective is to maintain the genetic variability and genetic composition of admixed populations at levels that are not statistically different from those of conspecific wild populations, particularly the recipient population. In stock enhancement of imperiled species, increasing genetic variability and restoring genetic composition to some predetermined levels may be an objective.

Maintaining the genetic diversity of broodstocks is one of the most important considerations in stock enhancement operations because the fitness of broods is often related to the levels of genetic diversity in their broodstocks compared with levels in recipient wild populations. Some genetic change from wild populations is inevitable in hatchery broods (Pullin, 1993; Waples and Do, 1994) because, in most cases, the numbers of individuals in broodstocks are considerably smaller than they are in recipient populations. Differences between genetic diversity values for broods and those values for recipient wild populations can be exacerbated if the numbers of individuals in the broodstocks are very small, if genetic diversity components of the broodstocks differ significantly from those of the recipient populations, or if gamete contribution to broods is unequal among broodstock individuals. Differences due to unequal gamete contribution can occur even if broodstock genetic diversity values are not significantly different from those of recipient wild populations.

Hatchery broods can generate genetic effects on admixed populations in several ways even if broodstock collecting and breeding procedures are genetically sound. Events that occur during the rearing process can lead to decreases in genetic variability and shifts in genetic composition of hatchery broods compared with the values of those genetic diversity components in recipient populations. Particular brood genotypes can be eliminated because they are poorly adapted to hatchery conditions or because they are biologically inferior compared with other brood genotypes (e.g., in ability to compete for hatchery resources or to avoid cannibalism by other brood individuals). Certain genotypes can be preferentially chosen by hatchery workers either inadvertently (e.g., if individuals with particular characteristics are accidentally culled) or purposefully (e.g., if individuals are chosen because they have particular traits). Allelic or genotypic variability can be reduced or allele or genotype frequencies can change in broods by chance if mortality of brood individuals is high.

Genetic diversity in admixed populations can change immediately after release of hatchery broods into recipient populations if the ratio of released hatchery animals to wild animals is high and genetic diversity values differ sufficiently between hatchery components and wild components. Over time, genetic diversity can be altered in hatchery components by natural selection against individuals carrying traits that were neutral or advantageous in the hatchery environment but are then disadvantageous in the wild. Selection could also reduce or eliminate particular hybrid genotypes with inferior performances in some environmental conditions. Natural selection regimes among population components can change after enhancement and lead to the reduction or elimination of particular genotypes in any population component of admixed populations. Compared with wild populations, significant changes in the genetic diversity of admixed populations can also occur when hatchery components and wild components with differing genetic diversity values interbreed or interact ecologically (e.g., through competition for resources or predation on one population component by another). Sufficiently large shifts in genetic diversity values of any population component can change those values in the entire enhanced population. The magnitude of the change depends on the proportion of individuals belonging to the affected component and the differences in the genetic diversity values between components.

A common cause of alterations in genetic diversity in hatcheries is inbreeding—mating between related individuals that results in the production of offspring. Because breeding and rearing protocols differ among hatcheries and genetic backgrounds differ among broodstocks, the amount of inbreeding necessary to generate genetic effects in broods can differ among species (Falconer, 1989) or even among hatchery strains of single species (Tave, 1993).

Inbreeding in broodstocks can reduce genetic variability in broods because related broodstock individuals likely have fewer alleles at many loci than analogous broodstocks composed of unrelated individuals. In addition, the frequencies of slightly deleterious recessive alleles (i.e., the genetic load; see Theodorou and Couvet, 2004) can be higher in inbreeding broodstocks than in the wild populations from which the broodstocks were collected, assuming that those populations were randomly mating and not inbred. These alleles are usually maintained in randomly mating populations because they occur in the heterozygous state in members of those populations and, therefore, are not expressed. The broods produced by inbred broodstocks have higher probabilities of being homozygous for those alleles than offspring of the wild populations because the probability that broodstock individuals heterozygous for the deleterious alleles will mate is also higher than in wild populations.

The use of hatchery brood animals as succeeding generations of broodstocks compounds inbreeding effects. The successive generations of broods become highly inbred (Gosling, 1982; Cross and King, 1983) and genetic variability continuously declines over the generations (Bert and Tringali, 2001). After a number of generations, broods can exhibit extremely low levels of polymorphism (Taniguchi et al., 1983; Crozier, 1993) and their genetic compositions can differ from those of the wild stocks as much as the genetic compositions of different species (Allendorf and Utter, 1979; Sbordoni et al., 1986, 1987; Durand et al., 1993; Bert and Tringali, 2001).

3.2. Decreases in Fitness

In the evolutionary sense, fitness at the individual level is the ability of an organism to successfully reproduce, i.e., to leave descendants. For each generation, average fitness at the population level is the mean capability of the individuals in an interbreeding population to produce sufficient numbers of reproductively viable offspring to sustain the population over the next generation. The long-term fitness objective is to maintain reproductive viability to sustain the population over generations so that it contributes to the continuation of the species over ecological or evolutionary time.

In stock enhancement, fitness is a relative term. Increases or (more commonly) decreases in fitness values can be observed in one population component relative to another or in one component of an admixed population relative to a population prior to stock enhancement (e.g., recipient population, hatchery brood). Fitness comparisons for admixed populations as a whole are measured relative to fitness values that were present in recipient populations or conspecific wild populations prior to stocking. Fitness changes in other species' populations resulting from stock enhancement activities are measured relative to those species' fitness levels prior to stock enhancement. Fitness comparisons can also be made between populations or population components and expected standards or other measured values.

Fitness considerations are important in stock enhancement programs because a purpose of stock enhancement efforts is to improve the reproductive fitness of a targeted wild population that is in a reproductive fitness decline. Because other measures of fitness (e.g., for health, morphology, physiological response, survival) are usually related to reproductive fitness, many types of fitness measures are important. In a stock enhancement program that also has a goal of contributing directly to a fishery, fitness characteristics specifically related to survival of the hatchery animals until they attain harvestable size is also important.

In most stock enhancement programs, fitness objectives include releasing hatchery broods with fitness levels comparable to those of recipient wild populations and developing admixed populations in which the fitness levels of all population components are comparable to or better than the fitnesses of the recipient wild populations before enhancement. For any measure of fitness, admixed-population values should not be significantly lower than recipient-population pre-stocking values. In stock enhancement of imperiled species, avoiding changes in wild-population fitness caused by broodstock selection and increasing specific types of fitness (e.g., probability of survival) in admixed populations compared with recipient-population pre-stocking values may also be objectives.

Hatchery managers and aquaculture researchers try to avoid reductions in brood fitness both before and after the broods are released into recipient populations. After stocking, hatchery components with lower fitness values than those present in the wild components can immediately reduce the fitness values of their admixed populations, if the brood contribution to the admixed population is high and fitness differences between the hatchery components and wild components are large. A decrease in the fitness of any particular characteristic or trait (e.g., behavioral, morphological, physiological, reproductive, life-history) reduces the overall fitness of an individual. Decreases in the fitness of individuals in a population reduce the average fitness of the population. A decrease in the fitness of any population component (hatchery, wild, or hybrid) reduces the overall fitness of the admixed population (McGinnity et al., 1997; Cross, 1999; Utter, 2000). Fitness effects in one population component can positively or negatively influence the fitnesses of other population components, either directly or indirectly. Many causes of change in fitness can act independently or in consort with other causes to amplify or negate the overall fitness effect. Fitness effects can extend into future generations but future effects cannot be predicted from fitness values observed in present generations.

In general, genetic diversity is directly related to fitness levels. Stock enhancement can decrease the overall fitness of admixed populations when released hatchery broods have altered genetic diversities, and especially lower levels of genetic variability, compared with conspecific native populations. Differences in genetic diversity among admixed-population components due to any of the reasons described in the previous section may alter the selection regimes for one component and, thereby, change the relative fitnesses of any or all population components. For example, considerable empirical evidence has shown that decreases in the genetic variability of hatchery fish broods can adversely affect their fitness. Typical problems include low survival rates at one or more life stages, low reproductive success (e.g., fewer gametes, gametes of poor quality, lack of spawning activity), slow growth, poor physiological adaptation, abnormal mechanical function (e.g., swimming, feeding), developmental alterations, and morphological abnormalities (see Bert and Tringali, 2001; Iglesias et al., 2003; Asahida et al., 2004).

Inbreeding within hatchery broodstocks produces broods that have low genetic diversity, high frequencies and increased homozygosities of normally low-frequency deleterious alleles, and altered allele frequencies compared to recipient populations. Each of these alterations in genetic diversity can decrease the fitness of these broods. After the broods are released into recipient populations, they can increase the probability that fitness problems will affect the resultant admixed populations. Through interbreeding between population components, hatchery components composed of inbred individuals can transfer rare deleterious recessive alleles into other population components at higher frequencies than would normally occur. The probability of transmitting deleterious alleles into admixed populations and the chance for allelic expression in the homozygous state increases with the degree of inbreeding in the hatchery component and the extent of interbreeding between the hatchery component and other population components. The interbreeding continues to increase the frequency and homozygosity of those alleles in future generations and can be exacerbated by the repeated release of inbred hatchery broods or the repeated use of hatchery brood individuals as the next generation of broodstock. Fitness decreases due to inbreeding in aquacultured fish can be dramatic. Some inbreeding problems may not manifest themselves until after the broods are released for stock enhancement because they are not detectable until comparisons with wild individuals in the same cohort can be made. This undetected loss of fitness in inbred broods increases the overall probability that admixed populations will have fitness problems related to inbreeding due to stock enhancement. Some of the best examples of fitness problems due to inbreeding resulted from marine fish aquaculture. In aquacultured rainbow trout (*Oncorhynchus mykiss*), inbreeding produced a high incidence of morphological deformation and a low rate of survival in fry and a significant decrease in average weight attained by age 1 in juveniles (Kincaid, 1976). In aquacultured guppies (*Poecilia reticulata*), inbreeding markedly reduced salinity and temperature tolerance of the broods (Fujio and Nakajima, 1992; Nakajima and Taniguchi, 2001; Shikano et al., 2001a, b).

Genetic effects related to fitness in admixed populations can also be due simply to the introduction of hatchery animals into wild populations. Hatchery-based stock enhancement results in large influxes of artificially propagated animals belonging to single size/age classes of single species. These influxes can alter natural selection regimes on conspecific wild individuals and generate accompanying genetically based, fitness-related changes in wild-population components (Waples, 1991), in admixed populations, in neighboring conspecific populations, or in other species' populations. For example, after enhancement, the wild-population component may be at a fitness disadvantage solely because the number of individuals in the admixed population significantly exceeds the number that was present in the recipient population (Waples and Do, 1994). The additional animals in enhanced populations can also change the dynamics of those populations relative to the dynamics of other species' populations in the community and, thereby, shift selection regimes for numerous species in the community. Broods may also affect the fitness of populations after their release by carrying pathogens or parasites into recipient populations. This is a common pathway for decreasing fitness of the wild-population component (e.g., Johnsen and Jensen, 1986; Bakke et al., 1990; Fries and Williams, 1996; Kirk et al., 2000).

Selection can change the relative proportions of the hatchery and wild components after release of the broods through direct competition between population components or through indirect mechanisms that differentially affect the population components. For example, one component may directly prey upon the other or out-compete the other for critical resources such as food or shelter from predators. Selection can operate through ecological or biological mechanisms to influence the reproductive contribution of particular population components in admixed populations. For example, a population component can have higher average values than others in fitness characteristics that ultimately influence its proportional contribution to reproduction (Reisenbichler et al., 2004). Examples of these types of fitness characteristics include the following:

1. behavior that enhances the probability of survival, such as avoiding predators or procuring critical resources such as food or habitat;
2. physiological ability to withstand particular environmental conditions;
3. reproductive performance that increases the production of viable offspring, such as success in mating or production of high-quality gametes;
4. high performance in critical life-history aspects such as growth, metabolism, or survival.

Selection can also affect the relative proportions of population components in future generations. For example, some offspring genotypes could have higher reproductive rates than others, thereby increasing the proportional contribution of their population component.

Fitness loss in admixed populations can also occur through outbreeding—the production of offspring by parents from different genetic backgrounds that, therefore, have gene complexes adapted to different environments (Lynch, 1991). Outbreeding may or may not be associated with decreases in genetic variability or shifts in genetic composition. In stock enhancement, outbreeding in the hatchery is due to poor choices of broodstock individuals. Outbreeding occurs when all or part of a broodstock is composed of individuals from one or more populations that are genetically differentiated from the recipient population. The differentiated populations may be adapted to environmental conditions different from those of the release area. Broodstocks composed of individuals from the recipient population plus individuals from genetically differentiated populations produce "outbred" broods composed of individuals with locally adapted genomes, individuals with genomes adapted to different conditions, and hybrids produced by matings between broodstock individuals from the two different populations. These broods, particularly the hybrids, may not be well adapted to the environmental conditions of either the hatchery or the release area. Similarly, broods produced from broodstocks originating from multiple non-local populations are outbred and probably will have low fitness after their release. Broodstocks composed entirely of individuals originating from a single population genetically distinct from the recipient population would not produce broods that are outbred, but those broods may perform poorly in some fitness components in the hatchery. In all of these scenarios, interbreeding between hatchery components and wild-population components after enhancement will generate some level of outbreeding and, therefore, possible reductions in fitness of the admixed populations.

Outbreeding can also occur when generations of hatchery animals are repeatedly released into single recipient populations. Over generations, the accumulated matings between hatchery animals, which have some degree of genetic differentiation from the original recipient population, and wild-component animals creates a type of outbreeding. This problem can occur if only one generation of broods with limited genetic variability is introduced into a population (Tringali, 2003), or even if genetic diversity in the introduced broods is maintained over all generations (Alexander and Hubert, 1995). Moreover, the genetic load can increase over the generations because the probability that the frequencies of rare deleterious alleles will increase is higher in broodstocks due to their relatively limited numbers of individuals.

Regardless of the cause of an outbreeding situation, the offspring produced from interbreeding between hatchery components and wild-population components and subsequent generations of progeny could suffer from "outbreeding depression." This is the loss of fitness in the progeny of outbreeding parents due to the breaking up of co-adapted gene complexes (multigene groups that have evolved to work harmoniously to perform a function; Templeton, 1986) adapted to local conditions. Outbreeding depression lowers fitness in admixed populations due to the introgressive transfer of maladapted alleles from the hatchery component into the wild component. Fitness reductions due to outbreeding depression are manifested more in later-generation backcross and intergrade individuals than in first-generation hybrids (Lynch, 1991; Waples and Do, 1994). Thus, further fitness declines could be seen in enhanced-population filial generations. The overall level of fitness reduction in admixed populations depends on the extent of interbreeding between hatchery and wild-population components and the extent of maladaptation in the released broods.

Outbreeding between hatchery and wild individuals can affect the genetic population structure of more than just the recipient populations. Most aquatic species, and particularly marine species (Conover, 1998), contain more local adaptation than previously believed. Even continuously distributed species with broad geographical ranges, such as many marine fishes and invertebrates, can have population-level genetic differences over space and/or time (Palumbi, 1994; Taylor and Hellberg, 2003; Cowen et al., 2006). They can be divided into more-or-less discrete interbreeding populations. Source populations can supply individuals to other aggregations of individuals in the surrounding area (e.g., Hindar et al., 2004). Minimally, the likelihood of mating between individuals can increase with their proximity to each other (e.g., Gold et al., 2001). Individuals within these reproductive groups are widely assumed to have coadapted gene complexes adapted to local conditions. Reproduction between individuals from different interbreeding groups can homogenate populations and generate progeny less well adapted to the environments experienced by one or both parents. Stock enhancement can produce the same effect. If the enhanced species is composed of locally adapted, genetically differentiated populations, then supplementing a population with broods composed of individuals that contain alleles from a different population may homogenize those populations and reduce the genetically based adaptive differences between them (Gold, 2004; Waples and Drake, 2004). Local adaptation is disrupted via introgression of non-local alleles through interbreeding between individuals with different genetic backgrounds.

The fitness of severely depleted wild populations can be reduced by stock enhancement activities both before and after introduction of hatchery broods into the population. If a large percentage of individuals in an imperiled population is removed to serve as broodstock, that population's genetic viability might be compromised before enhancement can be achieved. During enhancement of an imperiled species, careful breeding strategies are needed to avoid inbreeding or outbreeding in the hatchery and maintain or even increase genetic variability in the admixed population. The wild-population component is in greatest jeopardy when the fitness of that group is lower than the fitness of other population components.

From an evolutionary perspective, neither the overall fitness of admixed populations nor the fitness of any population component can be predicted over the long term. Fitness levels can change as long as stock enhancement proceeds and possibly after it ceases—at least until the enhanced population attains genetic equilibrium. Lack of predictive capability in fitness response is inherent in all stock enhancement efforts. Prior to using stock enhancement as a conservation or management tool, its possible long-term fitness effects on the targeted population should be carefully considered and compared to other, less invasive options for restoring the population.

3.3. Reductions in Effective Population Size

The effective population size (N_e) is defined as the number of individuals in an "ideal" population that would produce the same level of inbreeding or genetic drift[1] as observed in the population of interest (Hartl and Clark,

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[1] Genetic drift is the random change in allele frequencies due to chance alone and is due to the random sorting of alleles during meiosis for production of gametes and random uniting of gametes during fertilization. This possibility for changes in allele frequencies each generation can lead to the fixation or extinction of alleles in populations over generations (Hartl and Clark, 1997).

1997). Characteristics of an ideal population include random mating, demographic constancy, equal sex ratio, random variation in reproductive success among individuals, no effects of selection for or against any population component, no immigration of individuals from other interbreeding populations, and no detectible genetic mutation rate. Because few natural populations fulfill the criteria for being ideal, N_e is almost always less—sometimes much less—than the observed number of breeding individuals or the adult census population size (Frankham, 1995; Waples and Drake, 2004). Very large populations can have relatively very small N_es due to any of the following:

1. non-random mating patterns;
2. unequal sex ratios of breeders (Nunney, 1993, 1996, 1999; Vucetich et al., 1997);
3. behaviors that affect population size, growth rate, or reproduction (Anthony and Blumstein, 2000);
4. large changes among generations in census population size (Waples, 2002), age distribution, immigration or emigration, or other factors that affect any of the criteria for an ideal population (see Palumbi and Wilson, 1990; Hedgecock et al., 1992; Fiumera et al., 2000; Hauser et al., 2002; Johnson et al., 2004).

Decreases in N_e, can stimulate changes in other genetic effects on populations, including the following:

1. the loss of alleles, including those that are adaptive in some way, increases over generations through genetic drift, even if mating is random;
2. the loss of selectively neutral genetic variation increases, at a rate inversely proportional to N_e (Waples and Drake, 2004);
3. genetic variability decreases, and with it, some adaptive potential;
4. fitness declines because inbreeding increases and, thereby, the exposure of deleterious recessive alleles in homozygous genotypes increases.

Thus, large, sustained reductions in N_e may result in considerable genetically related damage to populations (Lande, 1994; Lynch et al., 1995), including a progressive decline in population fitness due to the fixation of new, mildly deleterious mutations.

In most stock enhancement projects, an objective is to increase the N_es of admixed populations through the enhancement effort and to maintain the N_es of their wild-population components compared with the pre-stocking N_e values for those wild populations. However, unless it is well planned for increasing genetic diversity, stock enhancement can reduce N_e of admixed populations compared with their potential values. The magnitude of reduction depends on the ratio of hatchery animals to wild animals in each population (Ryman and Laikre, 1991), the collective genetic diversity of the broods released per generation (Ryman and Ståhl, 1980; Diaz et al., 2000), and the extent to which fitness differences among genotypes affect their survival and reproduction in the admixed population (e.g., Reisenbichler and McIntyre, 1997: Reisenbichler and Rubin, 1999).

The long-term effects of stock enhancement on admixed-population and wild-component N_es have been of considerable interest to researchers involved in stock enhancement (e.g., Tringali and Bert, 1998; Tringali and Leber, 1999; Hedrick et al., 2000). These immigrant population components usually have less genetic variability and altered allele frequencies at few to many loci compared with their recipient populations and they are instantaneously combined with recipient wild populations usually depleted of individuals to some degree. Through interbreeding between hatchery and wild individuals, the N_es of admixed populations are reduced, sometimes by orders of magnitude. Numerous statistical models are available for analyzing the interactions of stock enhancement and N_e, including those that do the following:

1. predict and quantify the relationship between post-stocking levels of interbreeding and N_e (e.g., Pollak, 1983; Waples, 1989; Ryman and Laikre, 1991; Ryman et al., 1995; see also Palm et al., 2003; Säisä et al., 2003);
2. evaluate the relationship between stocking rate (change in the hatchery:wild ratio) and rate of replacement of neutral alleles from wild-population gene pools with alleles from the hatchery-population gene pools (Chakraborty and Leimar, 1987);
3. evaluate the effects of stocking over generations on selectively advantageous alleles (Felsenstein, 1977, 1997).

For supplemented populations, many researchers consider the important N_e value to be the N_e for admixed populations (Ryman and Laikre, 1991; Waples and Do, 1994; Wang and Ryman, 2001; Duchesne and Bernatchez, 2002). The N_e values for wild-population components can be equally important because, in an extensive stock enhancement effort, the number of individuals in that population component can be reduced to the point that threatens its viability (Ryman and Laikre, 1991; Waples and Do, 1994). Wild-population components can be reduced to a small fraction of admixed populations due to post-enhancement ecological interactions between the hatchery animals and wild animals, such as predation on wild individuals by hatchery individuals or elimination of wild individuals through competition with hatchery individuals. Anthropogenic activities such as inadvertent overharvesting of wild components by indiscriminant fishing (Ryman and Laikre, 1991; Waples and Do, 1994) or stocking high numbers of hatchery individuals (Nehlsen et al., 1991) can also reduce the proportional contributions of wild components or lead to genetic swamping of wild-population components. Repeated introductions of hatchery broods with low genetic variability or altered genetic composition can exacerbate genetic swamping over time, particularly if interbreeding between hatchery individuals and wild individuals is extensive. However, even without substantial interbreeding between hatchery individuals and wild individuals, the N_es of wild-population components can be reduced to potentially dangerous levels if hatchery animals numerically overwhelm wild-component individuals. Sufficient genetic diversity will not be maintained in the wild-population component to sustain it over ecological or evolutionary time (Waples and Do, 1994), particularly if some important aspect of the environment's carrying capacity, such as food or habitat, is limited (Leber, 2004, and references therein). Lastly, admixed-population N_es will also be small regardless of the ratio of hatchery individuals to wild individuals if large fractions of breeders in the admixed populations originated from relatively few broodstock individuals.

The problems with N_e described here, which can threaten wild-population long-term viability, are exacerbated when numbers of wild individuals are very low, such as in imperiled species. By necessity, broodstock numbers will be low. This increases the probability that genetic diversity values for broods will differ significantly from those for recipient wild populations. If stock enhancement is successful, the ratio of released hatchery individuals to wild individuals could be high. This increases the probability that genetic effects of many types, particularly effects on N_e will impact wild-population components in admixed populations. For imperiled species, the potential costs and benefits of stock enhancement should be carefully weighed against other population-replenishment methods.

4. GENETIC MONITORING OF STOCK ENHANCEMENT EFFORTS

The genetic concerns regarding maintenance of genetic diversity, fitness, and N_e as detailed above can be fully explored and addressed by including comprehensive, genetically based monitoring programs in stock enhancement endeavors. Sophisticated genetic methods exist that enable discrimination of animals in different groups (e.g., individuals in different population components of admixed populations, individuals in genetically differentiated wild populations) or of single individuals in large groups (e.g., specific hatchery individuals in admixed populations). Methods also exist that can reveal family relationships within and among broods or among individuals in admixed populations (e.g., parentage, sibling relationships). The genetic analyses for performing these identifications have evolved to be relatively inexpensive, rapid, and easy. Computer software programs have been developed to analyze these data; many are available through the Internet at no cost. Below, we describe the disciplines of genetics involved, types of genetics used, goals usually put forth, and tasks needed for most stock enhancement genetic monitoring programs. We also provide an example of a genetic monitoring program for a specific fish stock enhancement project. This example could serve as a guide for designing other stock enhancement genetic monitoring programs.

4.1. Monitoring Tools

Researchers have monitored stock enhancement programs since the 1980s (see e.g., Ward and Grewe, 1994). Prior to the advent of relatively expeditious methods for visualizing DNA and its products, aquaculture scientists used a variety of innovative morphological identifiers and physical tags to identify hatchery individuals after their release and to estimate their contribution to admixed populations. Many of these types of markers are used today in stock enhancement monitoring programs—alone, in combination with each other, or as supplements to genetic markers. Physical tags that have been successfully used include the following:

1. morphological characteristics such as pigmentation, fused nares (Bartley, 1999; Mana and Kawamura, 2002), coloration, and fin clips;
2. scale characteristics such as time series of scale samples and scale ring patterns (Lund et al., 1989; Lund and Hansen, 1991; Einarsson, 1998; Hansen and Youngson, 1998; Frenkel et al., 2002; Bo and Zhou, 2003; Iglesias et al., 2003);
3. internal and external tags such as anchor tags (Otterå et al., 1999), binary-coded microtags (coded-wire tags) (Agnalt et al., 1999), ink injections, and oxytetracycline-labeled otolith rings (Kristiansen, 1999);
4. specific to invertebrates, characteristics and applied tags such as natural-stress ring variations on genital plates, evidence of fouling on shells (Dao et al., 1999; Okei, 1999; Sakai et al., 2004), numbers placed on shells or plates, and markings on shells induced by feeding the animals special diets (Gallardo et al., 2003).

Statistical methods used to infer contribution of stocking programs include a time-series model using the ratio of number of animals released to juvenile recruitment (Chan et al., 2003) and correlations between stocking rate or quantity and catch (Abdlohay, 1996).

Physical tags have the advantage of providing absolute identification, but genetic markers eliminate the cost and handling problems of physical tagging, and there is no tag loss. In addition, genetic markers can be obtained from individuals at sizes too small to physically tag and, because they are based on inherited genetic material, genetic tags are stable features of organisms and of their offspring (Wilbur et al., 2005). Physical tags can unambiguously demonstrate movement of tagged individuals; but they cannot prove that the individuals contributed to the reproductive population. Genetic markers can be used to investigate not only the genetic contribution of individuals or groups to succeeding generations but also levels of interbreeding between individuals from different genetic backgrounds and the magnitude and direction of the resultant gene flow between populations or species. Although there is a tradeoff between the statistical probability of identification obtained through genetics and the absolute identification attained through physical tagging, the very high level of statistical reliability achievable using a battery of multiallelic loci to identify individuals and assign them to groups obviates the need for serious doubt that the observed results are erroneous.

4.1.1. Categories of genetics involved

Two genetic disciplines—population genetics and diagnostic genetics—are principally used to obtain answers to questions relevant to stock enhancement. Population genetics is the study of the hierarchical organization of the collective genetic diversity in species' populations and of the genetic relationships of those species and populations to each other. Population genetic analyses provide critical baseline information on the natural levels of genetic diversity and population structure of species prior to stocking. Standard population genetic measures such as estimates of allele frequencies, level and organization of genetic diversity, relatedness among populations, and geographic range of populations are used not only to determine where to collect broodstock and how many to collect but also to estimate the contribution and effect of stocked individuals after the enhancement effort. Diagnostic genetics is the identification and distinguishing of single or multiple individuals within a group. It is essentially the same as forensic genetics, but without enforcement or legal implications. Diagnostic genetics are based on the premise that each organism on earth (except identical twins, triplets, etc.) possesses a unique genotype that represents the individual's ancestry—its "genetic tag." The most precise genetic tags allow each individual to be distinguished from all other conspecific individuals with very high probability. The many uses of genetic tags for diagnostic genetics in stock enhancement include all of those for which distinguishing and tracking individuals are required.

Genetic monitoring for stock enhancement is centered principally on two types of genetic analyses—biochemical and molecular. Biochemical genetic analyses use gene products such as enzymes or proteins, which provide indirect estimates of the genetic diversity of the genes that code for these products. Molecular genetic analyses use the DNA molecule itself to evaluate genetic diversity. The "genetic markers" that researchers and aquaculturists use are the visualized products of laboratory analyses that elucidate and illustrate the variable entities of the genes under examination. These entities are genetic alleles, DNA nucleotides, or DNA fragments.

4.1.2. Genetic tags

The genetic tags developed for diagnostic genetics can be used for many purposes in stock enhancement monitoring including the following:

1. identifying single individuals, families, or pedigree groups for tracking their ecological or life-history characteristics (e.g., movement, migration, age of reproduction);
2. establishing familial relationships among individuals within subpopulations (e.g., schools of fish, patches of scallops);
3. distinguishing special individuals from common individuals (e.g., hatchery individuals from wild individuals; particular individuals in populations or species from all others);

4. assigning individuals to particular populations or special groups (e.g., wild populations or hatchery broods [Hansen et al., 2001]);
5. determining gender (e.g., Tringali et al., accepted, a);
6. establishing genealogical relationships among individuals.

Bert et al. (2002) described the types of genes and gene products commonly used as genetic tags; provided information and references for developing and using these tags; and discussed their uses for all types of aquaculture. They also identified ten uses of genetic tags for stock enhancement. Nine of those uses are centered on the three important needs in stock enhancement:

1. maintaining genetic diversity and N_e in the hatchery;
2. avoiding disruption of the genetic diversity, population genetic structure, and N_e of the recipient population through the stocking effort;
3. understanding the contribution and effects (both positive and negative) of the stock enhancement program.

Genetic tags can also be used to estimate the rate of physical tag loss (or failure of detection) when both physical and genetic tags are used; estimate the effects of parameters (e.g., animal size, time of year, location of release) on stocking success; and estimate the magnitude or rate of harvest of hatchery individuals by user groups (e.g., commercial fishermen, sportfishermen) (Liao et al., 2003).

The most precise genetic tags can describe an individual's genotype sufficiently to distinguish that individual from all others within a population (except genetically identical siblings) or species with an average accuracy of 99.999% or greater. Applying that degree of accuracy to genetic monitoring of stock enhancement, a researcher could distinguish a hatchery individual from all others in an admixed population, identify the brood from which it came, and identify its two parents in the broodstock that spawned the brood. That degree of accuracy is needed for some aspects of stock enhancement, but it is usually a luxury because it depends on development of a multilocus genetic tag composed of numerous (usually microsatellite DNA) loci, most of which have numerous alleles. The type of loci used and the level of marker specificity needed depend on the anticipated use of the genetic tag. The tag should be developed to fit the anticipated need (Liao et al., 2003), considering the level of identification required, the expertise and equipment available, and the cost of developing the tag and executing the work. Typically, the ability to discriminate hatchery animals from wild animals is sufficient to assess the contribution of hatchery individuals to admixed populations. Developing a genetic tag of greater sophistication may not be difficult because the DNA sequences of many genetic markers for species of economic or conservation interest have been accessioned in GenBank®, the principal international depository for gene nucleotide sequences. They can be obtained by querying GenBank through the Internet (http://www.ncbi.nlm.nih.gov/Genbank).

4.1.3. Genetic markers

Numerous types of DNA and DNA-based products are being used to develop genetic markers for aquaculture (see Bert et al., 2002). Currently, the most commonly used genetic markers for stock enhancement genetics include allozymes, DNA with variable numbers of tandem nucleotide repeats (VNTRs—microsatellite DNA and macrosatellite DNA), and mitochondrial DNA (mtDNA). The use of DNA with single-nucleotide polymorphisms (SNPs) is developing quickly. Each type of marker has clear advantages and disadvantages (Ward and Grewe, 1994; Shaklee and Bentzen, 1998; Schlötterer, 2004), and no single type is suited to all needs (Ferguson and Danzmann, 1998).

Allozymes. These are enzymatic proteins involved in metabolic pathways. Most of those commonly used are coded for by single nuclear genes with codominant alleles that conform to Mendelian genetic assumptions. In allozyme electrophoresis, a few other proteins are also examined (e.g., general protein), but they are not distinguished from the enzymatic proteins when allozyme, or protein, electrophoresis is discussed. Allozyme electrophoresis is the oldest widely used biochemical technique for assaying genetic variation (e.g., Alexander and Hubert, 1995). This technique is still being used today (e.g., Britten and Glasford, 2002). It has the advantages of being inexpensive, technically simple, and quick. Numerous publications provide detailed information on laboratory procedures and analytical methods used to resolve allozyme alleles (e.g., Selander et al., 1971; Richardson et al., 1986). Allozyme genetic markers are different forms of the targeted proteins and are produced by alleles at the loci coding for those proteins. These allozyme "alleles" (different molecular forms of the protein) move differentially in a semipermeable medium when an electrical current is passed through it. They can be stained using chemical reactions that activate the proteins. Numbers of alleles at polymorphic loci usually range between 2 and 7 but may extend up to 11 or more. The allozyme alleles, which substitute for the gene alleles that produced them, can then be read and scored as genetic alleles. However, because of the redundancy of the genetic code (see Hartl and Clark, 1997) and technical limitations associated with visualizing all of the alleles at highly polymorphic loci, the observed variation is inherently less than that of the DNA that codes for these gene products.

For stock enhancement monitoring, the frequencies of rare allozyme alleles are usually greatly increased in hatchery broods by selecting broodstock that carry those alleles (e.g., Bartley et al., 1995; Jørstad, 2004; Reisenbichler et al., 2004). The success of stock enhancement projects can be ascertained using assays of the proteins that have those alleles. The proportional contribution of hatchery individuals to admixed populations is estimated using mixed-stock analyses that compare the frequencies of the hatchery-selected alleles in an admixed population with those frequencies in wild populations (e.g., Murphy et al., 1983; Taggart and Ferguson, 1984, 1986; Knut et al., 1994; Reisenbichler et al., 2004). A hidden complication is that the manipulated loci and alleles may be linked to alleles at other loci that influence or control other traits or processes. Those linked alleles are then increased in the hatchery population along with the targeted allozyme alleles, with unknown consequences.

Rare allozyme alleles are also employed as genetic tags in the hatchery using the same approach—increasing the frequencies of those alleles through selection.[2] But here, too, the limitations and potential complications associated with selection of specific genotypes apply. Recent advances in statistical calculations for identifying hatchery individuals in the wild (Tringali, 2006) may allow batteries of polymorphic allozyme loci to be used for parentage analysis without selection for specific alleles, if polymorphism is sufficiently high.

Stock enhancement researchers have used allozymes either alone or in combinations with other genetic techniques or tagging methods (e.g., Garcia et al., 1994; Fleming et al., 2000; Koljonen et al., 2002; Jørstad, 2004) for the following purposes:

1. assessing the population genetic structure of species targeted for stocking (Bartley et al., 1995; Shaklee and Bentzen, 1998; Bell and Warwick, 2004);
2. genetically characterizing local wild stocks, broodstocks, and hatchery broods (Jørstad, 1986; Bartley et al., 1995);
3. estimate N_e (Bartley et al., 1995);
4. checking for and monitoring selection in hatchery populations (Sbordoni et al., 1986; Crawford, 2000);
5. estimating survival of hatchery fish after release (Jørstad, 2004);
6. comparing genetic diversity (Ferguson et al., 1993) and performance (Reisenbichler and Rubin, 1999; Reisenbichler et al., 2004) of hatchery fish and wild fish;
7. quantifying the interactions of escaped farmed fish and wild fish (Fleming et al., 2000).

VNTRs. The two classes of VNTRs commonly used for stock enhancement—microsatellite DNA (also termed SSRs [simple sequence repeats] or STRs [simple tandem repeats]) and minisatellite DNA—are sequential repeats of short nucleotide sequences (e.g., ACACAC ... or AGCCTAGTAGCCTAGTAGCCTAGT ...). The single-repeat number ranges from 2 to 5 base pairs (bp) in microsatellite DNA and from 10 to 100 bp in minisatellite DNA (Burke et al., 1996; Dowling et al., 1996). Allelic polymorphism in micro- and minisatellite DNA depends on the variability in the number of repeats of these sequences and is visualized as DNA fragments of different lengths. After polymerase-chain-reaction (PCR) amplification and processing in a DNA

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[2] Caution should be used when using rare allozyme alleles as genetic tags. If the stock enhancement endeavor is successful, the frequencies of those alleles will be significantly increased in the admixed population and the fitness effects of those frequency increases, or of concomitant increases in the frequencies of loci linked to the targeted locus, will not be known.

analyzer, the loci are visualized in computer printouts that illustrate the lengths[3] of the repeat-DNA segments in individuals. Heterozygous individuals have alleles of two clearly distinguishable lengths and homozygous individuals have alleles of only one length. Numbers of alleles at VNTR loci are generally high (4–9) to very high (e.g., 12 or more) within species or populations (e.g., O'Connell and Wright, 1997). Typically, the loci are independent of other genetic loci, the alleles are codominant, and genotype frequencies conform to Hardy–Weinberg expectations. Therefore, the probability that an individual has a particular multilocus genotype is the product of the probabilities that the individual possesses its particular genotype at each locus. Because each locus typically has several to many alleles, batteries of 5–10 loci can be used to identify individuals with exceptionally high specificity. Probabilities of correct identification of single individuals in populations can be virtually 100%. This level of genetic variability makes VNTR loci, particularly microsatellites, more effective than other DNA techniques at revealing population genetic structure and relationships among populations within species (e.g., Banks et al., 2000) and between closely related conspecific groups (e.g., hatchery and wild animals) (Koljonen et al., 2002). In addition, laboratory techniques to assay for VNTRs have become rapid and relatively inexpensive (e.g., Heath et al., 1993; Lunt et al., 1999). Wright and Bentzen (1994) and O'Connell and Dillon (1997) provide reviews of VNTR-marker development, applications, and utility for fisheries and aquaculture.

Microsatellite loci are essentially replacing allozyme loci as the molecular tool of choice in all types of studies that require discriminating populations, documenting genetic diversity of populations, understanding gene flow patterns and extent, elucidating relationships among individuals (including parentage; Jackson et al., 2003), and identifying individuals in a group (Bruford et al., 1996; Cross, 1999; Perez-Enriquez and Nobuhiko, 1999; Koljonen et al., 2002; Miller and Senanan, 2003). Because of its great sensitivity to genetic variation within species and its utility as a genetic tag, microsatellite DNA has also proven to be very useful for genetic monitoring of stock enhancement. Microsatellites have been used for many aspects of monitoring, including the following:

1. estimating the genetic variability, effective population size, and inbreeding coefficient of broodstocks (Taniguchi, 2004);
2. determining the parentage of hatchery brood individuals (Jackson et al., 2003; Sekino et al., 2003);
3. comparing the genetic variation of wild populations and hatchery broods (Hansen et al., 2000; Jackson et al., 2003);
4. genetically characterizing local wild stocks, broodstocks, and broods (Jørstad, 2004);

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[3] Each "length" is actually composed of the DNA fragment length characteristic of the allele and a distribution of DNA fragment lengths that differ from the principal length by one to a few nucleotide repeats.

5. assessing the effects of stocking on the genetic diversity and genetic population structure of recipient populations (Ruzzante et al., 2001);
6. estimating the overall success of stock enhancement projects (Jørstad, 2004).

MtDNA. Mitochondrial DNA, which is extranuclear DNA that resides in the mitochondria of organisms, is composed almost exclusively of genes that code for cytochrome *b*, RNA, and proteins. Those genes are arranged in tandem along the single-stranded, circular mtDNA molecule. MtDNA does not undergo genetic recombination and is effectively inherited without change from the mother to offspring (but see Zouros et al., 1994). Therefore, mtDNA can provide information on maternal contributions to succeeding generations. Because of the unique inheritance pattern, the mtDNA molecule is frequently considered to be a single, linked genetic unit. Nevertheless, different mtDNA genes vary considerably in their rates of mutation (reviewed in Kocher and Stepien, 1996; Palumbi, 1996). Some mtDNA regions that have relatively high nucleotide substitution rates can be used together in various ways or in combination with nuclear-gene markers to create highly specific DNA markers. One, usually hypervariable, non-coding region of mtDNA, the control region, is frequently used as a genetic marker (e.g., Bentzen et al., 1996; Stabile et al., 1996). Its overall nucleotide substitution rate is among the highest known, in part because it does not contain genes involved in the protein-coding process. MtDNA is also useful for detecting loss of genetic variability because it is four times more sensitive to reductions in broodstock N_e than nuclear DNA. Traditionally, mtDNA variability among individuals and among populations has been compared by restriction fragment length polymorphism, or RFLP, analysis (e.g., Laikre et al., 2002; Wasko et al., 2004). The mtDNA molecule is cut into pieces with restriction enzymes that recognize and cleave the molecule at or near specific nucleotide sequences. The pieces, of differing lengths, are separated in an electrically charged, semipermeable medium and stained to visualize the mtDNA lengths. MtDNA variability is also analyzed by obtaining the nucleotide sequences of targeted parts of the molecule (e.g., the control region) using PCR and DNA-analyzer technology (e.g., Seyoum et al., 2003; Wilbur et al., 2005). The nucleotide sequences of the entire mtDNA molecule are also sometimes used. However, nucleotide sequencing may not offer more resolution than RFLP analysis (Ferguson and Danzmann, 1998). More recently, streamlined methods such as PCR-based assays for the presence or absence of specific nucleotides or sequences have been used (Tringali et al., accepted, b).

For stock enhancement genetics, mtDNA has been used for the following purposes:

1. investigating species' genetic population structures prior to stocking (Seyoum et al., 2003; Ziemann, 2004);
2. calculating N_e of recipient populations (Ziemann, 2004);
3. comparing genetic diversity estimates among hatchery broods (Garcia et al., 1994), including those produced from various proportions of wild and hatchery-derived broodstocks (Asahida et al., 2003);

4. estimating the relative contribution of broodstock females to broods (Asahida et al., 2004);
5. estimating the contribution of hatchery-derived animals to wild populations (Wilbur et al., 2005);
6. estimating the survival of hatchery animals after their placement in the wild (Milbury et al., 2004).

SNPs and other markers. Analysis of SNPs in nuclear DNA and mtDNA is a relatively new tool in the molecular genetics toolbox, but has promise for stock enhancement genetics (Calcagnotto and de Almeida, 2000; Brumfield et al., 2003; Luikart and Wayne, 2004; Rengmark et al., 2006). SNPs are simply that—single-nucleotide substitutions in the nucleotide sequences of DNA molecules. They are widespread throughout the genome (Brumfield et al., 2003) but, by necessity, their level of variability is lower than that of microsatellite DNA. They are visualized in the computer output from DNA sequencing on a DNA analyzer. Rapid, high-throughput, cost-effective genotyping methods for analyzing SNPs are being developed (Milbury et al., 2004; Smith and Seeb, 2005; Smith et al., 2005a, b). SNPs can provide broader genome coverage and higher-quality data than either microsatellite DNA or mtDNA; data standardization among reseachers is easier than with microsatellite DNA (Morin et al., 2004; Smith et al., 2005a, b). However, because of the limitations in variability at each site, researchers are often biased toward highly polymorphic SNPs (Brumfield et al., 2003) and a large array of SNPs is needed for discriminating individuals in groups.

Other types of DNA are sometimes used as genetic markers (reviewed in Liu and Cordes, 2004). For example, nuclear gene introns were used by Shleser (1998) to evaluate inbreeding and performance traits in selected lines of shrimp (*Penaeus vannamei*) broods reared in a common production system. In another study, alleles for the enzyme transferrin were used by Calcagnotto and de Almeida (2000) to determine that genetic variability in Amazonian tambaqui (*Colossoma macropomum*) hatchery broodstocks decreased over generations because small numbers of tambaqui brood fish were taken to be used as broodstock over succeeding generations. In addition, genetic drift operating over the generations further reduced genetic variability in the broods.

Many researchers use multiple types of genetic markers, or a combination of molecular or biochemical markers and other markers such as morphological or physical tags to monitor and evaluate stock enhancement programs. The clear advantage of using multiple types of genetic markers is a more comprehensive perspective of the genetic effects of the stock enhancement program. When genetic markers are combined with physical markers, the absolute certainty that hatchery animals have been found can be combined with genetic information. With high confidence, projections can be made on the extent to which the stocked animals are contributing to, and becoming integrated with, the local population and on the effects that the enhancement program is having on wild populations.

Although genetic markers enable researchers and aquaculturists to understand the effects of stock enhancement activities and determine the results of stock enhancement projects with high accuracy and in great detail, there are limits in the ability to project the long-term implications of stock enhancement endeavors. Genetic monitoring can provide information on succeeding generations in enhanced populations (e.g., on survival rate, interbreeding, sex-specific gene flow patterns) but even detailed molecular genetic data provide only limited insights about long-term evolutionary processes. Consequently, and perhaps most importantly, *a priori* predictions regarding the consequences of specific stock enhancement projects over ecological or evolutionary time periods are not possible (Utter, 1998).

4.2. Goals and Tasks

The overall goals for genetic management of stock enhancement should include the following:

1. maintain the genetic diversity, fitness, and N_e of hatchery broodstocks and broods at levels that minimize the probability of generating negative effects on the broods during the hatchery breeding and rearing period and on the admixed populations after enhancement;
2. maintain the genetic diversity, fitness, and N_e of admixed populations and their wild-population components at levels that minimize the possibility of negative fitness effects or loss of potential long-term viability during and after enhancement.

Each of these goals has multiple subdivisions within the corresponding phases of stock enhancement that they address. But all can be addressed by conducting genetic assessments of the four populations involved in stock enhancement:

1. wild populations of the species to be enhanced (and, sometimes, other sympatric or neighboring populations of the same or closely related species);
2. broodstocks;
3. broods;
4. admixed populations (including wild, hatchery, and hybrid components).

Understanding the population genetic structure of a species to be enhanced and the genetic diversity of the species' recipient wild population (which may even be the species over its entire range) can be accomplished through a population genetics study that encompasses at least a large region of the species range around the area where stock enhancement will take place. If possible, the study area should encompass the species' entire range (see Shaklee and Bentzen, 1998; Bell and Warwick, 2004). This study should be constructed such that sources of recruitment can be identified, levels and patterns of gene flow among aggregations of individuals (e.g., populations, subpopulations) or over the targeted species range can be ascertained, and estimates of genetic diversity components can be calculated. The genetic markers must be sufficiently variable to elucidate genetic differences among populations, which are usually represented by samples taken from different geographic locations or over different generations; but they should not be of such variability that each individual is unique. Closely related species that also inhabit the region where hatchery broods will be released and that have the potential to interbreed with released hatchery individuals should be included in this and other relevant analyses involving recipient wild populations or wild components of admixed populations. If possible, multiple genetic tools should be employed in this study.

Population genetics studies will provide baseline information necessary for many analyses needed in genetic monitoring programs, including the following:

1. determining where to collect broodstocks;
2. estimating the numbers of broodstock individuals needed to adequately represent the genetic diversity in recipient populations;
3. planning breeding strategies and stocking regimes needed to maintain genetic diversity in the recipient population;
4. periodically monitoring the genetic effects of interbreeding between released hatchery components and wild-population components in admixed populations (i.e., the introgression and spread of hatchery alleles into wild components, changes in allele frequencies possibly due to selection on specific population components, declines in proportions of heterozygotes due to outbreeding or of particular genotypes due to decreased fitness in some population component) (Jørstad et al., 1999);
5. monitoring changes in the genetic diversity of wild-population components and in the population genetic structure of enhanced species;
6. estimating changes in N_e of admixed populations due to introduction of hatchery broods and interbreeding between population components in the admixed populations;
7. adjusting breeding and stocking protocols to maintain the genetic diversity and N_e values of admixed populations at desired levels (e.g., similarly to the values of the recipient populations before enhancement) and to avoid swamping the admixed populations with hatchery alleles, particularly when stocking continues over generations.

The level of precision required for monitoring some genetic aspects of stock enhancement and determining the success of stock enhancement programs requires the use of high-resolution genetic tags. For each genetic monitoring program, the degree of specificity of each marker (e.g., allele, banding pattern) can be ascertained by assaying numerous individuals in an appropriate group (e.g., recipient population, species) for the genetic entity (e.g., locus) containing the marker and calculating the probability of unambiguously distinguishing a single individual in that group using the marker. A subset of the individuals assayed in the baseline population genetics study may be used for this assay. From this preliminary assay for potential genetic tag markers, the specific set of genetic entities (e.g., loci, DNA fragments) needed to achieve a desired level of certainty in identification (i.e., the genetic tag) can be determined. Typically, the broodstocks are analyzed only for these loci.

If broodstocks are composed of individuals chosen randomly from breeding populations, all should be assayed for the genetic tag markers. If broodstock selection is based on predetermined ideas of genetic diversity levels that need to be maintained in the hatchery broods, the broodstock candidates are assayed for the genetic tag markers and then breeding groups with known genetic-tag genotypes are assembled. (In this case, care must be taken to avoid purposefully selecting for specific alleles.) The genetic data obtained for the broodstock provides information needed for the following monitoring components:

1. estimating genetic diversity measures and N_e of the broodstock;
2. checking for inbreeding or outbreeding potential in the broodstock;
3. estimating broodstock gamete contribution to the broods.

Genetic assessments of the broods can be made using the same loci as employed in the baseline wild-population genetics study as well as the genetic tag loci. Both assays will provide information useful for evaluating genetic effects on the admixed population, but the genetic tag assay will enable far more detailed analysis of both the effects and success of the stock enhancement endeavor. The data obtained from these studies provides information needed for the following genetic monitoring components:

1. determining parental contribution in the hatchery (broods must be analyzed because hatchery managers cannot ensure completely equal gamete contribution to the broods by all members of the broodstock);
2. estimating genetic diversity measures of the broods, for comparisons with appropriate wild-population values (the wild component of the admixed population, the recipient population prior to enhancement, regional population values, or the species);
3. estimating N_e of the broods, for comparison with the recipient population and, after each brood release, with the wild-population component; if needed, also for adjustment in breeding or release strategies to compensate for differences between the brood N_e and admixed-population or wild-component N_e;
4. checking for indications of genotype-specific selection in the hatchery or in the admixed population; i.e., checking for directional changes in allele or genotype frequencies in the broods prior to release or in population components after release (in the hatchery, this requires periodically assaying the broods during the entire rearing interval; in the wild, this requires intermittently assaying the population components);
5. tracking survival and dispersal of broods or brood individuals after their release;
6. determining the contribution of brood animals (e.g., percentage of individuals) to the recipient populations and regional wild populations.

Genetic assessments of admixed populations should be done periodically. These assessments require knowledge of the population genetics of the native populations, and particularly the appropriate recipient populations, prior to stock enhancement. This aspect of the genetic monitoring program provides information for the following:

1. estimating the genetic diversity and N_e of the admixed population and the wild-population component;
2. estimating levels of interbreeding between hatchery and wild individuals and effects of that interbreeding on the genetic diversity and N_e of the wild-population component (e.g., checking for genetic swamping or evidence of a decrease in numbers of individuals in the wild component);
3. checking for evidence of selection operating to the detriment of wild populations or project goals and identifying the genotypes that are affected;
4. comparing performance characteristics of stocked individuals with those of the same wild-population cohort;
5. determining if the wild population is being altered demographically (e.g., if breeders or juveniles are decreasing in number);
6. tracking genetic introgression between wild individuals and released cultured animals over generations (with some decay factor related to the inheritance patterns of the genes used);
7. determining whether project enhancement goals are being met and, if necessary, adjusting breeding and release strategies to attain those goals (e.g., Chakraborty and Leimar, 1987; Ryman and Laikre, 1991; Ryman et al., 1995; Tufto, 2001).

4.3. Example of a Stock Enhancement Genetic Monitoring Study

The estuarine and marine fish *Sciaenops ocellatus* (red drum) is one of the most important coastal sport fishes in the southeastern USA. In Florida, fishing pressure and environmental degradation have reduced the red drum population to a fraction of its former abundance. Years of state and federal regulations did little to replenish numbers of red drum. In the early 1990s, stock enhancement was chosen as a management tool for replenishing red drum in Florida. The Florida Fish and Wildlife Conservation Commission's (FWC's) Fish and Wildlife Research Institute (FWRI; formerly the Florida Marine Research Institute) developed a long-term hatchery-based stock enhancement program for this species. Red drum stock enhancement was first attempted in Biscayne Bay, located in southeastern Florida. Fishery catches of red drum had been extremely low for years; problems with juvenile recruitment were thought to be the cause (Crawford, 2000). Red drum in Tampa Bay, west-central Florida, were also in low and declining abundance. That stock was thought to be only about 5% of its original, unfished abundance and was thought to be reproductively unviable (Murphy and Crabtree, 2001). A large, lengthy stock enhancement project (Project Tampa Bay) was later planned for that area.

FWRI genetics staff is responsible for genetic monitoring of FWC's red drum stock enhancement program. They initiated development of a study for genetic monitoring of FWRI stock enhancement during a transition period when the Biscayne Bay stock enhancement project was ending and Project Tampa Bay was starting. The genetic monitoring study was composed of two distinct investigations:

1. A biochemical genetic (allozyme loci) investigation, which included two components: (1) a survey of the genetic diversity and genetic population structure of wild red drum throughout the species' range in the southeastern USA and (2) an assessment of the genetic effects resulting from the breeding and rearing practices used in the FWRI hatchery to produce juvenile red drum for stock enhancement.
2. A molecular genetics investigation (mtDNA + microsatellite DNA), which was much larger and broader in scope. This investigation has had many interconnected components, which, together, were designed to monitor for the presence of a broad spectrum of genetic effects on genetic diversity, fitness, and N_e in hatchery populations and in the recipient population. This investigation also enabled FWRI geneticists to advise FWRI hatchery staff on genetically sound broodstock selection and breeding practices.

The biochemical genetics investigation has been completed. The molecular genetics investigatioin is ongoing but in its final stage.

Prior to and during the initiation of the genetic monitoring study, several surveys of red drum population genetics were conducted in the southeastern USA (reviewed in Gold et al., 2001), but sampling in Florida was sparse in all of them. To better understand the population genetic structure of red drum in Florida, the FWRI genetics staff conducted detailed surveys of the population genetics of red drum in Florida. Because the initial FWRI work for stock enhancement monitoring was conducted using protein electrophoresis, one survey was conducted using that technique (Crawford, 2000). Because the FWRI genetics staff was examining the utility of mtDNA as a genetic tag for female red drum broodstock, another survey was conducted using that technique (Seyoum et al., 2000). These surveys provided baseline information about red drum natural genetic diversity and population structuring needed for comparisons with hatchery populations and admixed populations.

4.3.1. Biochemical genetics investigation

Samples for the baseline red drum population allozyme survey were obtained between 1992 and 1996. Tissues from 460 red drum were collected from 13 sampling locations distributed throughout Florida nearshore waters and 1 location offshore from Charleston, South Carolina. The tissues were surveyed for 26 proteins coded for by 35 loci. At a number of locations, multiple samples were collected in different years. Overall, samples collected from the same locations in different years were similar in all measures of genetic diversity, as were samples from different locations collected in the same year. In addition, gene flow among the populations and over time was sufficiently high to homogenize populations. Thus, all Florida red drum belonged to a single genetic population with regard to loci coding for allozymes (Crawford, 2000). Therefore, all samples except the South Carolina sample were combined and the data were reanalyzed to obtain values for estimators of genetic diversity and gene flow in wild red drum from Florida waters.

Crawford (2000) examined FWRI hatchery broodstocks from Biscayne Bay and their broods for the following:

1. evidence of selection during the brood rearing process;
2. differences in genetic diversity among the broods and between the broods and wild red drum (as defined by the values calculated for genetic diversity measures in the baseline red drum population genetics survey);
3. contributions of broodstock individuals to the broods;
4. variation among breeding groups in the effective number of breeders (N_{eb}) that produced the broods.

The typical breeding strategy in the FWRI hatchery was as follows. Red drum broodstocks, collected from the wild and verified for reproductive maturity, were divided into breeding groups of 6 or 7 fish in approximately a 1:1 sex ratio. One to several broods from each breeding group were reared for stock enhancement, and some breeders were used in more than one breeding group. Spawning in red drum is nocturnal, broadcast, coordinated among individuals in breeding groups, and complicated by breeding behavior that is poorly understood. Therefore, the contribution of each parent to a particular brood cannot be ascertained by observation.

The broods used in this investigation were spawned during the spring and fall seasons in 1994. The 7 spring broods were produced by a single breeding group of 6 fish. The 13 fall broods were produced by 4 different breeding groups composed of at least 6 fish per breeding group; a total of 29 fish produced the fall broods. However, 2 of the females had also been used to produce the spring broods. The broods were reared in the hatchery for 7 to 23 weeks. For the genetic analyses, 12 samples of juveniles were collected from the spring broods and 38 samples were collected from the fall broods. Samples composed of at least 15 juveniles were collected at 2- to 3-week intervals. The first sample of juveniles was collected approximately 3 weeks after the brood was spawned; the last sample was collected within the week before the broods were released. The 9 allozyme loci used for the analyses were those that had the highest levels of polymorphism, the clearest electrophoretic resolution, and the best conformation to Hardy–Weinberg genotype frequency expectations in the population genetics survey of wild red drum.

Hatchery induced selection was not apparent in the broods; no brood exhibited clear directional changes in alleles frequencies at any locus. Therefore, all samples of each brood were grouped for all analyses.

Both genetic diversity components were compared between the hatchery broods and between the broods and wild red drum. Genetic variability was measured as H_o, N_a, and P_{100}; genetic composition was measured as allele frequencies.[4] Many estimates of genetic variability differed significantly among broods, even within seasons. Nearly all genetic variability estimates were significantly lower in hatchery broods compared with wild red drum. Because the individual broods from within a season were usually combined just prior to release, Crawford (2000) grouped within-season samples and recalculated genetic diversity measures. This allowed him to examine the effects of using different numbers of parents (6 vs. 19) on the genetic diversity of the broods. Most measures of genetic variability in the broods produced by 6 breeders were significantly lower than those in broods produced by 19 breeders. Genetic variability measures for both brood groups were lower (usually significantly) than those measures for wild red drum. Because all broods produced in 1994 constituted a single year-class contribution to the local red drum population, the broods could be grouped into a single brood population and the measures of genetic diversity recalculated and compared with those of wild red drum. Genetic variability was lower in the brood population than in wild red drum, but brood-population measures of genetic variation were more similar to those of wild red drum than were the measures of less inclusive brood groups.

At all hierarchical grouping levels, allele frequencies differed significantly among the broods and between the broods and wild red drum at several highly polymorphic loci. Some alleles that were rare in wild red drum occurred in high frequencies in some hatchery broods and other rare alleles present in wild red drum were absent from broods reared in the hatchery. Differences between the brood population and wild red drum in allele frequencies at one locus were particularly pronounced.

Crawford (2000) estimated the minimal pedigree for each brood (fewest broodstock individuals with genotypes that contained only alleles found in the brood) by examining the genotypic complement of the brood and the broodstock that produced it. Although 6 or 7 breeders were available to contribute gametes to each brood, apparently in no case did all breeders in a breeding group contribute to a brood. The minimum number of breeders needed to produce any brood ranged from 2 to 4. In addition, brood allele frequencies suggested that proportional gamete contribution of breeders to the broods differed among breeders. Proportional contribution of breeders that contributed to more than one brood differed among those broods. Because of limitations in the data, the only reasonable estimate of N_{eb} (6) was for the entire 1994 brood population.

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[4] Of the three standard measures of genetic variability, average number of alleles in a population (N_a) and percent of loci that are polymorphic in the population (P) are considered to be better indicators of genetic variability than is average percentage of individuals that are heterozygous in the population (H_o) (Hartl and Clark, 1997). Despite a loss of alleles, H_o may not differ between the hatchery broodstock and recipient wild population because the remaining uncommon or rare alleles are higher in frequency (see e.g., Ferguson et al., 1993; Taniguchi et al., 1997) or because the loss of low-frequency alleles has little effect on H_o (Tessier et al., 1997).

Crawford (2000) noted that limitations in the hatchery facility and the large size of adult red drum were important factors in designing the breeding strategy for red drum stock enhancement. He also observed that the breeding strategy was limited in its ability to approximate the genetic diversity of wild red drum. However, this limitation could be partially compensated by combining numerous broods spawned from multiple broodstocks and releasing those broods such that they formed a single year-class. To maximize N_{eb} in this type of breeding strategy, broodstock individuals should be used in only one breeding group and the number of broods produced by each breeding group should be limited to as few as possible (only 1 is preferable).

4.3.2. Molecular genetics investigation

Project Tampa Bay was divided into a research phase and a production phase (c.f., Blankenship and Leber, 1995). The research phase was designed to examine the influences of location of release, season of release, and size of release on the short-term and long-term survival of hatchery-reared red drum stocked into Tampa Bay. From this work, production-phase release conditions could be developed to maximize the probability of hatchery fish survival to adulthood. These fish could then contribute to the local red drum breeding population and to the fishery. Bert et al. (2003) provide a detailed description of Project Tampa Bay. The project has involved five separate but integrated research and monitoring staffs at FWRI; the fisheries enhancement staff at Mote Marine Laboratory, a local non-profit marine laboratory; and the recreational fishers who fish in and near Tampa Bay. Bert et al. (2003) describe the tasks performed by the staffs of FWRI and Mote Marine Laboratory, the interactions among those groups, and the cooperation between those groups and the fishers that were needed to execute the enhancement project, particularly the genetic monitoring investigation.

Hatchery-reared juvenile red drum were stocked at two different times of the year (the natural fall recruitment time and that time offset by 6 months). Three size classes of fish (Phase 1: 25–45 mm standard length [SL], Phase 2: 65–110 mm SL, and Phase 3: >135 mm SL) were released at four locations along a salinity gradient in the estuarine regions of two rivers that flowed into Tampa Bay. All fish in the two larger size classes were coded-wire tagged; fish in the smallest size class were not physically tagged. Parts or all of this release protocol were repeated for five years (2000–2004).

The FWRI genetics laboratory staff has relied on the staffs of the five other research groups participating in Project Tampa Bay to provide them with tissue samples (fin clips from most fish or whole fish when specimens are very small). During the enhancement period, FWRI Fisheries Stock Enhancement staff, who were responsible for all aspects of hatchery breeding and rearing, provided fin clips from all broodstock fish and from all broods soon after hatching, shortly before release, and, usually, also at 2–3 week intervals during the rearing period. In each of the first three years of Project Tampa Bay, FWRI

Fisheries Independent Monitoring staff collected young-of-the-year wild red drum samples from selected stations throughout Tampa Bay prior to the stocking at the time of natural recruitment ($N \approx 250$ per sampling event). During and after the years in which fish were released, Fisheries Independent Monitoring staff and Mote Marine Laboratory staff regularly (semiweekly or monthly, depending on location) collected tissue samples from the admixed population at numerous stations throughout Tampa Bay and in the rivers where the releases occurred (up to 50 individuals per station; average N per year $\approx$ 1000). These two staffs also conducted special collecting trips for red drum in the subadult size classes poorly represented in other sampling efforts. Fisheries Independent Monitoring staff will continue routine sampling for subadult and adult red drum at least through 2007. During the years of enhancement, the FWRI Aquatic Health Group also contributed brood fish after they examined them for diseases and parasites. Fish identified by coded-wire tags were not sampled for genetic analysis in any of these sampling efforts.

Since 2002, both Fisheries Dependent Monitoring staff and Mote Marine Laboratory staff have routinely collected fin clips from red drum captured by recreational fishers. To increase the number of these tissue samples, Mote Marine Laboratory staff initiated an extensive advertising campaign to inform recreational fishers about Project Tampa Bay and encourage them to participate in the project by contributing fin clips from the red drum they catch. Fin clips from recreational fishers are among the most valuable because they provide clear evidence of the Project Tampa Bay's contribution to the fishery. Collection of red drum samples from recreational fishers by the Fisheries Dependent Monitoring staff and Mote Marine Laboratory staff continues today and will continue through 2008. The number of individuals genetically analyzed per year for all samples of larger size classes of red drum plus, during stock enhancement, potential broodstock fish has ranged from approximately 2000 to 4500.

Initially, female broodstock and all post-enhancement samples were analyzed for a 419 nucleotide-base-pair (bp) portion of the mtDNA control region plus nine microsatellite DNA loci because the genetics staff did not yet know if, together, the microsatellite DNA loci alone were sufficiently variable to serve as a genetic tag.[5] The mtDNA population genetics survey (Seyoum et al., 2000) provided information on the genetic diversity needed to decide whether the targeted portion of the control region contained sufficient unique genetic variability to continue including it as a component of the genetic tag. Tissue samples for this survey were obtained from 209 red drum collected between 1992 and 1997 from eight sampling locations distributed throughout Florida

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[5] Early in the stock enhancement project, female red drum with rare or unique mtDNA haplotypes were selected for use as broodstock, but males were randomly chosen (see Bert et al., 2003). In addition, sometimes more broodstock fish were collected than were actually used as breeders in breeding groups; all fish in the broodstock were analyzed for the genetic tag loci.

nearshore waters and three locations in the nearshore waters off other states in the southeastern USA. These tissues were analyzed for a portion of the control region that was contained in the genetic tag. The 209 individuals analyzed had 134 different haplotypes; 54 individuals had unique haplotypes. FWRI genetics staff decided that this level of genetic variability was insufficient for increasing the specificity of the genetic tag. Therefore, the mtDNA segment and one problematic microsatellite DNA locus were dropped from the analysis, leaving an 8-locus microsatellite DNA genetic tag that could be used for both sexes.

All fish are assayed for the 8-locus tag in two phases. Each tissue sample is first screened for four loci, which are assayed in a single multiplexed analysis. If all alleles at those loci are consistent with alleles of potential broodstock parents, the sample is analyzed for the remaining four loci. If all alleles at those loci are compatible with those of potential broodstock parents, the probability that both parents were members of the hatchery broodstock is calculated and a check to see if the two parents were indeed members of the same breeding group is performed. Brood fish can be distinguished from wild fish with an average error probability of approximately 1×10^{-5}. The brood from which the fish came and the parents of each fish can be identified with an average error probability of approximately 1×10^{-6}.

These samples can be processed by two genetics technicians, one full-time and one half-time, using a 96-well PCR machine and an ABI 310® DNA analyzer. The average cost per sample for the routine, microsatellite-DNA-based laboratory analysis, after the initial exploratory phase to develop the genetic tag and including salary, chemicals, expendable supplies, and laboratory maintenance charges is less than $5.00 US per sample. Facilities that specialize in analyzing DNA samples could be utilized for the laboratory analysis. These facilities can process DNA very expeditiously and cheaply (approximately $2.00 US per sample).

Nearly 1,586,000 red drum juveniles were released during the enhancement period—approximately 1,340,000 in the Phase 1 size class, 174,000 in Phase 2, and 72,000 in Phase 3. From fall 2000 through spring 2006, the genetics laboratory staff processed approximately 21,300 red drum tissues and identified approximately 10% as brood fish. By far the greatest fraction of those was composed of fish in the smallest size class; most of those fish were captured near the release sites within a few weeks of release. More recently, sampling and analysis have focused on fish in the large-sized size classes that the released fish now occupy. All fin clips analyzed are either from fish captured by recreational fishers or fish captured by Fisheries Independent Monitoring staff. That staff has analyzed the data on the red drum ≥20 cm that they captured through June 2006. Although recovery percentages of fish released in the three size classes are very small (0.01%, 0.01%, and 0.09%, for Phase 1, Phase 2, and Phase 3, respectively), preliminary information potentially valuable for the production phase of Project Tampa Bay (c.f., Blankenship and Leber, 1995) has been obtained. Based on proportions recaptured, the contribution of the broods to the red drum admixed population in Tampa Bay differed significantly among broods, seasons, and locations. Fish released during the natural recruitment season in the area of the river that they would normally occupy as wild fish (e.g., up-river for Phase 1 fish, mid-river for Phase 2 fish, near the mouth of the river for Phase 3 fish) have higher probabilities of long-term survival than fish released elsewhere and at other times of the year, and fish in the Phase III size class are nine times more likely to survive to subadult or adult sizes than smaller fish (B. Winner and M. Tringali, FWRI, personal communication). Thus, although this molecular genetics investigation may seem to yield a minimal return for the effort involved, it has provided the critical information needed to plan the release strategy for the production phase of Project Tampa Bay.

The long-range objectives of the molecular genetic investigation are to estimate the short- and long-term survival of the stocked fish, the contributions of these fish to the local red drum breeding population and fishery, and the genetic effects of these fish on wild red drum populations. The background information needed for the maintenance of genetic diversity and N_e in the hatchery population during the breeding and rearing process and the initial contribution of the hatchery broods to the Tampa Bay red drum population can be obtained from the genetics data collected thus far. Specifically, the staff can do the following:

1. document the genetic diversity, N_e, and level of relatedness for each young-of-the-year cohort in the wild population; determine the changes in these factors among cohorts over years;
2. determine the contribution of each broodstock fish to each brood;
3. determine the genetic diversities and N_es of the broodstocks and the broods;
4. check for evidence of selection in the broods during the hatchery rearing process;
5. estimate the levels of relatedness and kinship associations within and among hatchery broods;
6. ascertain the uniqueness of the genetic-tag genotype in each brood fish compared with the genetic-tag genotypes of wild red drum populations;
7. estimate the proportion of hatchery fish from each brood in the admixed population at various times after their release and at various distances from the release sites;
8. initiate the monitoring of the long-term genetic effect of Project Tampa Bay on the genetic diversity of the wild red drum population;
9. search for evidence of interbreeding between wild fish and brood fish;
10. estimate the rate of coded-wire tag loss or failure of detection (coded-wire-tag scanners or their operators fail to detect the tags in some red drum; these individuals can be identified as hatchery fish because they are listed in the database by both their coded-wire-tag numbers and genetic-tag genotypes).

Sufficient data is now accumulating to begin the process of understanding dispersal patterns, estimating long-term survival, estimating reproductive and fisheries contributions of hatchery red drum, and calculating N_es of the admixed red drum population and its wild-population component. Advances in the statistics for identifying hatchery fish in the wild (Tringali, 2006) and for determining relatedness and N_e (specifically N_{eI}, the inbreeding effective number) in hatchery broods will enhance the accuracy of estimating and predicting the genetic effects of Project Tampa Bay on wild red drum.

5. CONCLUSIONS

A principal goal of stock enhancement of fish and other aquatic animals, as defined in this chapter, is to increase the probability that a population is self-sustaining over generations because the population is valuable as a source of food, economic gain, or esthetic (e.g., conservation) interest (Marte, 2003). When coupled with habitat restoration and other conservation practices, stock enhancement can lead to increased fishery production and restore harvestable stocks. Stock enhancement can also accelerate recovery of depleted or threatened populations of imperiled species of national or international interest (Primavera et al., 2006); and change or restore animal community structure (Hulett and Leider, 1993; Guzman and Guevara, 1998; Bartley, 1999; Iglesias et al., 2003; Mustafa, 2003). Although stock enhancement is an attractive method of increasing fishery production, numerous experts have cautioned that it should not be employed until after other measures to supplement the population, such as habitat restoration, protection of spawning stocks, and improved fishery management (Meffe, 1992; Hansen and Youngson, 1998; Mires, 1999), have failed. It may be far easier and less costly to prevent overfishing (see Jackson et al., 2001) or to restore or create new critical habitats than to execute a stock enhancement program. For example, protection of breeding and nursery grounds can be improved or artificial reefs and other habitat structures can be installed (Mustafa, 2003). At the least, stock enhancement should be used in combination with other conservation measures (Waples and Do, 1994; Waples and Drake, 2004) and used principally when it could considerably speed up replenishment (Bell and Warwick, 2004). Conserving wild stocks is safer than augmenting those stocks through hatchery-based stock enhancement because the success of any supplementation program cannot be predicted. All hatchery-based stock enhancement has some level of risk for disease introduction, ecological damage to local ecosystems, and genetic diversity alteration.

Regardless of the purpose for stock enhancement, the hope in any stock enhancement effort is that, on a sustainable basis, the admixed population will form a larger, more viable population than previously existed and that no genetic or ecological effects will occur. Interbreeding between hatchery and wild individuals is an objective of stock enhancement, but it should not compromise the genetic integrity and diversity of wild-population components in admixed populations (Iglesias et al., 2003). Care must be taken to maintain levels of genetic diversity in admixed populations that are comparable to those of viable wild conspecific populations (Tringali and Bert, 1998). This can be done through genetically sound broodstock selection, breeding strategies, and stocking regimes that are based on knowledge of the genetic population structure of the species, the genetic diversity and geographical extent of the recipient population, and the genetic diversity of the hatchery population.

Despite abundant evidence for genetic effects associated with brood production in the hatchery and the release of broods into the wild, the importance of including genetic monitoring in stock enhancement programs is not widely accepted. For example, Hansen et al. (1998) questioned whether genetic concerns related to stock enhancement were more theoretical than real. Harrell (2002) questioned whether genetic effects from stocking are more severe than genetic effects from natural genetic load or from anthropogenic changes in natural environments. Miller and Walters (2004) believe that fears of genetic effects when stocking fish are generally unsupported by data because we know little about the ecological significance of genetic differences. Laurec (1999) asserted that it would be unwise to block any stock enhancement attempt because of potential genetic problems.

If the decision has been made to use stock enhancement as a tool for bolstering populations, good genetic management should be an integral part of the stock enhancement effort. Indeed, if other problems (e.g., disease, lack of suitable habitat) can be resolved, well-managed stock enhancement programs can conserve or even enhance components of genetic diversity, particularly genetic variability (Toro et al., 1999; English et al., 2000; Wang and Hill, 2000; Doyl et al., 2001; Fernández and Caballero, 2001) and especially when applied to severely depleted populations (Doyl et al., 1991; Johnson, 2002; Hedgecock and Coykendall, 2007). Genetic management can be accomplished by following these guidelines:

1. Monitor the stock enhancement program using genetics. Any genetic monitoring is better than no genetic monitoring. Use the most appropriate biochemical genetic or molecular genetic tools for the needed evaluations (Liao et al., 2003).
    a. Understand the genetic diversities, genetic population structures, and N_es of recipient populations and other relevant populations or species prior to initiating stock enhancement efforts for those species.
    b. During stock enhancement, monitor the broodstocks and, if applicable, the breeding groups and monitor the broods both before and after their release into recipient populations.
    c. During and after release of broods into recipient populations, monitor those populations; also monitor any other populations or species that might be affected by the stock enhancement program.
2. Maintain genetic diversity in broodstocks. The genetic diversity of broods depends on the genetic diversity of the broodstocks and the breeding strategies used to produce those broods.

   a. Avoid outbreeding by obtaining broodstock individuals from recipient populations or genetically similar groups of populations.
   b. Assemble broodstocks composed of individuals that collectively encompass a suitable range of the genetic variation available in their recipient wild populations (Waples and Drake, 2004). If possible, obtain broodstocks from multiple locations within the ranges of their recipient populations and over appropriate ranges of time, including the entire breeding and spawning seasons.
   c. Keep numbers of breeders in breeding groups as high as possible (Cross, 1999; Asahida et al., 2003). Monitor the contribution of each breeder to each brood. For uncontrolled breeding (e.g., night spawning), know the breeding strategy of the species as well as possible and work to compensate for unequal gamete contribution among individuals in breeding groups.
   d. Avoid the production of inbred broods (see e.g., Bartley et al., 1995; Toro et al., 1999; Wang and Hill, 2000; Bert and Tringali, 2001; Fernández and Caballero, 2001) by regularly infusing broodstocks with local individuals collected from the wild (Sbordoni et al., 1986, 1987; Bert and Tringali, 2001; Reisenbichler et al., 2004) or using new broodstocks at regular intervals not to exceed a generation.
3. Maintain genetic diversity and fitness in broods. Differences in fitness among hatchery brood genotypes may cause numerous genetic problems after release of the broods into recipient populations. Fitness differences can also negatively affect hatchery production and result in failure to meet production goals and increased cost-per-individual during the hatchery rearing period.
   a. Avoid selection of any type in the broods.
   b. Minimize domestication of the hatchery broods (Waples and Drake, 2004). Within the limits of capability, structure the hatchery environment to resemble the wild environment into which the broods will be released (e.g., rear in water into which they will be released, using the same salinity/temperature regimes).
4. Maintain N_e in hatchery populations and in admixed populations, including the wild components of admixed populations and, if applicable, in more inclusive groups such as the species (e.g., Waples, 1989, 1990a, b; Ryman and Laikre, 1991; Jorde and Ryman, 1996; Miller and Kapuscinski, 1997; Laikre et al., 1998; Tringali and Leber, 1999; Bert and Tringali, 2001; Hedgecock and Coykendall, 2007).
   a. Develop breeding protocols to maximize the N_es of the breeding groups (Blankenship and Kern, 2004). These N_es will be related to the genetic diversities and the N_es of the recipient populations. General guidelines suggest that an N_e of 50 is essential to minimize inbreeding effects and an N_e of 500 is needed to maintain adaptive genetic variation in wild populations (Rieman and Allendorf, 2001). These numbers apply also to

admixed populations, and may be lower than needed to maintain viable supplemented populations. Limitations of hatchery facilities may restrict broodstock size, but there are ways to compensate for this limitation (e.g., Bert and Tringali, 2001).

   b. Avoid depleting wild broodstocks to support hatchery breeding programs (Waples, 1991).
   c. Avoid introducing broods of limited genetic diversity or reduced fitness compared with the recipient populations.
   d. Avoid introducing brood individuals in numbers that could adversely affect the N_es of the recipient populations.

5. Set limits on the amount of genetic alteration in admixed populations and their population components that is tolerable. The genetic diversities of admixed populations are at least somewhat different than those of the wild populations prior to enhancement. Thus, except for isolated populations, stock enhancement can change the evolutionary dynamics of the admixed population and, therefore, interactions resulting from interactions between enhanced populations and other populations, in unpredictable and irreversible ways (Waples and Drake, 2004).

Because stock enhancement is increasingly practiced to mitigate for reductions in abundance of aquatic organisms due to overfishing, habitat loss, and pollution, it has the potential to be of considerable long-term importance in shaping the genetic diversities and population structures of freshwater and, increasingly, marine organisms. Because genetic diversity and its hierarchical organization within species can influence the sustainability of that species, stock enhancement practiced today can have implications over ecological and evolutionary time scales. Thus, the responsibility to conduct stock enhancement in a genetically and ecologically responsible manner is great. Conducting stock enhancement without paying attention to the genetic effects that the hatchery animals will have on wild populations, their surrounding communities, and the ecosystems in which they live is simply no longer an option.

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SECTION THREE

CASE STUDIES

CHAPTER 9

ENVIRONMENTAL IMPACTS IN AUSTRALIAN AQUACULTURE

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Abstract: Australian aquaculture consists of traditional salmonid and native oyster industries and a wide array of rapidly emerging new sectors. Consistency in the regulatory framework and controls administered by the various states to minimize potential environmental impacts from aquaculture is increasingly promoted in a national approach. The most apparent and significant environmental impacts arising from Australian aquaculture to date have occurred because some species associated with aquaculture activities have been translocated. The resultant impacts have included reduction or loss of native or endemic species to catchments and introduction of a range of pests and diseases. The latter, in some instance, has led to the abandonment of large areas of aquaculture infrastructure that were no longer viable. Impacts from pollution and infrastructure in aquaculture vary from contribution to overall nutrient load within a catchment to demonstrable localized impacts on fauna or flora, environmental morphology, and aesthetics. Here, a range of examples is examined and strategies to minimize risk of the impacts are discussed.

Key words: Australia, aquaculture, environment, management plans, oysters, policy, site selection, translocation

1. INTRODUCTION

Australia is a Southern Hemisphere, dry, island continent that has an area of approximately 7.7 million square kilometers. Its coastline of 36 thousand kilometers stretches latitudinally 4 thousand kilometers, from 44°S to 10°S. In the late 18th century, European settlement commenced in Australia; this opened the country to systematic and widespread contact with other countries and to the introduction of both native- and alien-species aquaculture.

Theresa M. Bert (ed.), Ecological and Genetic Implications of Aquaculture Activities, 177–189.

Aquaculture in Australia dates back to the establishment of the New South Wales (NSW) oyster industry in the 1860s. So serious did the indiscriminate gathering of oysters become along the NSW coast that the Oyster Fisheries Act was established by Parliament in 1884. This regulated the gathering of oysters and the leasing of beds and penalized the burning of live oysters for lime. The introduction of salmonids to Australia and the aquaculture of this species for stocking in streams also commenced around this time. Aquaculture in Australia has continued to expand in terms of species, area, value, and other performance measures (Allan, 1999). The Australian aquaculture industry now encompasses a diverse range of native and alien species farmed under various management systems and across temperate and tropical regions.

There is considerable difficulty in establishing causality and quantifying impact in the aquatic environment, particularly in ecological investigations where the possibilities for experimental design involving adequate controls and replications can rarely be achieved. Nonetheless, the efforts expended in quantifying and assessing impacts in Australian aquaculture-related environmental research are significant (Preston, 2000). In this paper, I examine environmental issues of concern (ecological, genetic, and disease-related) and associated with a range of Australian aquaculture industries. These are summarized in Table 1. Clearly these issues are similar to those in many other

Table 1. Summary of environmental impacts and associated responses resulting from aquaculture activities in Australia. NSW = New South Wales

Impact type	Case	Impacts	History	Response
Translocation of primary species	Carp	Opportunistic colonizer; reduction in aquatic plants and deterioration of water quality	Late 1800s—introduction into Australia; 1960s—vigorous hybrids escaped and spread	Multifaceted fish restoration and recovery programs
	Pacific oyster	Overran Sydney rock-oyster crops at major nursery site, resulting in abandonment of leases	1937—introduction into Australia; 1984—illegal introduction to Port Stephens, NSW	Strict limitation in Pacific oyster culture; zoning controls for native oyster stock movement
Translocation of secondary species	Fish gill herpes virus	Caused mass pilchard mortalities; suspected to be an exotic disease source	1990s	Review and import risk-assessment process for fish products
	Marteilia sydneii	Infected Sydney rock oysters	<1970s	Restrictions in the movement of host aquaculture species outside established zones

(*Continued*)

Table 1. Summary of environmental impacts and associated responses resulting from aquaculture activities in Australia. NSW = New South Wales—cont'd.

Impact type	Case	Impacts	History	Response
	Epizootic haematopoietic necrosis	An iridovirus caused mortality in freshwater native finfish and trout	Suspected exotic origin; 1987—first reported	Zoning to control movement of stock within infected catchments
	Viral nervous necrosis	Known host is *Lates calcarife*; caused high mortality in juveniles, uncertain impact on other species	First reported 1990	Strict translocation requirements and testing protocols for hatchery fry; quarantine of culture water
Site location	Abandonment of shrimp farm	Built too low on tidal plane, resulted in exposure of acid sulfate soils and inability to manage pond bottoms	1980s	Minimum tidal plane elevation required for location of estuarine land-based farms
	Farming nonindigenous species	Generated escapement concerns for translocated stock	1990s—Implemented in NSW	Minimum elevation above flood height required; no location in natural waterways with zero catchment
Operational	Recurrent blue-green alga blooms	Due to land practices in inland rivers; led to operational policy requirements for nascent, native-species, freshwater, finfish aquaculture industry	1990s—Implemented in NSW	Zero discharge for inland saline and freshwater native fish farms; load limits and water reconditioning infrastructure
Pollution	Raphidophyte flagellate, *Chattonella marina,* bloom	Caused southern bluefin tuna (*Thunnus maccoyii*) losses	1996—Boston Bay, South Australia	Locational loading and monitoring protocols; research and development of better diets

countries. The demonstration of, or causal link to, adverse impact may not be clear in all of the circumstances cited. However, they have prompted policy-makers and industry to respond. Therefore, I also outline strategies that have been implemented to address some of these concerns.

2. TRANSLOCATION

Translocation (defined as the movement of species or strains outside of their native range [Pollard and Hutchings, 1990]) can be either for aquaculture or for stocking. The impacts of alien or introduced species on native fish and invertebrates are many and can include competition for food and space, hybridization, predation, habitat disturbance, loss of species diversity, and disease transmission. Translocation can be purposeful and sanctioned by government, as is currently the case with trout in many catchments. In other circumstances it may be illegal or accidental. To date, the most apparent impact of fish translocations in Australia has been the establishment of reproducing populations that resulted from the escape or release of a translocated species. In some case, this has been a population of the translocated (primary) organism, such as carp. In other instances it has been a secondary organism, usually a pest or disease vector, translocated unintentionally with the primary organism. There are increasing concerns over the potential for genetic impacts on wild fish populations as the availability of aquaculture stocks expands.

2.1. Primary Introduced-Species Impacts

The introduction of exotic fish species, particularly from Europe, was widely practiced during most of the period since European settlement. Some of these species were deliberately and repeatedly introduced into waterways. Others escaped from aquaculture facilities. Twenty of the freshwater fish species introduced into Australia are now naturalized in our river and lake systems (Roberts and Tilzey, 1997).

The most notorious species to date is the common carp (*Cyprinus carpio*). The carp, also referred to as European carp (probably due to stock origin), was introduced into the continent in the mid- to late-1800s (Wharton, 1979). However, its present distribution is the result of a rapid expansion following hybridization between two varieties of European carp. This interbreeding produced the vigorous Boolara Strain, named after the fish farm in Australia from which it escaped in the early 1960s (Koehn et al., 2000). The carp has spread rapidly to every state except the Northern Territory; almost certainly, recreational fishers have aided this dispersal (Roberts and Tilzey, 1997). Carp now constitute 80% of the total fish biomass in the Murray-Darling Basin, which covers over 1 million square kilometres in southeastern Australia (Gehrke et al., 1995). High biomass densities of carp have been associated with loss of native species; reduction in aquatic macrophyte abundance; and deterioration of water quality, particularly through elevated turbidity levels (Driver et al., 1997).

In 1937, a leading federal research agency first proposed the introduction of the Pacific oyster (*Crassostrea gigas*) into Australia to establish a new oyster industry in the cooler waters of southern Australian states. A number of introductions of Pacific oysters occurred between 1947 and 1970. NSW remained opposed to the introduction of Pacific oysters (Medcof and Wolf, 1975). Numbers of Pacific oysters in the wild in NSW remained low until 1985, when large numbers of Pacific oysters appeared suddenly at Port Stephens, which was the major nursery area for the NSW native oyster industry. It is suspected that the establishment of this alien population occurred as a result of a deliberate illegal introduction around August 1984 (Holliday and Nell, 1985). There is also some conjecture that this was a different strain from that previously detected in NSW, which may account for its vigor in colonization (J. Nell, NSW Fisheries, personal communication). By the end of the 1980s, this colonization by Pacific oysters was a major factor contributing to the neglect and abandonment of large areas of oyster cultivation in Port Stephens. Over time, these colonized areas became smothered in Pacific oysters, which provided a reservoir of broodstock for the rest of the Port, where they rapidly began to overrun Sydney rock-oyster crops.

In 1986, all live Pacific oysters in NSW waters were declared noxious fish. Control programs were established. During the next decade, the Port Stephens oyster industry, which produced the vast bulk of juvenile oysters for other estuaries in NSW, was decimated. Elsewhere, the oyster industry has had to undergo considerable restructuring and modification of its practices. The ramifications of this outbreak have been considerable for the NSW oyster industry, both politically and economically.

2.2. Secondary Introduced Species Impacts

The spread of pathogens along with the uncontrolled movements of live aquatic animals has been clearly associated with disease outbreaks and significant losses of aquaculture production and revenue, and a number of instances of exotic disease introductions associated with aquaculture have been documented in Australia. This includes goldfish ulcer disease, caused by *Aeromonas salmonicida*, which was apparently introduced with goldfish from Japan (Langdon, 1990) and whitespot, caused by *Icthyophthirius multifilis*, which was possibly introduced through salmonid imports in the 1930s and now affects numerous native species. Fish parasites such as the anchorworm (*Lernaea cyprinacea*) are believed to have been introduced with carp and are believed to have significant impacts on the recruitment of native fish (Brown, 1995). An iridovirus associated with the introduced redfin perch (*Perca fluviatilis*) was first reported in 1987 (Langdon and Humphrey, 1987). It subsequently impacted both native fish and introduced salmonids. Recent mass pilchard mortalities associated with a gill herpesvirus have been tentatively linked to an exotic source such as imported frozen pilchards used in the bait and aquaculture industries (Jones et al., 1997; Whittington et al., 1997).

Incidents such as these have resulted in quarantine zoning in affected catchments and prompted a recent review of, and the development of an import risk assessment process for, fish products (Higgins, 1996). Concerns regarding the movement of these and other aquatic disease agents (e.g., *Marteilia sydneii*, carried by Sydney rock oysters, and epizootic haematopoietic necrosis virus, carried by trout) within Australia have led to the development of a range of regulatory controls and protocols that restrict the movement of their host aquacultured species to established zones, the testing of hatchery fry for pathogens and parasites (e.g., *Lates calcarifer* for viral nervous necrosis and *Pinctada maxima* for perkinsosis), and the establishment of operational requirements related to the quarantine of culture water discharged from the facility (e.g., as for water used to culture *Lates calcarifer* in nonendemic areas).

2.3. Genetic Impacts

Genetic studies are revealing cryptic biodiversity in the form of population genetic structuring, such as the presence of races, stocks, subpopulations, and even new species, in the aquatic animals that are cultured in Australia. However, there is still no generally accepted view of the genetic risk posed by translocation in terms of levels of gene flow that may cause impacts and longer term potential evolutionary consequences (Lymbery et al., 2000).

Most native fish species under culture in Australia have not been subject to any effective breeding program and no doubt suffer from limited genetic variation and possible inbreeding depression in the populations that aquaculturists manage. As technology for fish breeding becomes more commercially widespread and aquaculture in nontraditional species begins to expand, there is an increasing need for genetic studies to provide both commercial benefits and protection of the environment. The increased availability of native fish stocks from hatcheries has led to the proliferation of farm dam stockings that often fall outside of normal regulatory control. Farm dams are considered high risk in terms of fish escapement. Although occasional small escapes from farms should have less drastic effects on the genetic constitution and biodiversity of wild populations of the same species, it is impossible to generalize. One area of concern is localities where healthy wild stocks of conspecifics do not occur, as is the case with a number of Australia's freshwater native fish such as "strains" of silver perch (*Bidyanus bidyanus*) in localities of the Murray-Darling Basin. Impacts may also be expected where there is a high degree of allogeneity, such as in Australian freshwater crayfish (Lawrence and Morrissy, 2000), and when vagility (dispersal ability) is low and fishing pressure and competition have led to the disappearance of stocks, such as in abalone. The increasing trend in the use of interspecific hybrids in Australian aquaculture is an area of further environmental risk, particularly when the hybrids are not completely sterile.

Aquaculture as a means of enhancing stocks is increasingly being applied in Australia either as a compensatory measure to offset fishing pressure and modification of freshwater environments (Rowland, 1995) or to assist in the recovery of vulnerable or threatened native species (conservation aquaculture; Anders, 1998). However, concerns regarding impacts on native genetic resources are increasing (e.g., Keenan and Salini, 1990; Musyl and Keenan, 1992) because hatchery stocks generated from single or limited nonnative broodstocks are distributed to natural habitats over wide geographic areas. In other countries, indigenous populations have lost their genetic integrity following successful introductions (e.g., Garcia-Marin et al., 1999). Clearly, there is a need to understand the genetic structure of wild fish populations where a native species is bred for aquaculture and stock enhancement. Preservation of different stocks should be maintained in the wild and, if possible, through broodstock programs ("gene banks").

Despite these problems, aquaculture can be one important component of multifaceted fish restoration and recovery programs. Such stock enhancement or restoration projects should include careful breeding programs with strict genetic management protocols that maximize the opportunity for recovery of diversity within the population of interest, such as that used for the endangered Australian eastern cod (*Maccullochella ikei*) (NSW Fisheries, 1999).

3. SITE LOCATION

Environmental impacts arising from inappropriate siting of aquaculture facilities in Australia are not widespread. However, siting is a critical planning issue. Examples of impacts resulting from inappropriate siting in Australian aquaculture include the following:

1. abandonment of inviable enterprises that were poorly located;
2. wetland destruction and exposure of acid sulfate soils in excavated shrimp aquaculture ponds located in some low-lying estuarine areas;
3. escapement of nonendemic fish from flood-prone aquaculture facilities;
4. eutrophication in poorly flushed embayments due to high loading in fish cages;
5. increased sediment deposition in hydrodynamically sensitive areas due to oyster lease infrastructure;
6. impacted seagrass beds due to shading by aquaculture infrastructure;
7. elevated levels of endemic disease and chemical release in areas subject to temperature-induced stress due to inappropriately located, land-based, salmonid facilities.

Operational and marketing considerations are important factors in determining the location of an aquaculture facility, but a high priority also must be given to the environmental characteristics of the location. The appropriate location of an aquaculture facility is one of the most effective environmental management tools available. Appropriate site selection can avoid or reduce many problems inherent to aquaculture and can also accomplish the following goals:

1. reduce the need for technically based environmental mitigation measures and costly ongoing management and monitoring measures;

2. substantially reduce costs of establishment and operation;
3. reduce levels of public scrutiny;
4. streamline approval processes;
5. fundamentally improve overall viability of the project.

4. OPERATIONAL IMPACTS

In global terms, Australia has a very low level of aquaculture production relative to the available coastal area. However, impacts arising from operational characteristics in aquaculture facilities range from destruction of habitat (for example the past use of mangrove trees for oyster cultivation), to poor disposal of waste, such as direct discharge of untreated effluent from intensive large-scale culture facilities. Much of the recent focus on the reduction of aquaculture impacts has been on the minimization of pollution.

The Atlantic salmon (*Salmo salar*) industry dates back to the 1960s, when a stock of the species was brought into NSW from Canada, initially for sport-fishing purposes. As the economic success of salmon farming in the southern state of Tasmania became clearer, more area was sought for the establishment of cages, and increased planning controls came into effect. These included controls on water flow and exchange rates, water depth, carrying capacity, and distance between farms. Farm monitoring requirements were also developed (McLoughlin, 1996).

The southern bluefin tuna (*Thunnus maccoyii*) industry is a more recent development based on open-water cage culture of wild-caught juveniles. In 1996, the site for this activity was a relatively shallow, low-wave-energy environment in Boston Bay, South Australia. That year, the tuna farms suffered sudden, severe (up to 75%) losses of fish. A bloom of the raphidophyte flagellate, *Chattonella marina,* has been implicated in the mortality (Hallegraeff et al., 1998; Munday and Hallegraeff, 1998). The tuna are fed frozen imported pilchards with a feed conversion ratio of approximately 17:1. This has raised concerns that the bloom may have been caused by waste products from the aquaculture industry itself (Parliament of South Australia, 2000).

Oyster-lease timbers have been traditionally treated with tar prior to installation in the estuary. The extent to which tar products could leach from posts or other structures has recently been investigated in a limited sampling effort for the presence of hydrocarbons in and around lease areas (Umwelt Pty. Ltd., 2000). This study was undertaken in preparation for the removal of over 600 hectares of derelict oyster-lease cultivation material in the Port Stephens estuary (described above). The majority of samples taken within the lease areas contained polyaromatic hydrocarbons at levels above the relevant trigger levels recommended for further investigation (ANZECC/ARMCANZ, 2000). The likely impacts (and duration) of this sediment contamination are uncertain. The habitat within the abandoned lease area was found to be comparable to other similar estuarine habitats, was relatively undisturbed, and provided good habitat for the types of organisms found within the specific areas (Umwelt Pty. Ltd., 2000). Currently, the aquaculture industry is increasingly utilizing recyclable plastic materials and phasing out tar products, which will diminish this potential source of contamination.

As intensive aquaculture continues to expand in Australia, an increasing emphasis has been placed on minimizing pollution. Planning policies that take advantage of experiences in aquaculture development abroad have been instigated. These policies clearly indicated the environmental performance objectives expected from the existing aquaculture industry as well as from new investors. These expectations include, for example, zero discharge for inland saline and freshwater native-fish farms, load limits and water reconditioning infrastructure requirements for estuarine farms (Stone et al., 2000), robust benthic monitoring programs (Underwood, 1994) for marine cages, and staged (trial) developments with review mechanisms where precautionary principles apply. These policies are designed to enable aquaculturists and authorities to minimize and evaluate impacts as the industry grows.

5. RESPONSE STRATEGIES

The nature of Australia's aquaculture industries makes translocation within jurisdictions and across jurisdictional boundaries necessary. This has led to the preparation of National Translocation Policy Guidelines (Ministerial Council on Forestry, Fisheries, and Aquaculture, 1999). These guidelines set out a risk assessment process for considering translocation policy issues. Some degree of risk is inevitable with trade in live aquatic animals. Consequently, policies and practices must operate within the concept of *minimizing* the risk of ecological, genetic, and disease incursion while, at the same time, avoiding imposition of unjustifiable or unnecessary impediments to trade, aquaculture development, and aquatic food production.

Knowledge of the health status of aquatic animal populations or stocks is an essential prerequisite for risk assessment of pathogen transfer. Thus, health certification and associated quarantine measures are integral parts of the overall health consideration process. The national surveillance program for aquatic animals is a structured plan for the detection of specified diseases in susceptible aquatic populations. This surveillance applies to detecting the emergence of a "new" disease situation, as well as to monitoring the status (prevalence, geographic distribution, etc.) of established disease agents. It forms part of the national aquatic animal health plan known as Aquaplan (Commonwealth of Australia, 1999). The plan consists of eight programs that cover international linkages; quarantine; surveillance, preparedness, and response arrangements; awareness; research and development; legislation, policies, and jurisdiction; and resources and funding.

Regional management plans for aquaculture continue to evolve. These plans are multidisciplinary in approach, incorporate principles contained in national translocation and aquatic health plans and in industry Codes of Practice, and have defined environmental performance indicators to assess the implementation of these plans. The upfront integration of commercial, infrastructure, environmental, and public-participation considerations into the process is at the core of this strategic planning initiative.

The most recent of these management plans (Stone et al., 2000), known as the NSW Sustainable Aquaculture Strategy (SAS), incorporates a project profile analysis utilizing three "sieves" to evaluate options and assess risk. These are the following:

1. minimum Performance Criteria for projects to be permissible;
2. site Selection (Tier 1 and Tier 2);
3. operational Selection (Tier 3).

The site selection criteria (Tier 1 and Tier 2) provide the first two environmental sieves to determine the acceptability of risks. Tier 1 information is available from Government or Council sources. This has been incorporated into a mapping process that can establish permissible land areas for aquaculture located adjacent to estuaries. In the process, Geographic Information System tools are used to undertake constraint analysis. Tier 2 information, obtained from specific site investigations, provides a risk assessment of the site attributes. Following the selection of a site, Tier 3 evaluation criteria, the third sieve, provide for the evaluation of various options including species, design-layout, and operation factors on a per-site basis. The Tier 3 evaluation can serve as a cost-effective device to determine the relative risks associated with species, design, and operational options and to assist decision-makers in determining if certain options should be excluded from further consideration. Clear performance review triggers have been established within SAS.

6. CONCLUSIONS

The rapid growth of aquaculture in Australia brings a demand for resources such as land, water, feed, energy, employment, and infrastructure. It has also brought an increased focus on evaluating its potential environmental impacts. Although the industry is quite diverse when measured in terms of species, geography, or other parameters, most of the potential environmental impacts arise from similar fundamental principles. While much of the initial concern in Australia has arisen from rapid and sometimes unsustainable aquaculture developments in other western Pacific countries, there are also important lessons to be learned from domestic experience in providing direction and planning in the growth of the industry. This can be equally important for the viability and long-term sustainability of the industry. Experience has demonstrated that environmentally conscious aquaculture and sustainable aquaculture are inextricably linked. Although the rapid evolution of technical knowledge in aquaculture can be translated into improved planning and management practices, it has also brought an increased complexity and level of uncertainty in policy development. Notwithstanding this paradox, it is the author's opinion that the ecological risks associated with mainstream aquaculture activities are substantially and increasingly being addressed in Australian aquaculture. A major challenge remains with management of the "edges" (farm dams, unauthorized stockings, live-fish trade, etc.) where regulatory control, resourcing, and environmental awareness are difficult to promote.

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CHAPTER 10

EFFECTS OF HATCHERY REARING ON ASIAN SEABASS, *LATES CALCARIFER*, IN SABAH, MALAYSIA

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Abstract: Asian seabass propagated in a hatchery showed some anomalies in development and morphological features. The mouths of 1% of the hatchlings did not open after 72 hours, although their yolks were completely exhausted. None of these fry survived beyond 75 hours. Two other distinct anatomical abnormalities occurred together: upward bending of the caudal fin and thickening at the base of the distal end of the second dorsal fin. The deformed caudal fins also differed from normal fins in the number of fin rays. These anomalies were probably linked to inbreeding and could have a genetic basis.

Key words: aquaculture, Asian seabass, environment, inbreeding, *Lates calcarifer*, Malaysia, morphological deformities

1. INTRODUCTION

The Asian seabass (*Lates calcarifer*, Centropomidae) is widely cultured in sea cages in Malaysia and other Southeast Asian countries. It is a high-value food fish that supports a growing aquaculture industry. The popularity of seabass stems from its fast growth and palatability. Because fishery harvests are low, most of the commercial supply comes from aquaculture. Obtaining wild broodstock is extremely difficult. For this reason, hatchery managers use the same stock for seed production over successive years and raise some of the progeny to maturity for broodstock when the parental stock nears senility. In addition, hatcheries depend on a limited number of breeders because broodstock maintenance is expensive and hatcheries frequently lack sufficient space for holding

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large broodstocks. All of these factors can contribute to an inbreeding problem in the cultured fish. The first report of the founder effects and inbreeding in hatchery stocks of Asian seabass in Malaysia was published by Ransangan et al. (1999). Preliminary studies on fitness traits demonstrated growth depression in hatchery Asian seabass (Ransangan and Mustafa, 1999) compared to wild conspecifics. Follow-up investigations were motivated by thought-provoking views presented by Bert and Tringali (2001).

Many problems such as poor physiological adaptation, slow growth, high mortality, low reproductive success, alterations in developmental processes, and morphological abnormalities have been reported in broods with reduced genetic diversity (Chilcote et al., 1986; Leider et al., 1990). In this paper, we present information on morphological abnormalities that may be the product of using successive generations of hatchery-spawned brood individuals as Asian seabass hatchery broodstock in Malaysia. The focus of our attention is on developmental anomalies at the time of first feeding and morphological deformities. We also highlight problems associated with determining the possible effects of interactions between escaped, hatchery Asian seabass, which may be depleted in genetic diversity, and wild Asian seabass in local waters and we suggest measures for overcoming them.

2. MATERIALS AND METHODS

Test specimens of Asian seabass larvae were obtained from a local hatchery maintained by Ko-Nelayan in Kota Kinabalu, Sabah (on the island of Borneo). They were produced by induced breeding of broodstock descended from a limited number of brood fish obtained in 1988 from a hatchery in the State of Johor in west Malaysia (on continental Malaysia). Thus, the hatchery is located approximately 1500 km (811 nautical miles) across the South China Sea in the Pacific Ocean. The Ko-Nelayan hatchery has been producing offspring from 11 broodstock groups, each composed of 4 males and 7 females. It is not known whether the managers of the source hatchery in Johor received their broodstock from another hatchery or collected them from the wild. We were informed that the specimens used in our observations represented the third hatchery generation. Although the hatchery has not maintained separate lines or records of mating among siblings or crossbreeding between adult progeny and parents, we do know that there was no exchange of broodstock among the local hatcheries.

Fry were obtained from two spawning tanks. Each batch was composed of 200 specimens. The fry were maintained in tanks, each containing 2000 liters of filtered seawater at 31‰ salinity. Observations commenced from the time hatching took place. Temperature and dissolved oxygen of the water varied in the range of 27–30°C and 5–7 mg/l, respectively. Stocking density of the hatchlings was 75–80 per liter. Seawater was partially replaced on a regular basis. On the third day after hatching of the Asian seabass, rotifers were supplied to them as food at the rate of 12 individuals per liter. The feeding regime was changed on day 9, when *Artemia* replaced the rotifers. From day 25 onward, the diet was composed of minced meat of trash fish at the rate of 5% of the average body weight, given once daily. Using a Nikon microscope model Eclipse E600, individual fry were periodically examined to determine the extent of yolk-sac absorption and morphological abnormalities.

In a separate evaluation, three lots of fry, each composed of 100 specimens that were the products of previous spawning events, were maintained in sea cages at the same hatchery and sampled periodically during their grow-out phase. Specimens showing anatomical abnormalities were separated for further investigations. The angle of orientation of the caudal fin of each fish was measured using a geometrical protractor and the number of its caudal fin rays was counted. In addition, throughout the study, the fish were checked for the presence of pathogens or other adverse circumstances.

3. RESULTS

No incidence of pathogens or other adverse circumstances were observed.

The hatchlings had prominent yolk sacs. Yolk consumption was quite fast, as evidenced by rapid decreases in the yolk-sac volumes. In every fish, the yolk sac was fully absorbed after about 72 hours. At about that time, the hatchlings began to eat rotifers. One percent of the hatchlings failed to open their mouths after 72 hours, but their yolk reserves were exhausted. These hatchlings did not survive beyond 75 hours.

Two distinct anatomical abnormalities (Figure 1), which occurred together, were seen in approximately 2–5% of the fish of the three batches examined. One of these abnormal features was upward bending of the caudal fin. When measured at right angles to the lateral axis of the fish, the entire caudal fin lobe was at an angle of 65–85°, with its median line at 75°. This was unlike the caudal fins of normal fish, which had an average median axis of 90° and an average angle of 80° in the upper half and 100° in the lower half. Furthermore, the number of caudal fin rays in the fish with the deformed fins consistently differed from the number in the normal fish; abnormal specimens had 17–19 whereas normal fish had 13–15. Yet another feature of the deformed fish was a thickening at the base of the distal end of the second dorsal fin compared with the normal fish.

4. DISCUSSION

Although the time of mouth formation and onset of first feeding are variable in Asian seabass, this usually occurs when the larvae are about 3 days old and the yolk has been completely absorbed (Tookwinas, 1989). In our study, about 1% of the larvae deviated from this normal sequence of events. Their mouths had not opened by the early hours of the fourth day. A nonfunctional mouth, an entirely depleted yolk sac, and an absence of food in the alimentary canals of the fish with

Figure 1. Anatomical abnormalities of third-generation Asian sea bass (*Lates calcarifer*) reared in an aquaculture environment. Top, example of a normal individual; bottom, example of a morphologically deformed individual. Note the upward bending of the caudal fin and body contour. In addition, the number of caudal fin rays in deformed fish was always higher than it was in the normal fish. See text for further description

closed mouths ruled out the possibility that they were feeding in any way. Balon (1985) noted that some temperate fish species perform mixed feeding on exogenous food and yolk, but the condition in Asian seabass appears to be different.

This ontogenetic aberration may be the result of a deficiency in the yolk reserves needed until the formation of feeding organs or may be the product of inbreeding depression. If the problem is indeed a nutritional deficiency in the yolk, it may be due to poor nutritional status of broodstock, imbalance in transfer of nutrients from the somatic tissues of the maternal parent fish to the developing oocytes, or suppression of the intracellular mechanism for synthesis of yolk reserves. Egg chemical composition and fry viability have been linked to the diet of the parental fish (Hamor and Garside, 1977). Problems linked with broodstock nutrition can be remedied by changing the feeding regime of the broodstock. If the problem is associated with inbreeding depression due to generations of hatchery inbreeding, genetic improvement of the broodstock might be necessary. Sustained hatchery propagation over successive generations can adversely affect normal development and growth of farmed fish. A possible effect of inbreeding in a hatchery is the modification of the time sequence in the transition from endogenous nutrition from yolk to exogenous feeding. Failure in the development of a functional mouth before yolk depletion is an ontogenetic aberration that may result from a lack of synchronization in developmental pathways. Noakes and Godin (1988) have discussed the critical importance of first exogenous feeding for larval fish. Deprivation of food at this delicate stage can lead to irreversible starvation, a critical and fatal situation (Dabrowski, 1976; Hunter, 1981). Despite the fact that failure to begin feeding or to acquire food is a major cause of early mortality (Hunter, 1981), we are not aware of any attempt to examine this problem in relation to inbreeding in fish hatcheries. This anomaly does not apparently occur in Asian seabass hatchlings of wild broodstock (Tookwinas, 1989), or if it does, it occurs at a very low frequency. It is possible that inbreeding was responsible for this occurrence in the fry.

The caudal fin abnormality was such that it was pushed upward along the middorsal (median) axis. Likewise, the thickening at the base of second dorsal fin was also located along the median axis. These anomalies appeared randomly and in similar frequencies in many different lots. They occurred together and were independent of the irregularity in mouth/yolk-sac synchronization. Unlike the fatal developmental aberration of the mouth/yolk-sac problem, the fish can apparently live with the abnormal features associated with caudal and second dorsal fins. These abnormal features did not appear to cause any serious mechanical imbalance or disorientation, and were therefore not much of hindrance to swimming. The low level of occurrence amid a preponderance of normally developed individuals raised in a common environment suggests that the alleles causing the caudal fin abnormality are not widely distributed. Those alleles probably appear in the heterozygous condition and in only a few fish. If so, they could be maintained through some advantage to the heterozygotes but would be lethal as homozygotes.

The additional co-occurrence of a reduction in the number of caudal fin rays supports our idea that this abnormality is genetically based. It is unlikely that a mechanically induced disorientation of the fin will also change a meristic feature like the fin ray count.

A major problem in interpreting the source of the observed morphological anomalies is lack of information on the pedigrees of the broodstock and the broods. Testing these speculations would require crosses involving individual families, guided by careful observations of the parents for possible phenotypic differences.

According to unconfirmed reports, hatchery Asian seabass, including those showing abnormalities, enter the sea inadvertently. Given the extent of cage farming of Asian seabass and the proximity of hatcheries to the sea, it seems likely that these reports have some validity. Thus, it is possible that escaped hatchery Asian seabass interbreed with members of the depleted local wild Asian seabass population. Because Asian seabass catches from the wild are only occasional in Sabah, it is difficult to genetically characterize the wild population by standard population genetics methods, which require a large number of specimens captured from a local population. Thus, it is difficult to determine if such interbreeding is occurring and the extent to which it may be altering the genetic diversity of the wild population and affecting its ontogenetic development or morphological features. In addition, because the local population is small, other population biology characteristics such as stock size or population structure are difficult to investigate.

5. SUMMARY AND RECOMMENDATIONS

Use of hatchery-bred offspring as the next generation of Asian seabass broodstock at the Ko-Nelayan hatchery may have adversely affected the fitness of that hatchery stock, as evidenced by developmental alterations and anatomical abnormalities of the broods. As a precautionary measure, the managers of this (and other) hatcheries should take remedial measures to increase the genetic diversity of their broodstocks. Some of the measures include the following:

1. increase the number of broodstock,
2. use broodstock indigenous to the area,
3. exchange broodstock among local hatcheries,
4. supplement hatchery broodstock with wild fish,
5. prevent escape of hatchery fish to natural habitat, and
6. generate a gene bank.

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CHAPTER 11

DISTURBANCE OF KOREAN LAKE ECOSYSTEMS BY AQUACULTURE AND THEIR REHABILITATION

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Abstract: The many artificial, multipurpose reservoirs in the Republic of Korea (henceforth, Korea) have been used for water storage, flood control, hydroelectricity, sightseeing, fishing, aquaculture, and other activities. In 1978, cultured fish contributed 1,831 metric tons (t) of product per year to the inland fishery. By 1992, the cultured-fish contribution had drastically increased to 20,049 t per year. Aquaculture in reservoirs contributes most of this production. Most cultured fishes are alien fishes. Concomitant with the increase in the aquaculture industry, many ecological, limnological, and biological problems emerged. Among them, reservoir eutrophication and the spread of alien-fish species into Korean waterways are severe problems. Lake Soyang, the largest and the most important reservoir in Korea, was constructed in 1973 and has a water-holding capacity of 2.9 billion tons. From 1978 through 1997, the lake supported many fish farms for the production of alien species such as mirror carp (Israeli carp) (*Cyprinus carpio*), channel catfish (*Ictalurus puntatus*), and rainbow trout (*Oncorhynchus mykiss*). These fishes were raised with fish feed, which has a high phosphorus concentration. Prior to the introduction of aquaculture, the lake was very clean; Secchi-disk transparency was 9 m, and phytoplankton density was low. However, after 10 years of aquaculture, symptoms of eutrophication appeared, such as an anoxic zone in the hypolimnion, low dissolved oxygen layers in the metalimnion, increased *Anabaena* spp. density, and high phosphate concentration in the hypolimnion. It was believed that the eutrophication was due to an increase of phosphorus from the fish feed. In 1990, the annual total phosphorus (TP) loading into the lake from the watershed was 104 kg/yr, and that from the fish farms was 48 kg/yr. The critical TP loading for eutrophication of Lake Soyang is 87 kg/yr. The fish farms were thus believed to be a major cause of eutrophication. All of the fish farms were closed and removed between 1997 and 1999. The water quality of Lake Soyang should improve sooner or later. Also a new and different ecosystem will be established. Alien fishes also predominate in Lake Paldang, which is the major source of drinking water for 20 million people. Bluegill (*Lepomis macrochirus*), imported Crucian carp (*Carassius cuvieri*), largemouth bass (*Micropterus salmoides*), and other

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alien fishes released from fish farms are replacing domestic fish species. In 1996, more than half of the fish caught were alien fishes, which implies negative effects for the native species community. Among the severe problems generated by aquaculture in Korean lakes, eutrophication and the presence of alien fishes are the most important. Fortunately, the former problem can be solved, with government and citizen efforts, by clearing the fish farms; on the other hand, the latter problem cannot yet be solved.

Key words: alien fishes, aquaculture, disturbance, environment eutrophication, hypolimnion, Korea, Lake Paldang, Lake Soyang, metalimnion

1. INTRODUCTION

Twenty-three alien-fish species were released in the Republic of Korea (henceforth, Korea). Most of them are used for aquaculture, experimental research, and, in limited quantities, the aquarium trade. Alien species were introduced intensively during the 1960s and 1970s, when the Korean economy (e.g., the gross national product) was expanding and many people desired a higher quality of living, including diets higher in protein. At that time, cultivation and transportation techniques for fishes were also improved. These advances stimulated the development of fish farming, principally of alien fishes because, in general, they grow faster and bigger than do native fishes. The Korean people rapidly adapted some cultivated alien species as favorite foods, which further stimulated the fish-farming industry. It has continued to expand since 1978 and has become "big business" in Korea. Many fish farms were built in coastal areas for marine fishes, shrimps, and other animals and in lakes and streams for freshwater fishes and other animals.

One popular location for the introduction of alien fishes has been artificial reservoirs. During the time of economic expansion, many reservoirs were constructed in rivers to provide a steady supply of freshwater (more than 70% of the annual precipitation of 120 cm is concentrated during the summer monsoon season), to provide electricity to factories and cities, and to control floods and ameliorate the effects of droughts. For example, in the Han River, which is the largest river in Korea, eight reservoir lakes were constructed (Figure 1).

An important accessory usage of these reservoirs was for fish farming. Most of the fish species introduced into these water bodies were alien species. These newly created reservoirs have lake ecosystems that include alien species rather than the original riverine ecosystems with native species. For example, the building of the Lake Soyang reservoir in 1973 in a mountainous area of the upper Han River changed the limnological, ecological, and biological characteristics of that river in the region affected by the reservoir. Before the dam was built, the river was shallow and the water flow was rapid. The building of the dam created a 100-m-deep lake that has a cold hypolimnion. Native fishes could not adapt to this new environment and the cold hypolimnion remained a "dead zone." The Korean government Maritime Affairs and Fisheries Office

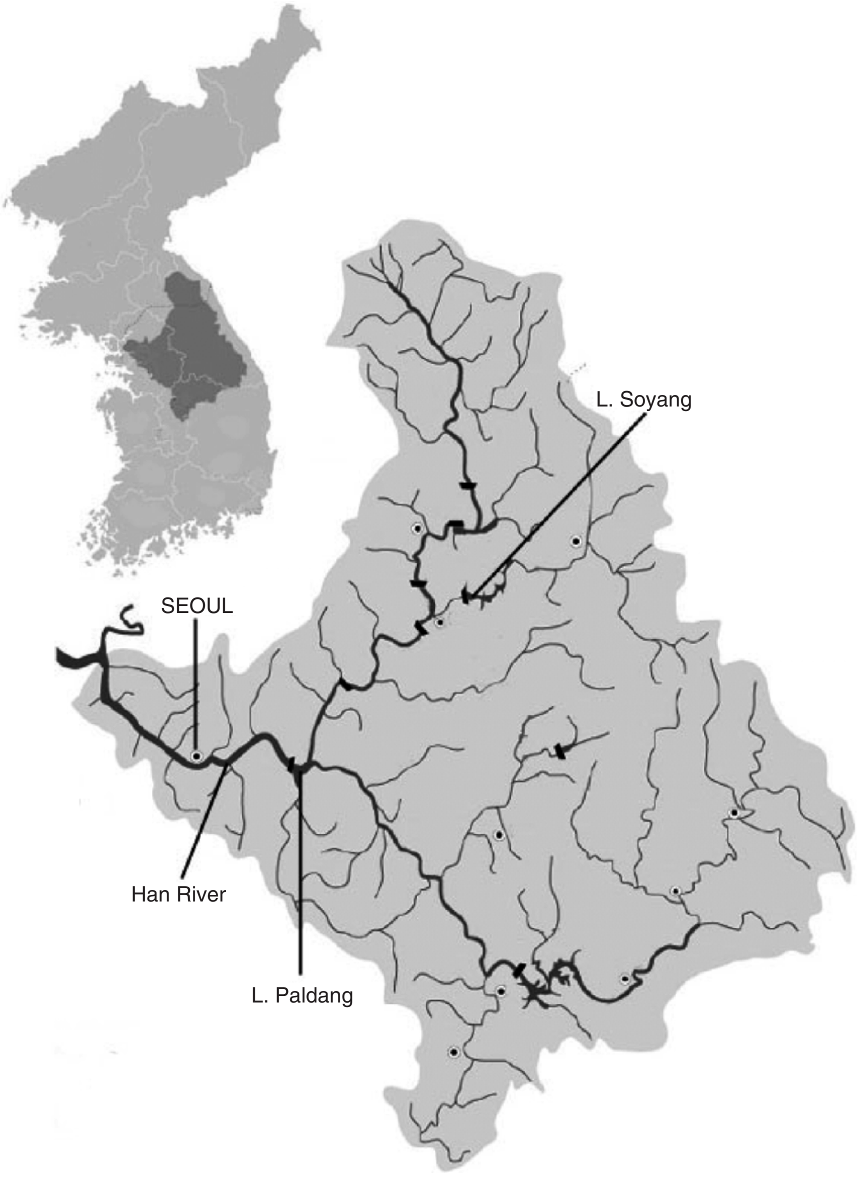

Figure 1. Han River system in the Republic of Korea. The Han River is largest in Korea and has many artificial reservoirs for flood control, electrical power, and human usage. Lake Soyang, the largest lake in Korea, and Lake Paldang, which serves as a water source for Seoul, are important reservoirs

introduced alien fishes into the lake to increase fishery resources and to utilize the dead zone.

Alien fishes introduced into reservoirs such as this one and alien fishes grown in fish farms are escaping from those water bodies into the inland water systems of Korea and are destroying native ecosystems. Alien fishes have been found in 78% of 250 surveyed freshwater ecosystems and in 93% of surveyed large reservoirs (Kong et al., 1996). These fishes destroy native-fish communities by competing with the native fishes for food and space and by preying on the native fishes.

Exacerbating the destruction of the lake ecosystems is eutrophication. Since 1986, symptoms of eutrophication have been detected in reservoirs that are intensively used as fish farms. Eutrophication, which is manifested as an intense proliferation and excessive accumulation of algae and other aquatic plants, can cause detrimental changes in water quality and to the biological population of the water body, and it can interfere significantly with human usage of the water resource (Rast et al., 1989). The OECD (1982) defined eutrophication as "the nutrient enrichment of waters, which results in the stimulation of an array of symptomatic changes, among which increased production of algae and macrophytes, deterioration of water quality, and other symptomatic changes are found to be undesirable and to interfere with water uses." Eutrophication, in the original sense, represents the natural aging process of a lake. A lake receives inflows of water from its surrounding drainage basin, along with materials carried in the water from the land surface. These materials are particularly concentrated in the inflows following a rainstorm or from irrigation drainage. Human settlement and activities in the watershed can greatly accelerate the eutrophication process because the phosphate concentration increases in the water (Dillon and Rigler, 1974) and phosphorus is the limiting nutrient factor in the production of phytoplankton and macrophytes (Schindler, 1978; Wetzel, 1983).

Now, in Korea, many freshwater ecosystems are in a state of chaos; fish farming contributes significantly to this chaos through both the introduction of alien fishes and increased eutrophication. Here, we describe the changes in the fish communities and the eutrophication associated with fish farming in Lake Soyang in Kangwon Province and Lake Paldang in Gyeonggi Province.

2. ALIEN FISHES IN KOREA AND THEIR EFFECTS

In Korea, the important alien fishes are the largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), Israeli carp (*Cyprinus carpio*; called the mirror carp or leather carp in Europe and the common carp in many countries), Imported Crucian carp (*Carassius cuvieri*), grass carp (*Ctenopharyngodon idellus*), silver carp (*Hypophthalmichthys molitrix*), rainbow trout (*Onchorhynchus mykiss*), and channel catfish (*Ictalurus puntatus*). Each of these has adapted to and dispersed in Korean natural waters.

The Korean government Maritime and Fisheries Office imported the largemouth bass from the USA in 1973. After experimental release, it was evaluated as "not suitable," but the released fishes have colonized Korean rivers and lakes. Bluegill were imported from Japan and released into Lake Paldang in 1969. Both the largemouth bass and bluegill have adapted to Lake Soyang and Lake Paldang. In Lake Paldang and other reservoirs, it has become the predominant fish. The Israeli carp is an economically important species and is very popular with Koreans. However, its reproductive rate in Korean natural water bodies is very low. Herabuna, imported from Japan in 1972, has morphological, ecological, and physiological characteristics similar to the local Crucian carp (goldfish, *Carassius auratus*). For example, the herabuna has a high fecundity: 149,396 eggs were found in an adult female of 381 mm body length (Kong et al., 1995). Herabuna colonization has been very successful; in some lakes, this species is more abundant than the local carp. Moreover, it may be hybridizing with the carp; some putative hybrids have been captured. The grass carp and silver carp were respectively imported from Japan and Taiwan in 1962. There is no evidence for their reproduction in Korean waters. Rainbow trout were imported from the USA and from Japan in 1965 and channel catfish were imported from the USA in 1972. The largemouth bass, bluegill, Israeli carp, herabuna, rainbow trout, and channel catfish were introduced for commercial fishing and sport fishing.

All are popular food fish except the channel catfish; the taste of this fish is not popular with the Korean people, thus its cultivation is decreasing. The silver carp and grass carp were introduced for control of aquatic weeds and algae. Other alien fishes were introduced for the aquarium trade (*Poecilia reticulata*) or experimental research (*Leuciscus idusand* and several trout species).

The characteristics of the naturalized alien fishes in Korea are listed in Table 1. All are eurythermal except the rainbow trout, which inhabits cool waters, and all are tolerant to habitat disturbance such as newly constructed lakes, so they have easily adapted to Korean freshwater ecosystems. The largemouth bass, bluegill, and rainbow trout are aggressive, carnivorous, and competitive; and their microhabitats, prey, and ethological characteristics differ from those of native fishes such that they are not affected by native predators. Moreover, largemouth bass, bluegill, and channel catfish have rapid growth rates and reproductive characteristics (e.g., excavating spawning sites, guarding eggs and fry, frequent spawning intervals, high fecundity) that increase their dispersal abilities by increasing their reproductive potential.

These alien fishes are dispersing by both intentional transplantation and escape from fish farms. In a survey of Korean freshwater habitats, the percentages of occurrence of alien fishes are as follows: herabuna, 81.1%; Israeli carp, 68.1%; bluegill, 63.8%; grass carp, 37.6%; largemouth bass, 26%; silver carp, 24.6%; channel catfish, 23.2%; and rainbow trout, 7.1% (Kong et al., 1995). Where they were found, bluegill and herabuna were in high abundance, and they predominated in many lakes. Largemouth bass and Israeli carp were moderately

Table 1. Biological characteristics of alien fishes in Republic of Korea natural waters (after Kong et al., 1995). Species scientific names are listed in the text

	Species							
Habitat or life history characteristics	Large-mouth bass	Bluegill	Imported Crucian carp	Israeli carp	Grass carp	Silver carp	Rainbow trout	Channel catfish
Salinity tolerance[1]	E	E	E	E	E	E	S	E
Temperature tolerance (°C)	0–38	1–35	1–30	<1–33	1–35	1–35	5–20	1–30
Optimum temperature (°C)	25–30	25–30	25–30	24–28	20–30	20–30	12–15	28–30
Natural habitat (adult)	Lakes, rivers	Lakes, rivers	Lakes, rivers, streams	Lakes, rivers	Lakes, rivers	Lakes, rivers	Lakes, streams	Lakes
Microhabitat	Littoral	Littoral	Littoral	Littoral	Littoral, pelagic	Littoral, pelagic	Benthic	Benthic
Rheophility	Lentic	Lentic	Lentic, lotic	Lentic	Lentic, lotic	Lentic, lotic	Lotic	Lentic, lotic
Spawning locality[2]	Benthic veg.	Benthic veg.	Surficial veg.	Surficial veg.	Pelagic	Pelagic	Benthic	Benthic
Spawning temperature (°C)	17–25	20–29	16–18	18–20	18–24	18–24	8–10	21–29
Annual number of spawns	Several	Several	Several	One	One	One	One	One
Spawning season[3]	May–Jul (Jun)	Jun–Aug (Jun)	Apr–Jul (May– Jun)	May–Jun (May)	Jun–Jul	Jun–Jul	Nov–Mar	May–Jul (Jun–Jul)
Number of eggs or fry ($\times 10^3$ per spawning time)	5–30	3–36	9–150	400–700	1,000–2,000	500–1,500	3–10	3–30
Spawning basin	Yes, by digging	Yes, by digging	No	No	No	No	Yes, by hiding	Sometimes
Parental care	Guarder	Guarder	None	None	None	None	Brood hider	Guarder
Mean adult size (cm)	50	15–20	25–30	30–40	100	90	40–50	50
Maximum adult size (cm)	70	25	40	70	150	120	70	1,270
Adult age (years)	5–6	2–3	3–4	3–4	4–5	4–5	4–5	5
Adult feeding mode[4]	Carn. (B, F)	Omn. (B, F, PZ)	Omn. (B, P)	Omn. (B, D, F, H, P)	Omn. (D, H)	Omn. (D, PP)	Carn. (B, F)	Omn. (B, D,F, H)

[1] E = euryhaline, S = stenohaline.

[2] veg. = vegetation.

[3] Parentheses = peak spawning season.

[4] carn. = carnivorous, omn. = omnivorous, B = Benthic-invertebrativorous: D = detritivorous; F = piscivorous; H = herbivorous; P = zooplanktivorous and phytoplanktivorous; PZ = mainly zooplanktivorous; PP = mainly phytoplanktivorous.

abundant and grass carp, silver carp, rainbow trout, and channel catfish were rarely observed. In Korea, all of the common alien fishes listed in Table 1 inhabit reservoir lakes; all but the channel catfish also inhabit streams and rivers.

These naturalized alien fishes have both positive and negative effects. The principal positive effect is increased fishery production through cultivation. In 1994, production from alien-fish cultivation was 76% of the total inland fishery production; and Israeli carp accounted for 59% (30,906 metric tons [t]) of that production (Kong et al., 1996). A secondary positive effect is water-quality improvement through a "top-down" effect. For example, largemouth bass reduce the numbers of planktivorous fish, which, in turn, increases zooplankton production. The zooplankton reduce the phytoplankton by grazing, which improves the water quality (Kong et al., 1994). In addition, grass carp and silver carp greedily eat aquatic weeds and are used to control aquatic macrophytes. However, the overall positive effect of this water-quality benefit has not been estimated.

Unfortunately, in many lakes, the negative effects have not been scientifically analyzed, but have been reported by fishermen. The most important effect may be eutrophication. Reportedly, all reservoirs that have been made into fish farms have become eutrophic; between 10% and 73% of the total phosphorus (TP) loading is due to fish feed. Other effects include habitat change through the feeding habits of the alien fishes. For example, Israeli carp dig into the bottom to feed, which agitates the bottom and can resuspend nutrients trapped there, thereby stimulating plankton growth. Grass carp and silver carp may overgraze the littoral zone and destroy vegetated habitats there. Largemouth bass, bluegill, and herabuna also co-occur with native fishes in those habitats and, along with the grass carp and silver carp, could compete for space in the littoral zone. Largemouth bass and bluegill could compete for food with the native Mandarin fish (*Siniperca scherzeri*), snakehead (*Channa arga*), and far-eastern catfish (*Silurus astous*). Predation on native fishes by alien fishes occurs (MOE, 1996). Chironomid larvae, *Ephemera orientalis* adults, other small fishes, and insects were found in the gut of a largemouth bass of 180 mm total length (TL) collected from Lake Paldang (MOE, 1996). Freshwater shrimp, a favorite prey of the largemouth bass, were not abundant in the lake. Chironomid larvae and other fry, along with other food items, were found in the guts of 150-mm-TL bluegill. In addition, herabuna are thought to feed on native-fish eggs. Alien-species competition for food and space and predation may have affected the fishery production of native fishes. At the national level, native-fish fishery production decreased after the abundance of largemouth bass and bluegill increased in 1986 and 1987 (Kong et al., 1996).

3. INLAND FISHERY HARVEST IN KOREA

In Korea, fishes have been cultivated for harvest since the 7th century AD. Prior to the 1960s, native fishes such as the carp and goldfish were cultivated. Since that time, species cultivated to increase fishery resources have included approximately 30 species of alien fishes, mollusks, and other aquatic animals (Kong et al., 1995). Most were cultivated only on a limited or experimental basis, but the largemouth bass, bluegill, Israeli carp, grass carp, rainbow trout, and channel catfish were widely cultivated and rapidly spread into the rivers, lakes, and reservoirs of Korea. The Israeli carp and rainbow trout were especially liked by the Korean people; the harvest of Israeli carp accounts for over 50% of the annual fish-farming yield in Korea (Figure 2).

In 1974, the annual Korean inland fishery yield was only 1,131 t, of which 155 t was obtained from commercial fish farming. The fishery yield dramatically increased in 1979 and continued to increase through 1987, when total yield was 57,463 t, of which 9,505 t was from fish farming. In 1988, the fishery yield precipitously declined, probably due to water pollution and overharvest, but the number and size of fish farms and their yield increased. During this time, fish aquaculture changed from the cultivation of native species to cultivation of alien species, predominantly the Israeli carp.

To obtain high yields of cultivated fish, large amounts of fish feed are required. The feeding coefficient of common carp is 1.5; i.e., 1.5 kg of fish feed is required to increase fish wet weight by 1.0 kg. Fish farmers want their fish to grow rapidly and think that increasing the amount of food beyond the feeding efficiency level will facilitate attaining that goal. The organic materials

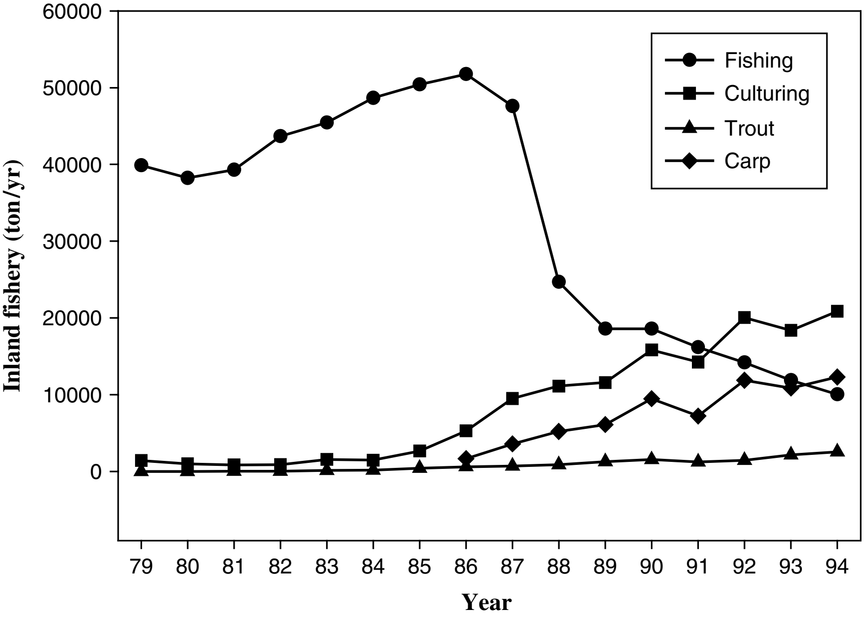

Figure 2. Annual variation in the inland fishery harvest in the Republic of Korea. Trout: rainbow trout (*Oncorynchus mykiss*); carp: Israeli carp (*Cyprinus carpio*)

from the unused fish feed are a source of pollution in water bodies used for aquaculture. Moreover, in fish feed, the phosphorus content is higher than the physiological requirement for fish growth (Kim and Heo, 1992). The unused phosphorus further exacerbates the pollution problem. The degradation of the unused fish feed and fish feces requires oxygen and generates anoxic zones in the deeper portions of lake reservoirs.

4. ECOSYSTEM CHANGES IN LAKE SOYANG

4.1. Abiotic and Biotic Changes

Lake Soyang, a dendritic reservoir, is located in the upper Han River (Figure 1). Its watershed is occupied by less than 60,000 people; only a small amount of anthropogenic sewage enters the lake. At capacity, this reservoir holds 2.9 billion tons of water; has a maximum depth of 120 m, a mean depth of 34 m, and a surface area of 45 km^2; and drains a $2,703\text{-m}^2$ watershed. As an example of the production level in this lake, in 1998, an estimated 300,000–500,000 common carp, rainbow trout, and other alien fishes were cultivated in 520 net cages (10 m length × 10 m width × 15 m depth). From this activity, the annual yield was approximately 1,600 t of fish and the annual consumption of fish feed was approximately 2,400 t.

The symptoms of eutrophication first appeared after 12 years of extensive commercial fish farming in Lake Soyang (Kim et al., 1989, as reported in a special issue of the Korean Journal of Limnology dedicated to this topic). The lake's transparency was 4–6 m in the early 1980s but decreased to less than 2 m in the late 1980s, principally due to algal growth in summer. Between 1984 and 1988, the chlorophyll *a* concentration was less than 5 mg/m^3 (Figure 3). In 1990, the chlorophyll *a* concentration dramatically increased; but after discharge of lake water in autumn 1990, the chlorophyll *a* concentration declined to less than 8 mg/m^3 (Lee, 1995). The hypolimnetic oxygen deficit (HODR) in 1986 was 0.032 mg O_2/cm^2/day (d). In 1987, the HODR increased to 0.052 mg $O_2/cm^2/d$ and in 1988, increased to 0.066 mg $O_2/cm^2/d$ (Kim and Cho, 1989). Ahn et al. (1992) also noted this eutrophication. In addition, since 1988, an oxygen minimum has been observed in the metalimnion at 15–20 m depth in summer (Heo, 1993). Similarly, during the winter lake-water turnover, the dissolved oxygen (DO) concentration was greater than 10 mg/l in 1985 but less than 10 mg/l in 1988; and in the latter year, the decreased DO was accompanied by an anoxic layer below 70 m depth. This anoxic layer increased in width and depth in 1989. Since that time, the chlorophyll *a* concentration has varied among years; but, overall, has been higher than it was prior to the introduction of intense aquaculture (Figure 3).

The temporal gap between the initiation of aquaculture and the appearance of eutrophic symptoms is due to the limnological characteristics of Lake Soyang. The concentrations of total phosphorus (TP) and nonapatite inorganic

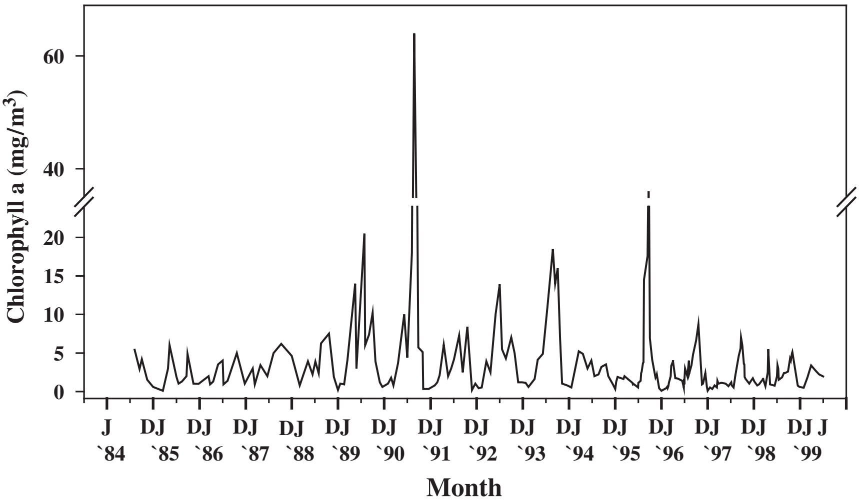

Figure 3. Interannual chlorophyll *a* variation in Lake Soyang, Republic of Korea (data for 1984–1995 is from Kim [1997])

phosphorus in the sediments of Lake Soyang have been higher than those in the central water mass of the lake itself (Jun and Park, 1989). The principal mechanisms of phosphorus input into the lake are biological uptake and chemical precipitation. In this type of system, phosphorus can be concentrated more than 10,000 times higher in the sediment than in the water column (Pettersson et al., 1988). Thus, the phosphorus from terrestrial watershed drainage and from fish farming could be preferentially stored in the lake's sediments. This phosphorus could be released into the lake water if the sediments become phosphorus-saturated and anoxic. This "internal loading" can be due to the depletion of oxygen in the hypolimnion and concomitant reduction of nitrogen, which causes ammonia and soluble reactive phosphorus to be released from the sediment (Kim and Cho, 1989). Internal loading is also suggested by the phosphatase activity (PA) in the lake (Ahn et al., 1993). During the turnover period, the PA and dissolved inorganic phosphate (DIP) concentrations were 3 nmol/l/h and 8.7 μg/l, respectively. However, during the summer phytoplankton blooming period, the PA and DIP respectively were 1,561 nmol/l/h and 1.4 μg/l. Because phosphatase is an inducible enzyme with DIP depletion (Berman et al., 1990), the low activity of PA during the turnover period (November) indicates that a substantial amount of DIP is being released from the deeper layer. Briefly, this is evidence of heavy "internal loading" of DIP. Lastly, the concentrations of chlorophyll *a* and TP, together with transparency (measured as Secchi-disk depth), can be used to estimate the Trophic State Index (TSI). The TSI values of Lake Soyang between 1981 and 1987 ranged 38–43; however, in 1997, the value was 50 (Kim, 1997).

The most notable biological change in Lake Soyang during the eutrophication process was a decrease in phytoplankton diversity. The Shannon-Weaver Diversity Index decreased from 0.81 in 1985 to 0.55 in 1988 (Lee, 1995). Lee and Cho (1994) estimated phytoplankton abundance in Lake Soyang monthly from 1986 through 1991. *Anabaena microspora*, which is an indicator of eutrophication, became the predominant phytoplankton species during the eutrophication process. Prior to eutrophication, the predominant phytoplankton species changed seasonally: the diatom *Asterionella* predominated in winter, *Spondylosium* in spring, *Peridinium* in summer, and *Anabaena* in fall. Since 1987, *Asterionella* has predominated in the cold season and *Anabaena* in the warm season. In 1989, *Anabaena* appeared in July. In August 1990, *Anabaena* cell density was approximately 35,000/ml, seven times higher than in September 1989. However, in the following year, cell density was only approximately 1,000/ml (Lee, 1995). The sudden decrease may have been due to a metalimnion discharge in 1990. Metalimnion water, which contained high phosphorus concentrations, was discharged in that year and in the following year due to heavy rainfall. After the discharge in 1990, the concentration of *Anabaena* was only 3% of that prior to the discharge. However, since 1991, the concentration of *Anabaena* has sporadically increased.

In general, eutrophication has changed the Lake Soyang ecosystem. Important limnological changes include altered nitrogen:phosphate ratio (Heo et al., 1992), increased TP and phytoplankton blooms (Lee, 1995), depleted silicate, and reduced transparency (Ahn et al., 1995). Eutrophication has also caused a change in the feeding behavior of zooplankton (Sim and Ahn, 1992) and an increase in nitrogen fixation through phytoplankton blooms.

4.2. Phosphorus from Fish Farms as a Eutrophication Agent

Phosphorus, an essential mineral for living organisms (Jansson et al., 1988), is usually defined as TP, which includes both particulate phosphorus (PP) and soluble phosphorus (SP); SP can be further divided into soluble reactive phosphorus (SRP) and soluble nonreactive phosphorus (SUP). Biologically available phosphorus is composed of SRP, which is entirely available; SUP, which is available after enzymatic hydrolysis; and labile phosphorus, which may dissolve into a liquid solution (Schaffner and Oglesby, 1978). Biologically available phosphorus is less than 60% of the TP in the USA Great Lakes and about 70% of the TP in municipal wastewater (DePinto et al., 1980). All forms of phosphorus can be regarded as potential agents for algal growth. Some eutrophication models formulated by Hakanson and Carlsson (1998) use TP as the measurement; thus we here also use TP as our measure.

From 1984 to 1988, TP concentration in the Lake Soyang surface layer increased from 3 to 16 g/l. Phosphorus enters Lake Soyang from various sources. In summer 1990, TP concentration reached 40 g/l and remained high each summer through 1994 due to blooms of *Anabaena*. Total phosphorus concentration near the fish farm net cages was 10 times higher than it was in the center of the lake (Lee, 1995), suggesting that a major source of TP in the lake was the fish-farming activities. A phosphorus budget was calculated for the lake in 1991 (Heo et al., 1992). Annual total phosphorus loading was estimated as 104 t (69%) from the watershed and 48 t (31%) from the fish farms (Table 2).

The phosphorus content in fish feed is 1.5% (weight TP/weight fish food). Only 30% is transformed into fish biomass; the rest is released as particulate and dissolved forms (Kim and Heo, 1992). Using this information, the phosphorus discharge from farming common carp in the lake was estimated in a closed laboratory experiment (60-l tank). Farmed common carp were fed using 16 different fish feeds with different phosphorus contents. Dissolved and particulate phosphorus concentrations in the discharge water were measured after 2 days. From these data, the phosphorus uptake by fish per unit growth was calculated as a function of the phosphorus content in the feed. Using this quantity, the TP excretion, and the feeding coefficient, the phosphorus discharge from fish cultivation was expressed as the function of TP content in the feed and the feeding coefficient:

$$LP = Pf - 0.98Pf/FC + 4.9/FC$$

where LP is the TP discharge per unit of feed (mg/g feed), Pf is the TP content in the feed (mg/g feed), and FC is the dry weight of feed per wet-weight growth

Table 2. Total phosphorus budget in Lake Soyang, Republic of Korea, 1990 (Kim and Heo, 1992)

Source	Amount of total phosphorus (TP)
Input	
Fish farm	
TP content in fish feed	1.5%
TP loading per kg fish feed	8.4 g/kg
Fish farm area	47,800 m^2
Supplied feed amount	120 kg/m^2
Annual amount of supplied feed amount	5,736 t
TP loading from the fish farm	48 t/yr
Watershed	
Inflow rate	7–335 t/s
TP concentration	9–46 μg/l
TP loading from watershed	104 t/yr
Total TP input	152 t/yr
Output	
Outflow rate	50–288 t/s
TP concentration	7–43 μg/l
Total TP output	62 t/yr
TP retention in Lake Soyang	90 t/yr

of the fish. From this equation and the plot of FC, TP loading per kg of fish feed was calculated as 8.4 g/kg. Using the LP value, fish farm area, and supplied fish feed per unit area, we calculated the annual TP loading into Lake Soyang from fish farming as ranging from 48 (Heo et al., 1992) to 55 t/yr (Kim and Heo, 1992), which was 32–35% of the TP loading into Lake Soyang for that year. In addition, the long residence time (0.72 yr) of Lake Soyang water (Kim, 1987) concentrates the TP in the lake. In Lake Soyang, an average of approximately 90 t of TP remains each year (Table 2); this is 59% of the 1992 TP loading.

The critical TP loading in Lake Soyang was defined by the Vollenweider OECD model (OECD, 1982) as follows:

$$\text{Lpp (permissible critical loading)} = 10 \times \text{Qs}(1 + (\text{Z}/\text{Qs})^{0.5})$$
$$\text{Lpe (excessive critical loading)} = 20 \times \text{Qs}(1 + (\text{Z}/\text{Qs})^{0.5})$$

where Qs is the surface hydraulic loading of the lake (47.2 m/yr) and Z is its mean depth (34 m). Using the hydrological values of Lake Soyang (Kim, 1987), Lpp = 0.87 g/m^2/yr, and Lpe = 1.75 g/m^2/yr (Heo et al., 1992). Total phosphorus loading into the lake was calculated as 3.4 g/m^2/yr from the fish farms and 2.3 g/m^2/yr without fish farms. These values suggest that Lake Soyang is eutrophic even without fish farms; the fish farms exacerbate the eutrophication process.

4.3. The Future of Lake Soyang

After confirmation of the eutrophic state of Lake Soyang, many limnologists and scientists tried to permanently eliminate fish farms from that lake. Initially, they notified nongovernmental organizations (NGOs) of the damages from and symptoms of eutrophication. Then, they had many meetings with governmental officials, NGO representatives, and fish farmers. Finally, in 1997, the government refused to permit the extension of aquaculture activities in all large reservoirs, including Lake Soyang. In 1997, five fish farms were removed from Lake Soyang and in 1999, the remaining nine fish farms were removed. Fish farming contributed substantially to the establishment of a unique ecosystem in Lake Soyang.

The eutrophication of Lake Soyang can be remedied now that all of the fish farms have been removed. Since 1997, the chlorophyll *a* concentration in Lake Soyang has decreased (Figure 3). However, most of the phosphorus in the lake has not yet been eliminated. As evaluated by the chlorophyll concentration, the water quality is now in good condition. The sudden decrease in chlorophyll *a* concentration after the 1991 discharge of lake water suggests that similar periodic flushing of the lake would stimulate its rehabilitation. The Lake Soyang ecosystem now has the opportunity to recover as a low-nutrient ecosystem, but the direction that this development could take cannot be predicted.

5. ECOSYSTEM CHANGES IN LAKE PALDANG

Lake Paldang is an important water source for Seoul, a city of almost 23 million people (nearly half of the Korean population). This shallow lake, constructed in 1973, has a 23,800-km^2 watershed area, a holding capacity of 244 million tons, and a large littoral zone.

Alien fishes were introduced just after the construction of the dam and they have established in the lake. To estimate the species composition and relative abundances of the alien fishes in the lake, trap nets were installed at two sites and were retrieved weekly from spring through fall, 1996 (Kong et al., 1996). The bluegill was by far the most commonly captured species; it accounted for 78.2% of all fishes captured and nearly half of the fish biomass obtained (Table 3). During its spawning season, the biomass of captured bluegill was approximately four times higher than during other seasons. The imported Crucian carp was the second-most commonly captured species. Numerous largemouth bass were also captured. Together, these three species accounted for approxi-

Table 3. Fishes caught in Lake Paldang, Republic of Korea, from May to November, 1996. Alien fishes are in bold print

	Numbers		Amount	
Family/species	No.	%	kg	%
Cyprinidae				
Carp (*Cyprinus carpio*)	18	0.5	20.7	6.5
Israeli carp (*Cyprinus carpio*)	**11**	**0.3**	**9.1**	**2.8**
Crucian carp (*Carassius auratus*)	28	0.8	2.0	0.6
Crucian carp(imported) (*Carassius cuvieri*)	**178**	**5.0**	**39.7**	**12.4**
Grass carp (*Ctenopharyngodon idellus*)	**1**	**>0.0**	**0.3**	**0.1**
Korean striped bitterling (*Acheilognathus yamatsutae*)	11	0.3	>0.0	>0.0
Korean oil shinner (*Sarcocheilichthys nigripinnis morii*)	1	>0.0	>0.0	>0.0
Steel barbel (*Hemibarbus labeo*)	75	2.1	11.9	3.7
Sky gager (*Erythroculter erythropterus*)	315	8.8	37.7	11.8
Bagridae				
Korean bullhead (*Pseudobagrus fulvidraco*)	11	0.3	1.6	0.5
Siluridae				
Far-eastern catfish (*Silurus asotus*)	67	1.9	12.4	3.9
Ictaluridae				
Channel catfish (*Ictalurus puntatus*)	**2**	**0.1**	**0.4**	**0.1**
Centrachidae				
Bluegill (*Lepomis macrochirus*)	**2798**	**78.2**	**148.4**	**46.3**
Largemouth bass (*Micropterus salmoides*)	**45**	**1.3**	**13.9**	**4.3**
Odontobutidae				
Dark sleeper (*Odontobutis interrupta*)	1	>0.0	>0.0	>0.0
Channidae				
Snakehead (*Channa argus*)	17	0.5	22.3	7.0
Total	3579	100.0	320.4	100.0
Alien-species fishery	3035	84.8	211.8	66.1

mately 85% of the fishes captured and 66% of the biomass from the lake. Israeli carp were also frequently captured after heavy precipitation. Kong et al. (1996) analyzed changes in the fish community of Lake Paldang. At that time, there were 40 fish species in Lake Paldang. The construction of the dam and the introduction of 6 alien species caused the fish community of the region to change: 6 native species were extinguished and 15 new species, including the 6 alien species, became established. Both sport and commercial fishing are prohibited in Lake Paldang because it is a drinking water source; thus, alien-fish abundance is limited only by the carrying capacity of the lake and other natural forces (e.g., selection, predation). Through natural processes such as predation and competition for food and space and through anthropogenic factors such as fishing restrictions, alien species can become predominant in reservoirs and they can displace native fishes, including economically important species such as the Mandarin fish (*Siniperca sherzeri*). Thus, the problem with Lake Paldang is not only eutrophication, but also alien fishes.

The government and citizens are trying to eliminate these alien fishes; but because all fishing is prohibited in Lake Paldang, at this time there is no suitable way to reduce the alien-fish population. The government planned selective harvesting and water-level control during the alien fishes' principal spawning period. The latter method was an attempt to dry the eggs and fry of the littoral alien fishes by lowering the water level. However, both methods failed. Controlling the water level generated problems in sustaining good water quantity. In reality, this new aquatic ecosystem with alien fishes can self-regulate. However, here, too, the direction of aquatic ecosystem succession cannot be predicted because no previous similar case exists. The Lake Paldang ecosystem may be permanently altered from that of a native lake ecosystem because an apparently stable ecosystem based on alien fishes has been established.

6. OTHER EFFECTS OF FISH FARMING

Numerous ancillary effects can be associated with the introduction of alien fishes and fish farms into native ecosystems. Among these are hybridization between the alien fishes and closely related native species; the introduction of fish diseases, pests, unintentional alien species, and antibiotic-resistant bacteria; and massive mortalities of the alien fishes. Unusual climatic events can also exacerbate damage to ecosystems that contain alien fishes.

Fishermen have reportedly caught fish that appear to be hybrid forms between common carp and endemic carp in Lake Soyang and between herabuna and local goldfish in Lake Paldang. Unfortunately, no scientific study has yet been conducted to examine this claim.

Unconfirmed but suspicious apparent introductions of fish diseases and invertebrates have occurred since the advent of alien-fish introductions. Cultured fishes have been examined for viral infections since 1982. Infectious Pancreatic Necrosis Virus (IPNV) was the first isolate, and several viral infections identified as IPNV have since been reported. Cultured chum salmon (*Oncorhynchus keta*), goldfish, eels (*Anguilla japonica*), and rainbow trout have reportedly been infected (Hah et al., 1984; Hedrick et al., 1985). Since 1987, colonies and statoblasts of the alien *Pectinatella magnifica* (Bryozoa) have been found in fish farms where Israeli carp and rainbow trout are cultured. In 1994, freshwater jellyfish were observed at Lake Daechung and Lake Soyang, two reservoirs used for fish farming (Cho, 1995). These species had not been reported prior to the initiation of fish farming in Korea; they may have been co-introduced with the alien fishes.

Korean fish farmers use many types of antibiotics to control fish diseases in their fish farms. This extensive use may result in the generation and spread of antibiotic-resistant bacteria. In 1995, Joe et al. (1996) isolated from cultured flatfish (*Paralichthys olivaceus*) a bacterial strain presumably responsible for hemorrhaging of the fishes' fins and abdominal surfaces. The bacterium, which was identified as *Bacillus brevis* without a plasmid, was resistant to 12 different antibiotics and could be transferred both intraspecifically and interspecifically.

Unexpected temperature changes can exacerbate ecosystem changes in lakes with alien fishes. For example, in 1998, the water temperature of Lake Soyang was unusually higher than in other years. On 24 April, it was 17.9°C, which is approximately 6°C higher than the average water temperature at that time of year. In that year, the first massive fish death—300 t of common carp—occurred, possibly through rapid spreading of parasites and diseases in the warm water or possibly through intolerance of that species to the comparatively warm water. In small reservoirs, massive fish deaths such as this are common during summer.

7. CONSEQUENCES AND ACTIONS

In some aquatic ecosystems where alien fishes have been introduced, native fishes still predominate and the fish community structure remains relatively stable. However, alien species usually predominate when they are introduced into newly constructed reservoirs, and in those lakes, they generate nonnative ecosystems. Prior to the construction of dams, species that prefer lotic (flowing) waters inhabit rivers. After dam construction, species that prefer lentic (quiet, not flowing) waters inhabit the reservoirs; the habitat is no longer suitable for lotic species. The alien species introduced into these lakes are lentic species and thus have an advantage in these water masses.

In addition to the problems described above, others are common because the littoral zones of reservoir lakes constitute high-quality, alien-fish habitats for several reasons. In these zones, large bivalves such as *Anodonta archaeformis*, *Anodonta woodiana*, and *Unio douglsiae* can explosively increase. After they die, small native fishes such as Korean striped bitterling (*Acheilognathus yamatsutae*) and Rose bitterling (*Rhodeus ocellatus*) use the bivalve shells as spawning habitats because the shells conceal their eggs. In areas of high shell density, the densities of these fishes can be high. The availability of these fishes can, in turn, generate a substantial increase in the pscivorous alien fishes that inhabit the littoral zone (e.g., bluegill and largemouth bass).

Many efforts, ranging from governmental to those of individual citizens, are directed toward the rehabilitation of lake ecosystems. Several actions to reduce the spread of alien species and to prevent additional introductions of those species can be taken by the Korean government and Korean citizens. Some of these actions have already been done or are presently being conducted.

1. Cage aquaculture in artificial lakes has been completely eliminated and new cage aquaculture is prohibited.
2. Aquaculture of native species could be developed and promoted. Incentives for this development could be provided. The fry of native-fish species are released into lakes. But the species are limited because there is a shortage of cultured fry.
3. Selective fishing of alien species could be allowed in areas where populations of these species predominate.
4. Water-level fluctuation during the spring spawning season of alien fishes was attempted, to desiccate their eggs, which are laid in the littoral zone. But this method was very complicated because artificial lakes are used for many purposes, such as flood control, electricity, and drinking water supply.

These actions and others that Korean scientists may devise, performed alone or in combination, would help to maintain Korean native aquatic communities. A good start in that direction has already been made.

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CHAPTER 12

MARICULTURE-RELATED ENVIRONMENTAL CONCERNS IN THE PEOPLE'S REPUBLIC OF CHINA

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Abstract: The People's Republic of China (China) is the world's largest producer of aquacultured products. In 2002, the total production of fisheries was 42.6 million tons; of that, 12.46 million tons was from mariculture. On the one hand, mariculture has produced plenty of food and especially additional protein for the Chinese people; on the other hand, the high level of mariculture activity has brought about many environmental issues. One of the largest impacts of mariculture on the ocean environment is self-pollution produced by the farming activities. Effluents, excess feeds, and excretions of organisms in hatchery culture, shrimp in pond culture, mollusks in raft culture, and fishes in cage culture are the major pollution sources. Excess phosphorous and nitrogen compounds from these sources have generated serious eutrophication and may even trigger red tide. The deteriorated aquatic environment has contributed to the spread of different diseases in aquacultural animals, which causes and greatly aggravates loss of production. Biodiversity changes due to mariculture activities are also an environmental concern. Losses in the genetic diversity of cultured shrimps and scallops have been found through biochemical analyses. Inbreeding and limited numbers of parental organisms may be the main causes. Adequate representation of germplasm diversity and high-quality offspring and seedlings should be the focus of greater attention in Chinese mariculture. Also, although the introduction of exotic species is an effective approach to promote the development of mariculture, it can be accompanied by some risk of genetic contamination. The introduction of the bay scallop from the USA is an example of a successful introduction of a species for aquaculture without apparent genetic risk to native species. To maintain sustainable development of Chinese mariculture, the author suggests several avenues of action that should be implemented in China to effectively and rapidly reduce the environmental pollution caused by mariculture.

Key words: algae, aquaculture, bay scallop, China, environment, genetics, impacts, fish, shrimp farming, mollusk farming, polyculture

Theresa M. Bert (ed.), Ecological and Genetic Implications of Aquaculture Activities, 219–228.

1. INTRODUCTION

Because the major wild inshore fishery stocks in the People's Republic of China (henceforth, China) are overexploited, the culture of aquatic organisms plays an important role in providing aquatic products for consumption by the Chinese people. At this time, China is the largest producer of aquatically cultured products in the world. About 71% of the world's aquaculture production comes from China (FAO, 2002).

Approximately 27.3% of the world's marine fisheries production comes from mariculture (the culture of organisms in brackish or salt water [i.e., the marine environment]). From 1978 through the present, mariculture in China has increased steadily and rapidly (Table 1). In 2000, mariculture production was 41.8% of the total marine fisheries production in China. In 2002, the total fisheries production in China was approximately 42.6 million metric tons (t), of which 12.46 million tons were from mariculture. On the one hand, mariculture produces plenty of food and especially additional protein for the increasing Chinese population; on the other hand, the high level of mariculture activity in China has brought about some unavoidable environmental issues.

Mariculture is a complex process that involves many interlinked components such as diet and nutrition, broodstock, disease control, culture technology, and management (Figure 1). The completion of any mariculture activity depends on the successful integration of all of these components. The aquatic environment basically supports mariculture. Anthropogenically derived environmental pollution can impact mariculture, mariculture can heavily impact aquatic environments, and self-pollution from mariculture activities can impact the mariculture operation itself.

Table 1. Output of seawater aquatic products in China (×1000 metric tons) (FBAMC, 2001)

Year	Seawater aquatic products	Wild catch	Mariculture
1978	3,598.0	3,145.0	453.0
1980	3,257.1	2,813.0	444.1
1985	4,197.4	3,485.1	712.3
1986	4,754.0	3,896.0	858.0
1987	5,482.0	4,382.0	1,100.0
1988	6,057.0	4,633.0	1,424.0
1989	6,612.0	5,036.0	1,576.0
1990	7,133.0	5,509.0	1,624.0
1991	8,001.0	6,096.0	1,905.0
1992	9,337.0	6,913.0	2,424.0
1993	10,760.4	7,673.4	3,087.0
1994	12,415.0	8,958.3	3,456.7
1995	14,391.3	10,268.4	4,123.0
1996	20,128.8	12,489.8	7,639.0
1997	21,764.2	13,853.8	7,901.4
1998	23,567.2	14,966.8	8,600.4

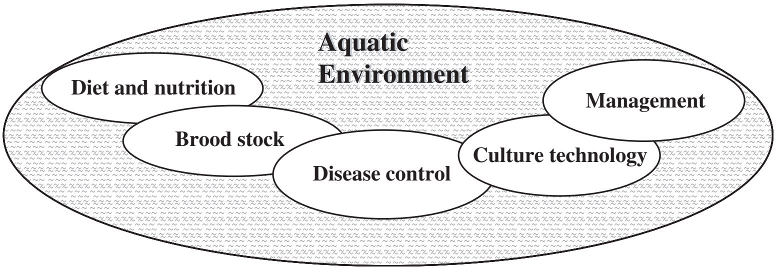


Figure 1. The mariculture chain in the aquatic environment

2. POLLUTION SOURCES RELATED TO MARICULTURE

Land-based pollution into marine environments in China has been and still is a major concern. In 1997, the effluent into the sea from the land in China was about 9.5 billion tons, including 0.79 million tons of nitrogen and 86,097 t of phosphorus (CAFS, 1998). Although incomplete, statistics gathered suggest that about 380 serious pollution incidents occurred between 1980 and 1997. Initially, serious pollution incidents averaged about 20 per year and, in the 1990s, increased to about 30 per year (Xiang, 1998).

As mariculture rapidly expands, effluents, excess feeds, and the excretions of cultured organisms from hatcheries, shrimp pond-culture facilities, mollusk raft-culture operations, and fish cage-culture facilities have been become pollution sources. The average annual total effluent from mariculture is 2.48 billion tons; total nitrogen and total phosphorus accounts for 10,175 and 1,874 t, respectively. These amounts are, respectively, 26.11%, 1.29% and 2.18% of the total effluent, nitrogen, and phosphorus that enters the sea from the land and ships. The total chemical oxygen demand and total inorganic nitrogen, inorganic phosphorus, and suspended matter effused into the sea from shrimp ponds and hatcheries each year in China is about 4,857, 343.9, 34.4, and 19,430 t respectively (CAFS, 1998). However, the cage culture of fish is by far the main source of effused nitrogen and phosphorus from mariculture activities. The average annual excess feed introduced into marine waters from the cage culture of fish is 106,035 t; inorganic nitrogen and inorganic phosphorus constitute about 9,330 and 1,838 t, respectively.

The production of mollusks and algae far exceeds other types of mariculture in China; it typically accounts for 85–90% of the total maricultured products of China. The amount of excrement produced by maricultured mollusks in China in 1997 was estimated to be 1.75 million tons. However, the organic nitrogen and organic phosphorus effused into the sea from that excrement was only about 715 and 109 t, respectively because, at the same time, maricultured mollusks and algae absorbed approximately 16,275 t of nitrogen and 1,558 t of phosphorus from the sea. Therefore, overall, the total phosphorus that effused into the sea from mariculture in 1997 was approximately 316 t, whereas approximately 6100 t of nitrogen were removed from the sea through absorption by maricultured mollusks and algae. From the data above, we can see that, as a whole, mariculture pollution has not yet significantly affected the sea environment in China compared with contamination from the land and other sources.

Another concern about the impacts of mariculture on the ocean environment is self-pollution produced by the farming activities. Mariculture activities can significantly pollute bays with poor water exchange, which, thereby, can negatively affect the mariculture activities conducted within that bay. Excessive phosphorous and nitrogen compounds have caused serious eutrophication and may even trigger red tide. In deteriorated water environments, various diseases of maricultured animals have greatly aggravated production. According to a preliminary estimate, in the 1990s, all kinds of diseases of maricultured animals in China caused an annual loss of billions of Chinese RMBs (Ren Min Bi, the Chinese currency).

3. GENETIC DIVERSITY AND HATCHERY-BASED MARICULTURE

Biodiversity changes due to mariculture activities are also an environmental concern (Beardmore et al., 1997; Avise, 1998). Genetic diversity is an important component of biodiversity (Bert et al., 2001). Genetic bottlenecks, genetic drift, inbreeding, and genetic introgression can reduce genetic diversity. Mariculture operations are frequently susceptible to these genetic problems. Originally in China, almost all maricultured organisms were derived from broodstocks collected from wild stocks. However, now in the operation of a hatchery, usually a limited number of parental organisms, often from small, captive populations, are used for broodstock. In addition, compared to agriculture and livestock husbandry, there are few varieties and strains of maricultured organisms and, thus, comparatively little genetic diversity to draw upon. This reduces the genetic diversity of the broods and renders them susceptible to forces that reduce viability, such as inbreeding depression. More and more seedlings and fries have been produced by hatcheries from limited numbers of broodstock individuals and from broodstocks that have been selected from successive hatchery broods. For example, in 1983, bay scallop (*Argopecten irradians*) fry were successfully cultivated in a hatchery; from that brood, successive generations and billion of offspring have been produced. This practice is known to reduce genetic diversity, sometimes to levels that can impact production (Bert and Tringali, 2001). Table 2 shows the numbers of seedlings or fries of different organisms produced in hatcheries during 1999 and 2000 in China (Xiang, 2002).

We used the randomly amplified polymorphic DNA (RAPD) technique (Williams et al., 1990) to examine the genetic variation of stocks from the natural population and hatchery-reared *Marsupenaeus japonicus* (Song et al., 1999). For this study, we extracted genomic DNA from each of 20 individuals

Table 2. Numbers of seedlings or fry of different organisms produced in hatcheries in China, 1999 and 2000; species within groups are combined

	Number produced	
Maricultured organism	1999	2000
Scallop	100,073,000,000	175,326,000,000
Shrimp	51,915,000,000	58,367,000,000
Kelp	6,894,000,000	15,532,000,000
Fish	1,988,100,000	3,882,000,000
Porphyra (shell)	2,810,000,000	2,202,000,000
Abalone	890,000,000	1,030,000,000

from the natural population and from the hatchery stock. Amplification with 20 random primers under predetermined optimal reaction conditions generated in the natural-population sample and the hatchery-stock sample, respectively, 157 and 153 fragment patterns, of which 85 and 58 were polymorphic. The average heterozygosities of the natural population and the hatchery stock were 0.25 and 0.13, respectively. Clearly, the genetic diversity of the hatchery stock was decreased compared with that of the natural population.

In a previous study, isozyme electrophoresis was used to analyze genetic variation at 20 enzyme loci (12 different enzymes) in two populations of *Fenneropenaeus chinensis* (Liu, 1995) in the Yellow Sea. One population was from the Korean side of the Yellow Sea; the other was from the Chinese side. We hypothesized that the occasional escape of cultured *F. chinensis* from the plentiful coastal ponds or the release of juvenile, hatchery-bred *F. chinensis* through a large-scale restocking program in China may have affected the genetic diversity of this species on the Chinese side of the Yellow Sea. For example, from 1985 to 1990, 658 million hatchery-bred juvenile *F. chinensis* were released into Jiaozhou Bay close to Qingdao, for restocking (Liu et al., 1993).

In the Korean *F. chinensis* population, the percentage of polymorphic loci, the average observed heterozygosity, and the expected heterozygosity were 20%, 0.028, and 0.037, respectively; whereas, in the Chinese population, these values were 15%, 0.016, and 0.028, respectively. Preliminarily, we estimated that, in the Yellow Sea, the Korean *F. chinensis* population possesses slightly higher genetic diversity than does the Chinese population. The extensive stock enhancement activities of the Chinese may be reducing the genetic diversity of the *F. chinensis* population on the China side of the Yellow Sea.

4. CASE STUDY: BAY SCALLOPS

To meet the need for new species or strains of aquatic organisms suitable for culture, people are both domesticating and breeding more wild native stocks and introducing into China exotic aquatic stocks with good characteristics. The purposeful introduction of exotic aquatic species has been done in China since

Table 3. Some exotic mariculture species introduced into China

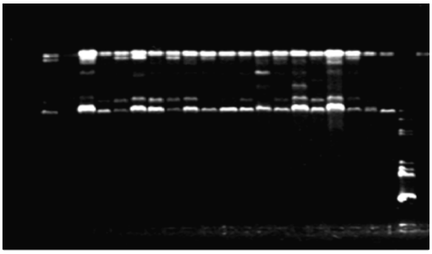
Species	Native area	Year of first introduction
Bay scallop, *Argopecten irradians*	USA	1982
Pacific oyster, *Crassotrea gigas*	Japan	1985
Puffer fish, *Fugu rubripes*	Japan	1996
Giant freshwater prawn, *Macrobrachium rosenbergii*	Southeast Asia[1]	1976
Giant kelp, *Macrocystis pyrifera*	Mexico	1978
California perch, *Micropterus salmoides*	USA	1983
Hybrid striped bass, from *Morone saxatilis*	USA	1997
Japanese scallop, *Patinopecten yessoensis*	Japan	1980
Tiger shrimp, *Penaeus monodon*	Thailand	1986
Blue shrimp, *Penaeus stylirostris*	South America[2]	1999
White shrimp, *Penaeus vannamei*	South America[3]	1989
Rainbow trout, *Salmo gairdnerii*	USA	1983
Red drum, *Sciaenops ocellatus*	USA	1990
Flounder, *Scophthalmus maximus*	England	1992
Tilapia, *Tilapia nilotica*	Africa	1978

[1] Introduced into China from Japan.
[2] Introduced into China from Hawaii.
[3] Introduced into China from the USA.

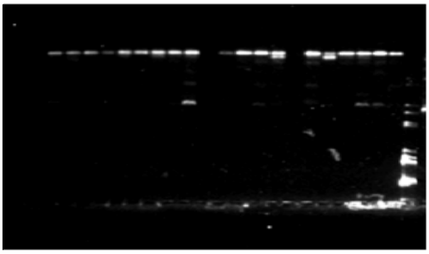
the late 1950s. More than 70 species have been introduced into China, and about 30 species have been propagated to a large extent. Some introduced species are listed in Table 3.

One of most successful introduced species is the bay scallop *Argopecten irradians*. In 1982, 128 scallops from the Virginia Institute of Marine Science in the USA were transported to the Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China. Twenty-six of the transported individuals survived the journey and spawned in January 1983 (Chew, 1990; Zhang et al., 2000). A series of breeding and grow-out technologies were successful developed in China. From 1982 to 1996, the total production of cultured bay scallops, which are characterized by rapid growth and a short production cycle, reached 1.5 million tons (in-shell live weight). Thus, the bay scallop has developed into one of the most important fisheries species in China.

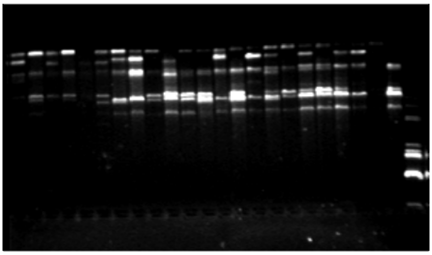
However, after more than 10 generations of culture, the average body size of the bay scallop has become smaller and the organism is easily affected by diseases (Zhang et al., 1997). This may be due to a loss of genetic diversity, perhaps because of the very small number of founders for the Chinese bay scallop population and the continuous inbreeding of their offspring. Using RAPD technology, we studied the genetic variation of the natural population in Massachusetts, USA, and a cultured stock of bay scallops brought to China from Massachusetts in 1998, to evaluate the change in genetic diversity of the cultured stock. Figure 2 illustrates the loss of genetic variation in the cultured population compared with the natural population.



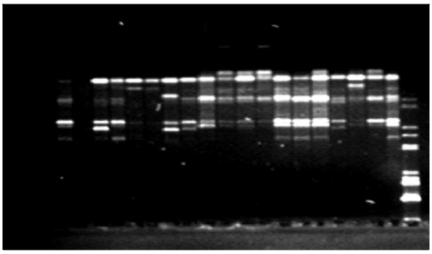
natural population, primer s-108



cultured stock , primer s-108



natural population, primer s-48



cultured stock, primer s-48

Figure 2. The electrophoresis patterns from randomly amplified polymorphic DNA (RAPD) analysis of genomic DNA from the source population (Massachusetts, USA) and a cultured stock of *Argopecten irradians*. Using the primer s-108, we found at least seven different banding patterns in the natural-population sample but only three banding patterns in the cultured-population sample. Using primer s-48, we found at least 10 different banding patterns in the natural-population sample but only approximately 5 different banding patterns in the cultured-population sample

The loss of genetic diversity in the cultured population was also documented in collaborative work with American scientists (Xue et al., 1999), in which horizontal starch gel allozyme electrophoresis was performed. The collaborators documented a significant deviation in allele frequencies and a deficit in heterozygosity at the phosphoglucomutase (*PGM*) locus in the cultured scallops compared with wild-population samples from six different locations in the USA. The heterozygosity of the wild bay scallops from the USA was 0.116, whereas the heterozygosity of the 9th-generation farmed bay scallops in China was 0.091(Zhang et al., 1997). In addition, Blake et al. (1997) speculated that the mitochondrial DNA haplotype variation in 11th-generation cultured bay scallops in China was indeed different from that of wild bay scallops in the USA.

All of this evidence implies that some genetic variation in the bay scallops cultured in China was either lost over the generations and/or was never present in the original founding stock. The decline in quality of the Chinese cultured bay scallop population may have been caused or exacerbated by continuous inbreeding over many years, which resulted in loss of vigor of the broodstocks. To overcome this genetic bottleneck and to counteract genetic drift in the cultured bay scallops, different populations and a different subspecies, *A. irradians concentricus*, were transported from the USA in April 1993.

At present, bay scallop culture is practiced in the Bohai Sea, Yellow Sea, and East China Sea, and South China Sea. Although the introduced bay scallops are cultured on a very large scale in China, no feral populations have been found in any of the farming areas of China. For this species, widespread mariculture apparently has resulted in neither the establishment of feral populations nor introgression of bay scallop alleles into local native scallop populations.

5. DISCUSSION

The worldwide effort to protect the environment started in the 1970s; at that time, China's aquatic environment began to suffer disturbance from industry development. More and more people have realized that mankind should not wait to act until the environment has been irreversible destroyed, and many developed countries have taken measures to reduce environmental destruction. It is of great importance for China, which has the largest population in the world, to promote sustainable development as the state strategy.

Several avenues for reducing the environmental pollution caused by mariculture could be implemented in China.

1. To decrease pollution from mariculture, the culture structure must be improved. Polyculture is more advantageous than monoculture. Seaweeds play an especially significant role in removing excess nitrogen and phosphorous from the aquatic environment (Fei et al., 1999). Large-scale cultivation of macroalgae has the potential to absorb and utilize the main eutrophication

elements—carbon, nitrogen, and phosphorus—from the surrounding seawater. When cultivated macroalgae are harvested, a substantial amount of carbon, nitrogen, and phosphorus are removed from the sea.

2. Recycled-water systems, which can significantly reduce hatchery effluents, are very useful aquaculture engineering technologies. Recently, several institutions in China have become involving in a collaboration to develop appropriate new technologies for recycled-water systems.
3. As mentioned above, fish in open-water cage culture and shrimp ponds are the main sources of effused nitrogen and phosphorus, which are principally the products of excess feeding. Therefore, rational and scientific feeding management is important. In addition, more effective artificial diets, which can replace the commonly used and wasteful frozen fish bait, should be produced.
4. A better understanding of the sources and transport pathways of disease and parasites could reduce the incidence of these problems in mariculture operations. A National Key Fundamental Research Program entitled "Study on the epidemic mechanism of disease and defense basis of the maricultural organisms in China" was launched in 1999. A total of 30 million RMB will fund the program. My collaborators and I (the Chief Investigator) are studying the interactions between pathogens, host organisms, and the environment.
5. In a review of the impacts of aquaculture on biodiversity, Beardmore et al. (1997) consider a range of impacts, including the competitive and introgressive effects from farmed stocks on wild stocks. Because farmed marine organisms frequently escape or are released and then could displace or interbreed with wild conspecifics or closely related species, the maintenance of reasonable effective population sizes (Crow and Kimura, 1970; Hynes et al., 1981) in the farmed populations is very important.

China should implement these measures for environmentally sustainable mariculture. As a world leader in aquaculture and in mariculture, the example set by the Chinese in mariculture production techniques could influence the people of other Asian countries to improve mariculture practices in their countries.

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CHAPTER 13

INDIGENOUS SPECIES FOR AFRICAN AQUACULTURE DEVELOPMENT

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Abstract: From the history of introductions and the development of successful aquaculture elsewhere, it appears that the use of exotic species to speed up the rate of aquaculture development in Africa is unlikely to be an efficacious strategy. The major sustained aquaculture industries worldwide evolved from close working relationships between pioneering investors and local research-and-development institutions. The use of indigenous species avoids many environmental risks, facilitates broodstock and hatchery management at the farm level, and can increase the effectiveness of selective breeding programs. Public-sector involvement in the domestication and marketing of indigenous species can strengthen research, development, and education; broaden the range of investors; create more jobs; and increase the social benefits accruing as a result of aquaculture development.

Key words: Africa, alien species, aquaculture, Cameroon, ecosystem, environment, ecological impacts, indigenous species, introduction, Malawi

1. INTRODUCTION

Aquaculture has made steady progress over the past 40 years, but environmental constraints are now being imposed either by natural ecosystems or man-made regulation. While many negative environmental impacts can be ameliorated through improvements in fish feeds, facility design, and waste processing technology (Boyd, 1995; Mires, 1995a), the impact of escapees from aquaculture on indigenous biodiversity is, in almost all cases, unavoidable (Shelton and Smitherman, 1984; Beveridge and Phillips, 1993).

In this article, I examine the context and history of aquaculture-related introductions of exotic freshwater finfishes into Africa and propose that an

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emphasis on the domestication of indigenous species can decrease environmental consequences of escapement while simultaneously stabilizing and diversifying the industry and ensuring the equitable distribution of benefits. Although many of the comments made here may be broadly applicable, the author's experience is predominantly in African systems and it is these to which the following arguments specifically apply.

2. HISTORY OF AQUACULTURE INTRODUCTIONS IN AFRICA

Increasing poverty and human population sizes in developing countries increases the pressure on governments to maximize food production as rapidly and as cheaply as possible. Urgency often results in a failure to carefully review costs and benefits. Policy-makers trying to feed hungry people and investors seeking quick returns are strongly compelled by the perceived magic bullet of importing for aquaculture an alien species that has proven its worth in aquaculture in other countries or regions (New, 1999).

The track record of aquaculture-related introductions (Table 1) shows that bringing in exotic species to get quick results seldom produces the desired outcome (Satia, 1991). In reviewing 212[1] international[2] introductions of freshwater fishes into Africa for aquaculture, only 33 (16%) were found to have resulted in the establishment of an industry with output of more than 10 metric tons (t) per year in 1997 (FishBase, 1998; FAO, 1999). Of these, 10 (30%) were of common carp (*Cyprinus carpio*) from Asia and Europe and 7 (21%) were of Nile tilapia (*Oreochromis niloticus*) from other African countries. The balance was of mixed cyprinids and rainbow trout (*Oncorhynchus mykiss*). Typical is the case of Zambia, where 39 introductions resulted in sustained aquaculture of only Nile tilapia and common carp (Thys van den Audenaerde, 1994; FAO, 1999). Production of these two species in 1997 was only 133 and 275 t, respectively, compared to 2680 and 1010 t for the indigenous *Oreochromis andersonii* and *Tilapia rendalli*, respectively (Table 2).

In terms of weight produced, over 99% of the total production of exotic species in Africa was of common carp in only two countries: Egypt (22,000 t) and Madagascar (6,000 t).[3] Currently, the common carp industry in Egypt is in serious decline due to the reduction of government subsidies and consumer preference for the indigenous Nile tilapia. In total, exotic species account for only 15% of African aquaculture output (Garibaldi, 1996; Bartley and Casal, 1998). In Asia, the powerhouse of world aquaculture, 517 introductions of primary and secondary freshwater species have resulted in a total contribution of only 5% to total output (Garibaldi, 1996).

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[1] FAO (1999) reports a total of 470 freshwater and marine introductions to Africa.

[2] Most available datasets do not permit the comparison of production statistics with species translocation within a country.

[3] Recently, two projects in Zimbabwe have started operating at a combined output of 6,000 t per annum of Nile tilapia (Cecil Machena, Africa Resources Trust, personal communication, November 1999).

Table 1. Effects of some characteristic aquaculture-related introductions. Of 212 introductions of freshwater species, 33 have generated sustained aquaculture of over 10 metric tons (t) per annum; only 14 produce more than 100 t

Aquaculture introduction	Environmental impact	Tons cultured	Reference
Oreochromis niloticus to Kenya	Displaced endemic *O. esculentus* in Lake Victoria	124	Lowe-McConnell, 1988
Tilapia zillii to Uganda	Displaced *O. variabilis* in Lake Victoria	20	Fryer and Iles, 1972; Lowe-McConnell, 1988
Osphronemus goramy to Mauritius	Naturalized, minimal	0	Moreau et al., 1988
Oreochromis macrochir and *Tilapia rendalli* to Cameroun	Naturalized, unknown	0	Nguenga, 1988
Cyprinus carpio to Kenya	Displaced local species	<0.5	Lever, 1996
C. carpio to Zambia	Not established	275	Woynarovich, 1997
C. carpio to Malawi	Not established	<10	Msiska, 1993
C. carpio to Zimbabwe	Naturalized	0	Lever, 1996; Binali, 1997
O. niloticus to Zimbabwe	Introgression and reduced catches of indigenous tilapias	133	Lever, 1996; Binali, 1997
Clarias gariepinus to Cameroun	Naturalized	<0.5	Lever, 1996; FAO, 1999
Carassius auratus to Madagascar	May have introduced parasites	0	de Moor and Bruton, 1988; Moreau et al., 1988
Chinese carps to Ethiopia	Reportedly naturalized	2	Moreau et al., 1988; Lever, 1996
Ctenopharyngodon idella to the Republic of South Africa	Introduced fish tapeworm	<0.5	de Moor and Bruton, 1988
C. carpio to Madagascar	Naturalized	6,105	Moreau et al., 1988; FAO, 1999
C. carpio to the Republic of South Africa	Reduced catches of local species, introduced 7 exotic parasites	35	de Moor and Bruton, 1988
Heterotis niloticus to Côte d'Ivoire, Cameroun, Central African Republic, Gambia, Congo	Naturalized	2	Lever, 1996; FAO, 1999
Oncorhynchus mykiss to Morocco	Unknown	100	FAO, 1999
Salmo trutta to the Republic of South Africa	Eradicated local species	0	de Moor and Bruton, 1988
O. niloticus to Madagascar	Genetic introgression, replaced local species	0.5	Moreau et al., 1988; Lever, 1996

One reason why exotics have failed to produce rapid growth of the aquaculture sector in Africa is because the germplasm being cultivated is only one (but not currently the most important) constraint to development. African fish

Table 2. Production of indigenous species in selected African countries, as reported to FAO (1999). Of 49 industries that produce over 10 metric tons (t) per annum, only those with outputs of ≥100 t are listed. Data for Malawi were extrapolated from ICLARM-GTZ (1990) and Fisheries Department internal reports

Country	Species or species group	1997 production (t)
Côte d'Ivoire	Siluroids	192
Egypt	Clariids	2,301
	Mugil cephalus	1,931
	Oreochromis niloticus	30,416
Ghana	*Clarias gariepinus*	100
	Oreochromis niloticus	300
Kenya	*Oreochromis niloticus*	124
Malawi	Mixed tilapias	>300
Nigeria	Characoids	3,480
	Clariids	5,357
	Heterotis niloticus	2,956
	Oreochromis niloticus	1,589
	Synodontids	550
Sudan	*Oreochromis niloticus*	1,000
Tanzania	*Oreochromis niloticus*	250
Tunisia	*Mugil cephalus*	485
Zambia	*Oreochromis andersonii*	2,680
	Oreochromis macrochir	407
	Tilapia rendalli	1,010

possess adequate aquatic biodiversity to sustain aquaculture development. Asia relies on indigenous species for 95% of total production, and the number of indigenous freshwater fish species in Asia and Africa is approximately the same: 2943 and 2660, respectively (Fishbase, 1998; Christine Casal, WorldFish Center, personal communication, November 1999). However, far more important than the lack of species are inadequate inputs (van der Mheen and Haight, 1997; Williams, 1997); shortage of seed (Ruddle, 1993; Coche et al., 1994); lack of the necessary research, development, and extension (R, D, & E) to backstop industrial growth (Lazard et al., 1991; ALCOM, 1994); and poor market development (Hecht, 1997). While inadequate inputs affect indigenous and exotic species alike, indigenous species may have an advantage in seed production, R, D & E, and markets.

Well over 90% of the African fish-farming sector is composed of smallholders (King, 1993). To be viable and self-sustaining, the smallholder sector needs species that can be reproduced without complicated and/or expensive interventions. Encouraging dependence upon exotic species that require hatchery facilities for propagation will only exacerbate the fingerling supply problem (Satia, 1991). Eknath (1991) identified inadequate hatchery reserves of broodfish as a major cause of inbreeding depression in cultured stocks. For indigenous species, ready reserves of broodstock are already adapted to local environmental and climatic conditions for their reproduction (Lowe-McConnell, 1988).

New feeds, disease therapies, reproduction techniques, and sometimes even pond designs are needed when species additions or changes are taking place (Beardmore et al., 1997). The R&D process, through which new management strategies are developed, is probably the best way to produce both the needed technology and the skilled scientists and extension personnel to support aquaculture development (Gaillard, 1990; Lazard, 1992; Van Crowder and Anderson, 1997). Because of cost and/or environmental concerns, exotic species are normally introduced to only one research facility at a time. In situations where high-quality human resources are in short supply, this may limit the number of researchers who study the domestication of a particular species to only one or two. With indigenous species, any student, scientist, would-be farmer, or extension agent in the country can get involved. This not only increases the number of minds focused on the problem, but enhances the opportunities for collaboration and synergism.

Many technology-driven development initiatives introduce complete production systems (including the culture species) more or less without regard to markets (Ruddle, 1993; Christensen, 1994). The common carp industry in Egypt is a good example. Carp were introduced as an ideal fish for culture in rice paddies. Millions of carp fingerlings were produced in government hatcheries and delivered at subsidized prices to rice farmers. At give-away prices, these fish were a source of cheap protein to the urban poor, but as government subsidies declined and the price of carp rose to cover costs, consumers with sufficient income switched back to consumption of the indigenous tilapias while poorer segments of the market simply did not buy fish. Such an outcome was anticipated by Street and Sullivan (1985). Carp production in Egyptian rice fields collapsed from a reported 21,000 t in 1996, to less than 7,000 t in 1997 (FAO, 1999).

For whatever reasons, the track record shows that indigenous species are more likely to contribute to local economic growth and put food into local markets faster than exotics. They are also much less likely to damage the environment when they escape from aquaculture facilities.

3. ENVIRONMENTAL CONSEQUENCES OF ESCAPEMENT

For aquaculture, the most commonly introduced groups have been the carps and tilapias. The opportunistic habits that have made these fishes good aquaculture candidates also render them highly competitive for resources and potentially disruptive of the environment (Barlow and Tzotzos, 1995; Bartley and Casal, 1998). The planktivorous Chinese carps, for example, have the capability to distort food webs by targeting primary producers and consumers in their feeding activities (Leventer, 1981; Costa-Pierce, 1992). The aggressive and territorial tilapias alter food webs (de Moor and Bruton, 1988; Bruton, 1990) and reproduce so effectively that they can rapidly displace indigenous species (Moreau, 1983; Lowe-McConnell, 1988). The widely dispersed common carp muddies water, thus destroying aquatic vegetation and phytoplankton that form the basis of most aquatic food webs (Moreau et al., 1988). The introduction of carps in particular has been implicated in the spread of exotic diseases and parasites to indigenous species (de Moor and Bruton, 1988; Paperna, 1996).

The threat to indigenous ecosystems from exotic fish introductions is considerable (de Moor and Bruton, 1988; Courtenay and Stauffer, 1990). Many cases exist where the importation of species has resulted in the destruction of indigenous fish populations or habitats (McNeely et al., 1995; Moreau, 1997). The importation of the common carp to North America and the stocking of Lake Victoria with the Nile perch are only two examples of the disastrous effects that might be expected from introduction of exotics.

Many of the worst impacts from introductions have occurred in disrupted environments (Moreau et al., 1988; Courtenay and Stauffer, 1990; McNeely et al., 1995). While it is difficult to separate causes in such situations, much current ecological theory (Barlow and Tzotzos, 1995; McNeely et al., 1995) supports the hypothesis that introduced species may not have much impact until a stressed environment opens a sufficiently broad niche into which "weedy" species, such as those often used in aquaculture (Beveridge and Phillips, 1993), might expand (Courtenay and Stauffer, 1990). The history of the common carp in the Columbia River (northwestern USA) is a case in point. Introduced in the 1800s, the carp had no significant adverse environmental impact until extensive dam construction in the 1940s and 1950s slowed currents and warmed the water to the point where it had a competitive advantage over the indigenous cold-water species. Common carp have since contributed substantially to decreased water quality, loss of aquatic vegetation, and consequent declines in indigenous species—the salmonids in particular (Lever, 1996).

4. IMPROVED GERMPLASM FOR AQUACULTURE

That improvements in germplasm can increase production is almost unarguable. However, how these improvements are made can have a large impact on the rate of progress and on who benefits, and how. There are two general approaches to improving germplasm for aquaculture:

1. import an exotic species or improved variety developed elsewhere (centralized approach);
2. locally develop a new species or variety (decentralized approach).

In the past, the option of domesticating or breeding a new variety in a central location and then subsequently disseminating seed or broodstock has been favored by the international R&D establishment. This approach requires the international and often intercontinental transfer of genetic material and involves questions of genotype × environment (G × E) interactions, which render improved genotypes less competitive in culture systems that differ from those under which they were bred.

A major advantage of the centralized approach is that complicated technologies can be more easily handled and controlled in larger, more sophisticated labs. Breeding progress is faster. For example, the genetically improved farmed tilapia (GIFT) strain of *Oreochromis niloticus*, developed by ICLARM, the Asian Development Bank, and the United Nations Development Program in the Philippines, grows 20–70% faster than most domesticated *O. niloticus* strains. However, in Thailand and China, the GIFT fish exhibits signs of G × E interaction and is not substantially superior to locally adapted and bred strains. The GIFT fish, though, was produced in 4 years while the strains in Thailand and China have been domesticated for 30 and 20 years, respectively (ICLARM, 1998).

Well-documented examples of successful introductions of exotics for aquaculture are not plentiful. In most places, systematic comparison of local and exotic species was not conducted, either before or after the introduction (Pillay, 1992). Nevertheless, if G × E interactions and possible environmental impacts are negligible, one could argue that this approach provides more food to more people faster than the longer process of developing local species or strains.

In addition to growth rate of individual fish, however, governments contemplating introduction of exotic germplasm must consider the equitable accrual of benefits and distribution of environmental risks. In Africa, fingerling production is not generally based on centralized hatchery systems, and this situation is not changing. African governments that have tried in the past to produce low-cost fingerlings for support to low-income farmers are now increasingly unable to manage their hatchery programs and are, in fact, divesting themselves of this responsibility (Coche et al., 1994; Vincke, 1995). The private sector is unlikely to take up hatchery technology unless it has a market that can pay for the product.

In this situation, larger, vertically integrated farms are the most likely beneficiaries in the short term (over which time frame the centrally bred varieties have the advantage of being more quickly developable). This is what has happened in the USA catfish and Norwegian salmon industries (Forster, 1999). In Africa, where the vast majority of consumers are also producers, people cannot afford to pay for fish grown on large commercial farms and so most of the produce is sold to luxury markets or exported (Satia, 1991; Corbin and Young, 1997).

Figure 1 presents a model for how total aquaculture output might be enhanced while keeping more investors and laborers in the industry. As production and the number of farmers increases, market limits or increases in efficiency favor some producers who come to dominate the market for a particular species. Without alternative markets, less competitive producers begin to fall out, with associated loss of employment and waste of developed infrastructure. Equilibrium 1 is the level of investment supported by a highly

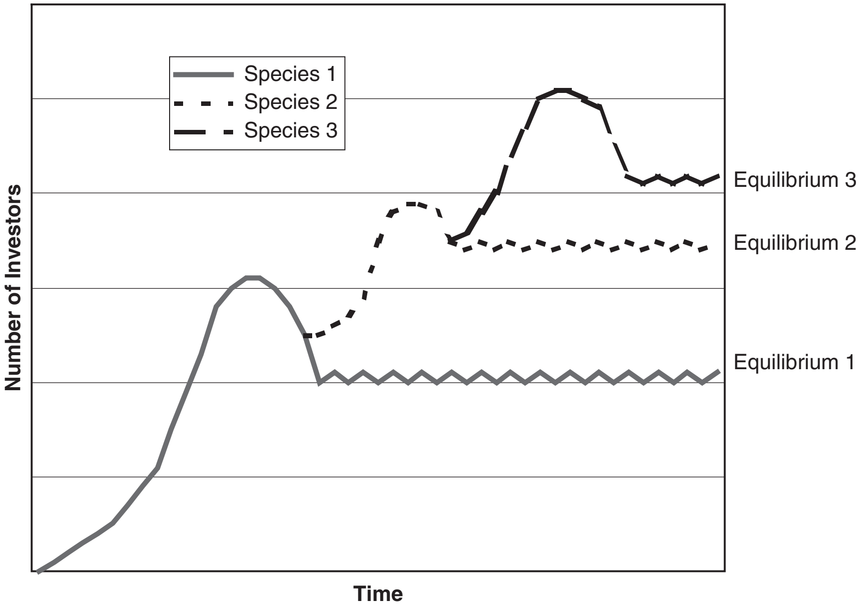

Figure 1. A theoretical model of how domestication of new species can enhance employment and investment in aquaculture. Equilibrium 1 is the point where the initial aquaculture industry stabilizes with the culture of one main species. Equilibrium 2, based on the domestication of a second species, has taken advantage of existing infrastructure to add quickly but marginally to investment levels. At Equilibrium 3, even less of an increment has been added, but opportunities for employment and investment have been further increased

efficient, single-species industry. With alternative species and markets, additional investment and employment can be supported (Equilibria 2 and 3), although overlap among producers will probably mean lower overall investment levels for each new species added. On the other hand, lead-time to full market exploitation should become shorter as more experienced farmers lead the transition to each successive new species. Since the markets for many species overlap (Brummett, 2000), this model would produce the greatest impact if new species brought in actually increase the overall size of the market or access new markets. In Israel, for example, polyculture of cyprinids and tilapias served largely to increase yield, but did not develop new markets. Only when striped bass and salmonids were introduced did new buyers start to eat fish. There is a clear role for market analysis prior to making major investments in the development of new species.

Almost any kind of economic growth in Africa is welcome, but evidence exists that directing assistance to rural poverty alleviation is more efficient than just making rich people richer and hoping for trickle-down effects (Delgado et al., 1998; Winkleman, 1998).

Local improvement of an already-domesticated species normally takes longer than the centralized approach. The decentralized approach requires more people that become involved and is consequently less efficient in terms of capital use. It also tends to be more difficult to implement within the short-term projects preferred by the donor community. However, as described above for more general R&D directed toward improved aquaculture technology, the benefits of developing local capacity to do biological assessments and hatchery management at the same time as the germplasm is being enhanced might outweigh the increased cost.

In terms of beneficiaries, the decentralized approach can include local economic and management constraints in the species selection and modification process, thus making new germplasm available to a broader range of local users. In terms of risk, local dissemination of indigenous species would seldom require more than the movement of genetic material from watershed to watershed (which may or may not involve national borders). In addition, G × E interactions in these "horses for courses" approaches are expected to be minimal.

Successful applications of the decentralized approach are widespread. In Malawi, common carp were considered for introduction and rejected when their performance was tested and judged inferior to local species (Msiska and Costa-Pierce, 1993). Instead, programs to domesticate and improve local tilapias (Brooks and Maluwa, 1997) and *Barbus* species (Brummett and Katambalika, 1996) were successfully undertaken. In Côte d'Ivoire, the domestication of *Heterobranchus longifilis* doubled growth rates over the previously cultured *Clarias gariepinus* (Breine et al., 1995); *H. longifilis* now contributes substantially to local aquaculture (Otémé, 1994). Ongoing research within the International Network for Genetics in Aquaculture (INGA) is aimed directly at this approach for the development and dissemination of improved indigenous germplasm in Africa and Asia.

5. A DIVERSE AND STABLE INDUSTRY

Within specific agroecological zones, the aquaculture industry has tended to specialize. States on cold oceans with sufficiently protected areas along their shores produce Atlantic salmon (*Salmo salar*). Tropical countries with suitable coastal areas produce shrimp (*Penaeus* spp. and related species). Throughout the Mississippi delta in the USA, farmers with bottomland grow channel catfish (*Ictalurus punctatus*). Concomitant with specialization has been a convergence of technology so that systems vary little from place to place. This has been fostered by the close working relationship normally established between pioneering entrepreneurs and R&D institutions supported by public funds. Once technology is standardized and shown to be profitable, investors pour in.

Since all investors are competing in very similar (if not the same) markets, economic viability comes to rely increasingly on smaller and smaller profit margins. Such cycles have resulted in large numbers of dropouts as ventures with comparative advantages for a particular species increase production and push prices below the break-even point for others. While some go out of business due to production inefficiency, many others are simply victims of circumstance. Increased efficiency and reduced numbers of farms means fewer jobs. Some bankrupt installations are sold to competitors, but others are simply abandoned for lack of a buyer in a saturated market. The Norwegian Atlantic salmon and the USA channel catfish industries have followed this general pattern, as indeed have many other agrobusinesses (Forster, 1999).

An example for the Israeli common carp industry is shown in Table 3. Until 1965, virtually all of Israel's aquaculture production was of common carp. From 1955 to 1965, efficiency increases lead to improvements in average yield, which precipitated (from 1965 to 1987) a decline in total area under water of 2325 hectares (almost 50%) and a decline in the number of farming businesses from 88 to 58. During this entire consolidation period, overall production steadily increased from 8680 to 13,979 t per year.

Over recent years, the enthusiasm for private-sector-driven economic expansion has led to a reduction in the financial resources available to public-sector research. The reduction in government hatcheries in Africa is only one symptom of this trend. In the USA, more and more aquaculture research is paid for by species-specific commercial aquaculture firms or associations. This research aims to only slightly improve profit margins and reduce environmental impacts (New, 1999) and is very seldom aimed at giving competitors options in the market.

While the loss of productive infrastructure and jobs may be affordable in Norway or the USA, it is much less so for developing countries. Under these conditions, it makes sense for public research expenditures to be directed at diversification of the aquaculture industry so as to open niches for a wide range of producers.

One way to do this is to establish long-term R, D, & E programs aimed at constantly domesticating new species and developing markets for them. The development of the Atlantic salmon and channel catfish industries illustrate how a close working relationship between researchers and farmers can lead to the elucidation of efficient aquaculture technology. Marketing, however, is often overlooked. An excellent case in point was the rapid growth and collapse of the South African clariid catfish industry. Scientists and farmers working together fostered rapid expansion from 10 t in 1987 to 1200 t in 1990. The industry however, collapsed to 150 t in 1992, due to inadequate market development (Hecht, 1997). Both species domestication and market development should be public-sector activities because the private sector is unlikely to finance technologies or market development schemes that are broadly applicable and designed to keep as many players as possible, particularly lower-income operations, in business (Corbin and Young, 1997).

Table 3. Development of the aquaculture industry in Israel from 1939 to 1997. Species diversification from 1955 to 1969 was primarily for purposes of polyculture with the principle species, common carp. Increases in efficiency during this period increased competition and led to a major reduction in number of farmers and infrastructure. Changes in government support for aquaculture research and development included increasing the number of species available to investors, which led in the early 1990s to renewed increases in investment. Data from Dill and Ben-Tuvia (1988); Sarig (1989, 1996); and Snovsky and Shapiro (1999). Avg. = average; Ha = hectares; t = metric tons

					Percentage of total production by species or species group						
Year	Number of farms	Total area (Ha)	Average yield (t/Ha)	Total production (t)	Common carp	Cichlids	Mullets	Silver carp	Other carp	Salmonids	Striped bass
1939		15	0.93	14	100						
1941		120	1.07	128	100						
1943		560	1.23	689	100						
1945	30	993	1.26	1,260	100						
1947		1,380	1.64	2,250	100						
1949		2,100	1.76	3,700	100						
1951		2,580	1.49	3,850	100						
1953		2,950	1.58	4,650	100						
1955		3,630	2.01	7,320	98.3	1.6	0.1				
1957		3,640	2.07	7,530	98.6	0.5	0.9				
1959		3,890	2.03	7,990	97.2	0.2	2.6				
1961		4,520	1.96	8,870	96.3	2.6	1.1				
1963		4,900	2.04	10,050	92.2	6.0	1.8				
1965		5,100	2.00	10,180	94.3	3.3	2.4				
1967	88	4,960	1.76	8,680	88.1	8.0	3.9				
1969	83	4,780	2.15	10,260	81.8	11.6	6.6				
1971	84	4,870	2.57	12,530	85.4	8.6	4.1	1.9			
1973	82	4,790	2.88	13,780	83.3	8.1	3.5	5.1			
1975	80	4,457	2.91	12,984	69.8	13.5	3.7	12.9		0.1	
1977	79	4,153	3.24	13,454	60.6	15.7	4.4	19.2	0.1		
1979	77	3,529	3.57	12,619	62.4	21.6	4.7	10.3	1.0		
1981	72	3,425	3.33	11,419	66.4	18.6	6.6	7.3	1.1		

(*Continued*)

Table 3. Development of the aquaculture industry in Israel from 1939 to 1997. Species diversification from 1955 to 1969 was primarily for purposes of polyculture with the principle species, common carp. Increases in efficiency during this period increased competition and led to a major reduction in number of farmers and infrastructure. Changes in government support for aquaculture research and development included increasing the number of species available to investors, which led in the early 1990s to renewed increases in investment. Data from Dill and Ben-Tuvia (1988); Sarig (1989, 1996); and Snovsky and Shapiro (1999). Avg. = average; Ha = hectares; t = metric tons—cont'd.

					Percentage of total production by species or species group						
Year	Number of farms	Total area (Ha)	Average yield (t/Ha)	Total production (t)	Common carp	Cichlids	Mullets	Silver carp	Other carp	Salmonids	Striped bass
1983	61	3,100	3.53	10,936	70.4	19.0	5.2	5.0	0.4		
1985	60	3,034	4.14	12,667	54.0	32.3	6.1	6.4	0.2	1.0	
1987	58	2,775	4.91	13,979	59.7	29.2	3.9	5.3	0.3	1.6	
1989	58	2,863	4.94	14,535	56.3	31.1	6.1	4.3	0.1	2.1	
1991	55	2,887	5.07	15,100	51.9	38.4	5.9	1.4	<0.1	2.4	
1993	56	3,010	4.30	13,540	55.4	31.8	6.1	3.1	0.1	3.5	
1995	55	3,037	5.38	16,341	46.8	36.8	7.9	4.0	0.1	4.1	0.3
1997	72	3,950	5.39	16,671	44.5	37.2	10.7	2.0	<0.1	4.0	1.6

Diversification to support stable industrial development is not a radical idea and has been a component of successful aquaculture development in many countries (Corbin and Young, 1997). (1) Since 1985, Norway has developed successful commercial systems for at least five new species (FAO, 1999). (2) Israel has been steadily increasing the number of species under cultivation (Table 3). Until 1967, when the decline in farm numbers began, the number of species grown on Israeli farms had been three. The decline reversed in 1991, when government increased its role in R, D, & E and encouraged the domestication of new species (Mires, 1995b). By 1993, over 16 species were being cultured (Dill and Ben-Tuvia, 1988; Sarig, 1989, 1996; FAO, 1999) and new investments were being made even while the carp industry was still consolidating (Mires, 1995b). (3) When USA aquaculture was in its infancy and no one knew which technologies were going to prove the most successful, research centers studied at least 16 finfish species (including 8 exotics) for application to USA warm-water aquaculture and numerous others for applications to marine and cold-water aquaculture. (4) In a recent survey of Mediterranean aquaculture, Abellán and Basurco (1999) discovered that 20 marine finfish species are currently under investigation for culture.

Clearly, through use of indigenous species, diversification, and involvement of local interests, low-cost, low-environmental impact, high-quality aquaculture can operate on local scales at productivity levels that benefit local and regional economies. The use of indigenous species for aquaculture should receive far more attention than it does now, particularly in developing countries with abundant potential for domesticating native species.

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CHAPTER 14

THE INTRODUCTION OF NONNATIVE FISHES INTO FRESHWATER SYSTEMS OF PERU

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Abstract: Since the 1930s, alien fishes (fishes not native to Peru) have been introduced into the freshwater systems of Peru for different purposes such as fish farming, the ornamental fish trade, public health applications, and sport fishing. The fish were introduced either deliberately or casually into the three hydrographic systems of the country (Amazon, Pacific coastal rivers, and Lake Titicaca). To date, 20 alien species have been found in the continental water systems of Peru: *Aristichythys nobilis*, *Carassius auratus*, *Cichlasoma nigrofasciatum*, *Ctenopharyngodon idella*, *Cyprinus carpio*, *Gambusia cf. affinis*, *Hypophthalmichthys molitrix*, *Odonthestes bonariensis*, *Oncorhynchus mykiss*, *Oreochromis aureus*, *Oreochromis hornorum*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Oreochromis urolepis*, *Poecilia reticulata*, *Poecilia velifera*, *Tilapia rendalli*, *Trichogaster leerii*, *Xiphophorus helleri*, and *Xiphophorus maculatus*. Native-species transfers have also occurred; seven Peruvian species have been transferred from lowland forest waters to water systems of both the highland forest and the coast (reservoirs): *Arapaima gigas*, *Astronotus ocellatus*, *Brycon cephalus*, *Cichla monoculus*, *Colossoma macropomum*, *Piaractus brachypomus*, and *Prochilodus nigricans*. Herein, we present an overview of the current situation of these species introductions and transfers in Peru based on both fieldwork and a review of the pertinent literature. We then focus on the three alien species most frequently found in natural environments but not previously evaluated for their impacts. Our surveys in the aquatic basins of the Parque Nacional Río Abiseo (PNRA; high-altitude, Amazon River system) show that the alien *Oncorhynchus mykiss* (rainbow trout) is the dominant species and that the three native species usually common in Peruvian highland Andean river basins (*Astroblepus* spp.) are present only in low numbers. The other two alien species—*Oreochromis niloticus* (tilapia) and *Poecilia reticulata* (guppy)—are well established and widely distributed in both the Huallaga (highland forest, Amazon River system)

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and Rio Grande (Pacific Ocean coastal system) river basins. We also discuss other introductions and transfers. For example, the introduction of *Odonthestes bonariensis* (pejerrey argentino) and *Oncorhynchus mykiss* into Lake Titicaca caused a negative impact on native *Orestias* species and the transfer of the giant Amazonian fish *Arapaima gigas* (paiche) initiated a chain of introductions and impacts in Sauce Lagoon. The introduction of species into nonnative waters is a complex problem without a unique solution. We give some suggestions for the control of both *O. mykiss* in the PNRA and *O. niloticus* in the Huallaga River basin and for the practice of environmentally sustainable aquaculture. Minimally, it is necessary to establish biological monitoring programs in the affected river basins and, for comparison to the affected basins, to obtain adequate data on the distributions and relative abundances of native species in analogous unaffected basins. We also recommend that environmental education programs be developed and promulgated to inform the public of the general problem.

Key words: alien species, aquaculture, ecosystem, environment, exotic species, fish, freshwater impact, Peru

1. INTRODUCTION

Due to its particularly high number of species and habitats and the genetic diversity of its species, Peru is acknowledged as one of the ten biologically megadiverse countries of the world (Gentry, 1992; Rodríguez et al., 1993; Carrillo and Icochea, 1995; Chang and Ortega, 1995; Pacheco et al., 1995; CONAM, 1999). Freshwater fish diversity in Peru is very high; 855 species of freshwater fishes have been reported (Chang and Ortega, 1995) from sea level to 4080 m altitude (Ortega, 1992; Ortega, personal observation). They are unevenly distributed in the three main drainage systems of the country: (1) Amazon River, (2) Pacific Ocean coastal river, and (3) Lake Titicaca (Figure 1).

However, despite such wealth in fish biodiversity, numerous alien fish species have been introduced into the cold and warm waters of the country, for various reasons. For example, fishes have been introduced into Peru for aquaculture and fisheries purposes since the 1930s. The first introductions were principally into aquatic basins of the Andean region (FAO, 1998), which had few native fish species. The alien cold-water species *Oncorhynchus mykiss* [=*Salmo gairdneri*] and *Odonthestes bonariensis* (Everet, 1973) were introduced to increase local fisheries production and for sport fishing. The alien *Poecilia reticulata* was introduced into the coastal region during the 1950s to control malaria insect vectors. Other species such as *Cyprinus carpio*, *Oreochromis aureus*, *Oreochromis hornorum*, *Oreochromis niloticus*, and *Tilapia rendalli* were introduced repeatedly into coastal and central Amazon forest river basins to increase food availability to local communities (Bartley, 1993). Within Peru, species have also been transferred from one river system to others. For example, during the 1970s, species from lowland tropical forests were transferred into both highland forest and coastal river basins, and species have been transferred to Lake Titicaca with amazingly negative results.

Twenty alien species have been recorded from the freshwater systems of Peru and seven native species have been transferred from lowland forest river systems to other water systems. Here, we present a comprehensive portrait of the current state of the introduction of alien fishes and native-fish transfers in the freshwater systems of Peru. Using both current data and historical records, we evaluate the distribution and biological impacts of exotic species introduced into different Peruvian river systems. Together, these data and records allow us to synthesize a comprehensive picture of the effects of species introductions and transfers on the water systems of Peru. Our results will be useful for making decisions and establishing measures for management, use, and conservation of Peru's native fish fauna, and may be applicable to other regions as well.

2. MATERIALS AND METHODS

In multiple expeditions to different areas, we surveyed three river-system components, each of which is located in a different type of environment. These are as follows: (1) the Parque Nacional Río Abiseo (PNRA) basin in the highlands Andes component of the Amazon River system, (2) the Huallaga River basin in the highland forest component of the Amazon River system, and (3) Rio Santa and the Rio Grande basins in the Pacific Ocean coastal river system (Figure 1). We also exhaustively surveyed the relevant literature concerning these river systems and a third Peruvian freshwater system—the Lake Titicaca system. We combined that information with our field observations to comment on changes in native-species fish diversity and relative abundance after the introduction of alien species and transfer of native species into nonindigenous locations.

2.1. Study Areas

The sampling locations, areas, regions, and departments mentioned in the text are shown in Figure 1. Some small rivers and reservoirs are not shown, but their general locations are provided in the text.

2.1.1. Parque Nacional Río Abiseo

This national park is located in the Andes, Cordillera Nor Oriental, approximately between 07°25′ S, 76°58′ W and 80°5′ S, 77°33′ W (Figure 1), in the Department of San Martin. The valley of the Marañón River is to the west and the Huallaga River basin is to the east. The PNRA was established in 1983. It encompasses approximately 264,520 ha and is composed of a variety of habitats, including six zones of life (Tosi, 1960; Young and León, 1989). The main rivers are the Montecristo, Tumac, and Abiseo, all of which are tributaries of Huallaga River. They extend from approximately 1680 to 3990 m above sea level (m.a.s.l.) and drain more than 40% of the PNRA.

The fieldwork was done in two expeditions (July 1989 and July 1990) during which we made 61 collections (Table 1). During the 1989 evaluation, we

A.

Figure 1. Geographic and hydrographic features of Peru important for documenting the nation's freshwater fish fauna. Multicolored: departments and field sampling locations (red dots). Black-/white/yellow: hydrographic basins and field sampling areas (in yellow)

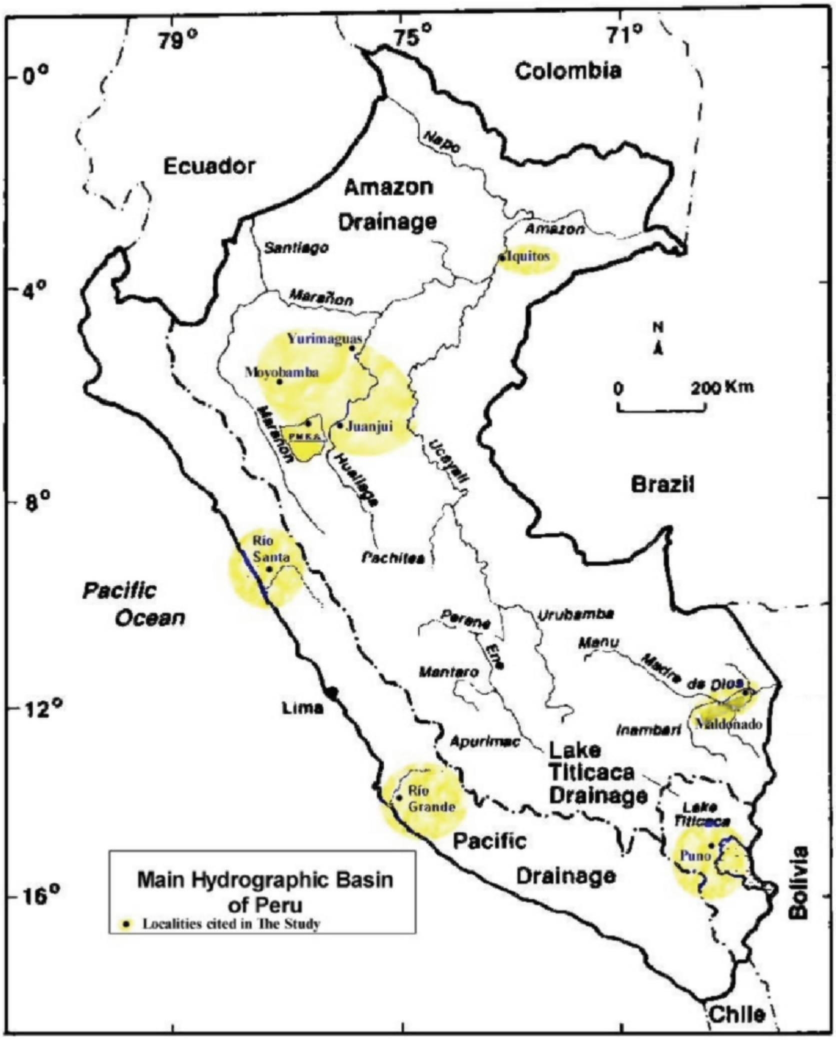

Figure 1. Continued

sampled 23 stations that ranged between 2000 and 3990 m.a.s.l. The air and water temperatures respectively varied between 8°C and 24°C and 5°C and 21°C. The pH values of the waters were neutral or slightly alkaline. Fish and aquatic insects were collected from the rivers, variously sized tributaries, and lagoons. Samples of plankton were also taken, mainly from those lagoons where no fishes were recorded. The following year, we sampled 38 stations. The air temperature varied from 5°C to 25°C; the water temperature varied between 3°C and 22°C. Water pH values were approximately neutral (7.0–7.5);

Table 1. Stations, field data, and samples collected in the aquatic environments of the Parque Nacional Río Abiseo, July 1989 and July 1990. No. = number; Str. = stream. *Oncorhynchus* = *Oncorhynchus mykiss*; *Astroblepus* = one or more of three native species in this genus

Station	Altitude (m)	pH	Temperature (°C)		Species captured	No. specimens
			Air	Water		
Stations sampled in 1989						
Chirimachay Str.	3,600	7.5	24	13	*Oncorhynchus*	309
El Oso Lagoon	3,052	7.0	22	20	Plankton	
El Susto Str., site 2	2,650	7.0	12	7	*Astroblepus*	10
Del Pato Lagoon	3,253	7.0	17	15	*Oncorhynchus*	101
Jaboncillo Str.	2,660	7.0	23	18	Plankton	
La Playa River	2,650	7.0	20	17	*Oncorhynchus*	3
Las Palmas River	2,063	7.0	22	20	*Oncorhynchus*	93
Laplap Lagoon, site 3	3,990	7.5	12	11	Plankton	
Los Alisos Str.	2,650	7.0	22	18	*Astroblepus*	11
Manachaqui Str.	3,400	7.0	15	11	*Oncorhynchus*	205
Pamapa Hermoza Str.	3,600	7.0	10	9	*Oncorhynchus*	116
Paredones Lagoon	3,252	7.0	21	18	Plankton	
Puerta del Monte Str.	3,190	7.0	22	18	*Oncorhynchus*	66
Shochos Str.	3,290	7.0	17	15	*Oncorhynchus*	65
Stations sampled in 1989 and 1990						
Cerro Central Str., 1989	2,300	7.0	24	20	*Oncorhynchus*	31
1990	2,600	7.0	24	20	*Oncorhynchus*	16
El Eco Lagoon, 1989	3,054	7.0	18	12	Plankton	
1990	3,050	7.0	18	12	Plankton	
El Susto Str., site 1, 1989	2,650	7.0	18	9	*Astroblepus*	3
1990	2,600	7.2	19	15	*Astroblepus*	55
Laplap Lagoon, site 1, 1989	3,990	7.5	19	15	Plankton	
1990	3,990	7.5	5	5	Plankton	
Laplap Lagoon, site 2, 1989	3,985	7.5	12	10	Plankton	
1990	3,985	7.5	5	3	Plankton	
Montecristo Str., 1989	2,600	7.0	23	21	*Oncorhynchus*	1
1990	2,480	7.0	10	16	*Oncorhynchus*	11
Negra Lagoon, 1989	3,252	7.0	10	8	*Oncorhynchus*	1
1990	3,640	7.2	12	10	Plankton	
Pajaten Str., 1989	2,000	7.0	23	20	*Oncorhynchus*	66
					Astroblepus	1
1990	2,680	7.0	22	18	*Oncorhynchus*	2
				16	*Astroblepus*	103
					Plankton	
1990	2,100	7.0	19		*Oncorhynchus*	168
					Astroblepus	1
Pampa del Cuy Lagoon, 1989	3,400	7.0	10	8	Plankton	
1990	3,400	7.9	8	5	Plankton	
Stations sampled in 1990						
Abiseo River	2,200	7.2	16	9	*Oncorhynchus*	11
Abiseo River, Jucusbamba	1,870	7.0	15	10	*Oncorhynchus*	3
Abiseo River, Las Palmas	2,650	7.2	19	13	*Oncorhynchus*	36
					Plankton	

(*Continued*)

Table 1. Stations, field data, and samples collected in the aquatic environments of the Parque Nacional Río Abiseo, July 1989 and July 1990. No. = number; Str. = stream. *Oncorhynchus* = *Oncorhynchus mykiss*; *Astroblepus* = one or more of three native species in this genus–cont'd.

Station	Altitude (m)	pH	Temperature (°C) Air	Temperature (°C) Water	Species captured	No. specimens
Alpamachay Str.	3,500	7.2	16	8	*Oncorhynchus* Plankton	49
Amarillas Str.	1,760	7.0	18	16	*Astroblepus* Plankton	27
Blanca Str.	2,280	7.2	14	10	*Astroblepus*	7
Casa de Tejas Str.	2,600	7.0	14	12	*Astroblepus*	2
Chorobamba Str.	1,680	7.0	20	22	*Astroblepus*	50
Colorada Lagoon	3,680	7.2	12	10	Plankton	
El Acre Str.	1,700	7.0	15	12	*Astroblepus*	10
El Colpar Str.	2,600	7.0	14	12	*Astroblepus*	9
El Llanto Str.	2,400	7.0	24	20	*Oncorhynchus* *Astroblepus*	1 10
Huairurito Str.	1,720	7.0	17	16	*Astroblepus*	8
Hualanga Str., El Molino	2,580	7.2	20	15	*Astroblepus*	37
Hualanga Str., La Quinta	2,400	7.2	12	10	*Astroblepus*	24
Hualanga Str., Zarumilla	2,500	7.0	23	18	*Astroblepus*	17
Iparraguirre Str.	2,650	7.2	14	12	*Astroblepus*	47
Jucusbamba Str.	1,940	7.2	25	15	*Astroblepus* Plankton	46
La Doncella Str.	2,200	7.0	15	10	Plankton	
La Empedrada Lagoon	3,620	7.2	10	8	Plankton	
Montecristo R, La Playa	2,400	7.2	19	17	*Oncorhynchus*	31
Negra Str.	2,100	7.0	15	10	Plankton	
Paredones Lagoon	3,252	7.2	10	8	Plankton	
Peligrosa Str.	2,045	7.0	22	18	*Oncorhynchus* Plankton	47
Ruibardo Str.	3,600	7.2	10	12	*Oncorhynchus* Plankton	116
San Marcos Str.	1,840	7.0	18	15	*Astroblepus* Plankton	30
Sausal Str.	2,250	7.2	19	16	*Oncorhynchus* Plankton	21
Verde Lagoon	3,600	7.2	12	10	Plankton	

water transparency was high, even in steep terrains, because we sampled during the dry season. As in the previous year, samples of fishes, insects, and plankton were collected from many different types of water bodies in the study area.

2.1.2. Lower Huallaga River basin

This study area (07°16′ S, 76°44′ W to 06°36′ S, 76°10′ W) included the basin of the Huallaga River from Moyobamba to Yurimaguas (Department of San Martin) and included, among others, the drainage basins of the Cumbaza, Mayo, Saposoa, and Sisa rivers.

The assessment of the ichthyological fauna in the lower Huallaga River basin was carried out by sampling 27 stations in each of two expeditions: November–December (rainy season) 1997 and September–October (dry season) 1998. Twenty water bodies were surveyed: lagoons, reservoirs, streams, and medium-sized and large-sized rivers, including the Huallaga.

In Table 2, the station locations and physical characteristics of the water masses sampled during the Huallaga River basin expedition are given. Water temperatures fluctuated between 21°C and 33°C both in the rainy season and the dry season. The pH values of the water bodies measured in 1997 were between 6.3 and 8.0 and of those measured in 1998 were between 6.6 and 9.1; most water bodies had slightly acidic pH values during the rainy season and slightly basic pH values during the dry season. All salinity values except that for Limón Lagoon during the dry season ranged from 0.0‰ to 4.4‰; most values were 1.0 or less. In 1997, the Mishquiyacu Stream had the highest salinity value because it has a saline upstream basin. In 1998, all values were <1‰ except those for Mishquiyacu Stream (4‰) and, notably, Limón Lagoon (25‰).

2.1.3. Santa River and Río Grande

The Santa River borders La Libertad and Ancash departments in the north-central Peruvian Pacific Coast (7°51′ S, 77°11′ W to 10°14′ S, 78°50′ W). It extends more than 350 km in length and originates at more than 5000 m.a.s.l. Within the last 200 km, the river descends from 4000 m.a.s.l. to sea level. The river widens from approximately 30- to 40-m width in the upper part to approximately 120 m at the outlet. Average flow rate at the mouth of the river is highly seasonal: approximately $972\,m^3/s$ during the rainy season and only $24\,m^3/s$ in the dry season. We sampled this river and many of its tributaries in both the rainy and dry seasons during 1989 and 1990.

The Rio Grande (Department of Ica; 13°30′ S, 75°15′ W) is in the south-central Peruvian Pacific Ocean coastal region, 400 km south of Lima. It is a coastal, permanent-water river, although the volume of water diminishes drastically from April to November and, as a consequence, numerous shallow ponds and riffles form. The river's bed averages 100 m in width but is reduced to 25 m width during the Southern Hemisphere winter. A survey (4 stations) was carried out in July 1994. The survey area extended from 40 km upstream of the Pan-American Highway to the river outlet (a total of approximately 50 km).

2.2. Biological Samples and Analyses

In the PNRA, Huallaga River basin, Santa River, and Rio Grande, the fishes were captured by intensively sampling shallow water bodies with shore seines of two sizes (2.4-m length × 1.8-m height and 7.0-m length × 1.8-m height) and made of 4-mm mesh. Each station was repeatedly sampled so that qualitative assessments of the relative abundances of the species present could be made.

Table 2. Huallaga River basin (Department of San Martín) sampling locations and their physical and chemical parameters, numbers of species collected, and relative frequencies of occurrence of alien species, 1997 and 1998. Transparency was measured using a Secchi disk. Alien species: O = *Oreochromis niloticus*, P = *Poecilia reticulata*, C = *Cyprinus carpio*. Relative frequency (rel. freq.): present (x), moderate (xx), abundant (xxx). R. = River; Tot. = total transparency; NA = not available

		Temperature (°C)		pH		Salinity (‰)		Transparency (cm)		Total number species		Alien species/ rel. freq.	
Water body	Coordinates	’97	’98	’97	’98	’97	’98	’97	’98	’97	’98	’97	’98
Ahuashiyac-u Stream	06°30′38″ S 76°20′12″ W	29.0	27.5	6.6	8.8	2.00	0.11	Tot.	Tot.	18	17	P	O, P
Cumbaza R., San Antonio	06°28′16″ S 76°22′48″ W	30.5	26.4	6.5	9.1	0.50	0.07	Tot.	Tot.	9	7		
Cumbaza R., Juan Guerra	06°35′13″ S 76°20′10″ W	26.0	33.0	6.6	8.8	0.12	0.11	Tot.	Tot.	12	16	O, P	OO, P
Cumbaza R. & Mayo R. junction	06°30′10″ S 76°24′20″ W	26.0	33.0	6.6	8.8	0.12	0.11	Tot.	Tot.	9	18	PPP	OOO, PP
Gera Reservoir	06°07′00″ S 76°53′09″ W	23.0	21.0	6.3	7.1	0.00	0.14	45	58	2	2		OO
Gera R. (mouth)	06°05′37″ S 76°52′27″ W	23.0	22.0	6.3	7.8	0.00	0.04	20	80	4	18		O
Huallabamb-a R. (mouth)	07°21′43″ S 76°50′16″ W	22.0	25.7	6.5	7.4	1.00	0.11	20	Tot.	10	9		
Huallaga R., Bellavista	06°40′39″ S 76°16′49″ W	23.1	27.8	8.0	7.5	1.00	0.15	13	83	17	16	PPP	P
Huallaga R., Chazuta	06°46′08″ S 76°17′26″ W	25.7	27.8	8.0	7.5	0.50	0.14	5	30	21	24		P
Huallaga R., Juanjui	06°40′39″ S 76°16′49″ W	23.1	27.8	8.0	7.5	1.00	0.15	13	83	34	12		
Huallaga R., Shapaja	06°34′53″ S 76°15′44″ W	27.0	26.3	8.0	7.5	0.00	0.18	12	20	13	14		
Indoche R.	06°02′52″ S 77°02′28″ W	23.5	24.4	6.5	7.4	0.00	0.11	5	60	6	7		O
Limón Lagoon	06°43′40″ S 76°10′10″ W	NA	29.8	NA	8.0	NA	24.90	NA	80	3	4	OO	OO
Mashuyacu Reservoir	06°06′29″ S 77°11′19″ W	23.3	24.3	6.8	6.6	1.00	0.04	12	58	4	8	OO, PP	OO, PP, C
Upper Mayo R., Tahuishco	06°03′59″ S 76°54′45″ W	22.5	23.3	6.6	7.3	1.00	0.11	11	34	11	26		OOO, PP
Mishquiyac-u Stream, Pilluana	06°06′29″ S 77°11′19″ W	25.5	28.8	7.5	7.8	4.00	4.36	100	76	22	14		
Potochico Stream	07°01′05″ S 76°29′53″ W	26.5	24.9	6.5	6.7	2.00	0.36	100	76	14	10	OO, P	P
Pucayacu Stream	06°33′33″ S 76°20′00″ W	26.0	30.7	6.6	8.8	0.00	0.11	Tot.	Tot.	14	16		
Sacanche Stream	07°10′48″ S 76°45′14″ W	28.0	24.3	6.5	7.4	1.00	0.87	20	50	11	16		P
San Pablo Reservoir	06°48′36″ S 76°34′40″ W	28.0	28.6	6.5	7.3	2.50	0.11	15	13	9	15		
Saposoa R.	07°03′51″ S 76°42′37″ W	33.0	22.9	6.6	7.6	1.00	0.30	35	20	14	16		
Sauce Lagoon	06°43′44″ S 76°13′06″ W	23.0	28.8	7.5	8.2	2.00	0.40	Tot.	205	6	6	OOO, P	OOO, PP
Shanusi R.	05°54′44″ S 76°06′46″ W	26.0	28.0	6.9	7.5	0.00	0.11	20	Tot.	22	25		
Lower Sisa R.	06°53′26″ S 76°34′00″ W	29.5	28.8	6.5	7.4	1.00	0.14	40	30	12	14		P
Upper Sisa R.	06°43′40″ S 76°41′36″ W	29.7	26.7	6.5	7.4	1.00	0.13	Tot.	20	11	13		
Tonchima R.	06°02′56″ S 77°08′55″ W	28.0	24.3	6.6	7.4	3.00	0.11	5	52	7	9		
Yuracyacu R.	05°54′44″ S 76°06′46″ W	21.5	27.0	6.9	7.5	0.00	0.11	20	Tot.	15	12		

The fishes were fixed in 10% formalin. Specimens larger than 150-mm total length were also internally injected with the same solution. For transportation back to the laboratory, the fixed fish specimens were wrapped in cotton gauze, placed in plastic bags, and humidified in 10% formalin. The bags were hermetically sealed in plastic carboys.

At the facilities of the Museo de Historia Natural of San Marcos University (MUSM) in Lima, Peru, the species collected and relative abundances of the aquatic biota and the necton were recorded following the methodology established for Amazonian water bodies (Roldán-Pérez, 1992). The limnological analyses were performed in the Laboratorio de Limnología del Instituto de Investigaciones de la Amazonia Peruana in Iquitos. Identification of the introduced species was accomplished using the original descriptions and the approach of Smith and Stearley (1989) and Ortega (1991). The determination of native species in the PNRA was done using the works of Regan (1904) and Eigenmann and Allen (1942). Most of the fish species from the lower Huallaga River basin, the Santa River, and the Rio Grande were identified using taxonomic keys and descriptions of different taxonomic categories, mainly those of Gery (1977) and Burgess (1989) and the classification according Reis et al. (2003) for native fishes and Bussing (1987) and Trewavas (1983) for alien fishes such as poecilids and cichlids.

From the Huallaga River collections, the stomach contents from the alien species, including 200 *O. mykiss*, and from a number of native species were sorted using a stereomicroscope. Identifications of the stomach contents and of the arthropods collected were made with the aid of taxonomic keys.

From PNRA, plankton was collected using a standard 45-µm-mesh net. The samples were preserved in 10% formalin; 5 ml of the solution was added to each 100-ml sample. Analyses of the plankton samples were carried out in the Department of Limnology of the MUSM.

3. RESULTS

The introductions of the 20 alien fish species and transfers of the 7 native species have impacted each of the river basins sampled, and each basin has developed particular problems due to these invasions. Here, we evaluate the introductions and transfers by location and then comment on the alien fish species known to be in Peru.

3.1. Case Studies

3.1.1. Amazon River system

Parque Nacional Río Abiseo. Four species were recorded from water bodies of the PNRA—one alien and three native. The dominant species was the alien *Oncorhynchus mykiss*. The three native species were siluriforms of the genus

Astroblepus (Family Astroblepidae) and were found, among other places, in the Rio Pajaten (*A. simonsi*), in waters near the town of Los Alisos (*A.* sp. A), and in El Susto stream (*A.* sp. B).

At most stations we sampled, *O. mykiss* was the only species we found (Table 1). In 1989, *O. mykiss* was recorded at 12 of the 23 stations, whereas the *Astroblepus* spp. were found only at 4 stations. In that year, *O. mykiss* also overwhelmingly predominated in both number of specimens (1081; 98% of all individuals collected) and biomass (grams total weight: *O. mykiss* = 282,900; *Astroblepus* spp. = 750). In 1990, *O. mykiss* was recorded at 13 of the 38 stations, and *Astroblepus* spp. was found at 17 stations (Table 1). In that year, the numbers of fishes captured for the alien and native species were very close (512 and 483, respectively), but *O. mykiss* again markedly predominated in biomass (grams total weight: *O. mykiss* = 153,600; *Astroblepus* spp. = 12,075).

The native species were more common in the southern area of the PNRA, where mountain slopes are steeper, whereas the exotic species were common in the northern area, where mountain slopes have a more gradual inclination. The alien and native species were found in sympatry in two streams (Pajatén and El Llanto); however, they occupied different microhabitats. In waterfalls with slopes of 45° or more, the native fishes were often separated from the salmonids; they occupied reduced and isolated water bodies, and some populations seem to be in a state of starvation.

The accompanying fauna was composed mainly of insects, principally of the families Leptoceridae and Helicopsychidae (Order Tricoptera), Chironomidae (Diptera), Baetidae (Efemeroptera), and Perlidae (Plecoptera). They were found in the stomach contents of *O. mykiss* in similar proportions to those found in the ambient environment. In addition, in the collections from three stations, native fishes were also found in the stomach contents of the alien species.

Several high-altitude or isolated (by waterfalls or rapids) lagoons surveyed did not contain fishes of any kind (e.g., Laplap, El Eco, El Oso). Colonization of both native fishes and *O. mykiss* was apparently impeded at those locations. Those water bodies had high diversities, but low abundances, of phytoplankton; the representative species were in the Chlorophyta (39 species), Bacillariophyta (26 species), and Cyanophyta (10 species). Their zooplankton fauna was scarce and was represented by just two forms of Rotifera and one of Copepoda.

Lower Huallaga River Basin. The diversity of habitats surveyed in the lower Huallaga River basin included both lotic and lentic natural water bodies and man-made reservoirs. The ichthyological diversity of these environments varied widely. The natural lotic water bodies were the most diverse; diversity was low in the lentic lagoons and reservoirs and in Potochico stream, where human influences had occurred (Table 2). In 1997, we recorded 21 species from the Huallaga River at Chazuta, 34 species from the lower Huallaga River at Juanjui, and 22 species from the Mishquiyacu Stream at Pilluana and Shanusi River. In contrast, we recorded only 2 species from Gera Reservoir, 4 species from Mashuyacu

Stream, 9 species from the San Pablo Reservoir, and 6 species from Sauce Lagoon. Other water bodies with less than 10 species were torrential-water tributaries of the Alto (upper) Mayo River basin (Indoche and Tonchima rivers) and the Bajo (lower) Mayo River basin (Cumbaza River), the mouth of the Gera River, and Limón Lagoon.

The number of species recorded in the lower Huallaga River basin during 1998 was more than 74 (if we include those identified as unknown species in several genera). This number was higher than that obtained in 1997 because in 1998 we collected during the dry season, when water levels were lower and the fish were more concentrated. Nevertheless, the patterns in species diversity that we saw the previous year were generally maintained (Table 2).

The species collected in the Huallaga River basin were distributed among 9 orders and 23 families (Table 3). The Characidae family was the most diverse (at least 22 species), followed by the Loricariidae (at least 13 species), and Cichlidae (7 species). The remaining families were each represented by only a few species; however, in the rivers, some of those species were widespread (e.g., *Hoplias malabaricus*, a widely distributed predator, and *Synbranchus marmoratus*, a long-bodied, carnivorous, snake-like fish) or abundant (e.g., the hematofagous Trichomycterid *Vandellia cirrhosa*). Other widespread species included those of small-sized fishes such as *Astyanax bimaculatus*, *Bujurquina huallagae*, and those in the genera *Bryconamericus*, *Cheirodon*, and *Knodus*. Only 3 species collected in the Huallaga River basin were alien. These introduced species, *Cyprinus carpio*, *Oreochromis niloticus*, and *Poecilia reticulata*, were, respectively, recorded at 1, 11, and 11 stations during our study (Table 2); and they were sympatric at 7 stations. In 1997, *O. niloticus* was recorded in two lotic environments: the Cumbaza River (at Juan Guerra) and Potochico Stream (Table 2). Both of these introductions may have resulted from fish-culture activities. The Cumbaza River is located 5 km from the mouth of the Ahuashiyacu Stream, which receives the drainage of tilapia farms. The waters of the Caño Potochico drain into a flooded area and, during the rainy season, join the Huallaga River basin.

Stomach content analyses were performed on a number of species. Most species were microfagous. The native *Bryconamericus* spp., *Bujurquina huallagae*, *Cichlasoma amazonarum*, *Hypostomus emarginatus*, *Knodus* spp., and *Steindachnerina* spp. all share this feeding niche with *O. niloticus*, and *P. reticulatus*. Herbivorous species included *Ceratobranchia* sp., *Creagrutus* spp.; insectivorous species included *Aphyocharax pusillus*, *Ctenobrycon hawuxwellianus*, *Galeocharax gulo*, *Paragoniates alburnus*, and *Tatia perugiae*; and omnivorous species included *Astyanacinus multidens*, *Astyanax bimaculatus*, *Moenkhausia* spp., and *Scopaeocharax rhinodus*.

3.1.2. Pacific Ocean Coastal River system

Alien species nearly totally predominated in the coastal rivers that we sampled. *Poecilia reticulata* has been the most frequently captured alien species in the

Table 3. Fish species recorded in different water bodies of the lower Huallaga River basin, 1997 and 1998. Alien species are highlighted in bold print. R. = River, Str. = Stream, Re. = Reservoir, x = present

ORDER family	Species	Ahuashiyacu Str.	Cumbaza R.	Gera R.	Huallabamba R.	Huallaga R.	Indoche R.	Limón Laboon	Mashuyacu Re.	Mayo R.	Mishquiyacu Str.	Potochico Str.	Pucayacu R.	Sacanche Str.	San Pablo Re.	Saposoa R.	Sauce Lagoon	Shanusi R.	Sisa R.	Tonchima R.	Yuracyala R.
BELONIFORMES																					
Belonidae	*Pseudotylosurus microps*				x	x												x			x
CHARACIFORMES																					
Anostomidae	*Schizodon fasciatus*					x															
Characidae	*Aphyocharax pusillus*			x		x					x			x				x			x
	Astyanacinus multidens	x								x			x								
	Astyanax bimaculatus	x	x			x	x	x	x		x	x	x			x	x	x	x	x	
	Astyanax fasciatus	x	x			x				x		x	x						x		
	Astyanax sp.	x	x	x		x	x			x				x	x	x					
	Bryconamericus spp.	x	x	x	x	x		x	x	x	x	x	x		x	x	x	x		x	
	Ceratobranchia sp.	x	x							x											x
	Chaetostoma sp.																				x
	Characidium spp.		x	x	x	x						x	x		x	x					x
	Charax tectifer																				x
	Cheirodon sp.																				x
	Clupeacharax anchoveoides				x				x												
	Creagrutus spp.		x	x		x				x			x	x		x			x	x	x
	Ctenobrycon hauxwellianus		x			x				x		x			x	x					x
	Cynopotamus amazonus					x															
	Galeocharax gulo						x							x	x	x		x	x		
	Hemibrycon sp.		x	x			x		x	x										x	
	Knodus spp.		x		x	x				x			x	x	x			x			x
	Moenkhausia comma		x			x				x											
	Moenkhausia dichroura					x				x											

(*Continued*)

Table 3. Fish species recorded in different water bodies of the lower Huallaga River basin, 1997 and 1998. Alien species are highlighted in bold print. R. = River, Str. = Stream, Re. = Reservoir, x = present—cont'd.

ORDER family	Species	Ahuashiyacu Str.	Cumbaza R.	Gera R.	Huallabamba R.	Huallaga R.	Indoche R.	Limón Laboon	Mashuyacu Re.	Mayo R.	Mishquiyacu Str.	Potochico Str.	Pucayacu R.	Sacanche Str.	San Pablo Re.	Saposoa R.	Sauce Lagoon	Shanusi R.	Sisa R.	Tonchima R.	Yuracyala R.
	Paragoniates alburnus	x				x							x	x	x	x		x			x
	Prionobrama filigera		x			x															
	Pygocentrus nattereri					x															
	Roeboides sp.									x					x						
	Scopaeocharax rhinodus	x	x	x		x							x	x		x			x		
	Serrasalmus sp.																				x
	Triportheus albus					x															
Curimatidae	*Curimatopsis macrolepis*	x	x				x			x								x			
	Steindachnerina guentheri		x	x					x	x		x				x		x			
	Steindachnerina hypostoma					x								x						x	x
Erythrinidae	*Erythrinus erythrinus*		x											x	x						
	Hoplias malabaricus			x						x			x		x	x		x	x		
Gasteropelecidae	*Thoracocharax stellatus*					x					x										
Parodontidae	*Apareiodon* sp.		x	x	x	x				x											
	Parodon sp.		x		x	x								x	x				x		
Prochilodontidae	*Prochilodus nigricans*		x											x				x			
CLUPEIFORMES																					
Engraulididae	*Anchoviella* sp.				x																
CYPRINIFORMES																					
Cyprinidae	***Cyprinus carpio***							**x**													
CYPRINODONTIFORMES																					
Poecilidae	***Poecilia reticulata***	**x**	**x**			**x**		**x**	**x**	**x**		**x**	**x**	**x**	**x**		**x**	**x**	**x**	**x**	
Rivulidae	*Rivulus* sp.																				

GYMNOTIFORMES																					
Apteronotidae	*Apteronotus albifrons*																	x			
Sternopygidae	*Eigenmannia virescens*			x														x			
PERCIFORMES																					
Cichlidae	*Bujurquina huallagae*	x	x	x		x	x			x		x	x		x	x	x	x	x	x	
	Bujurquina ortegai		x			x															
	Crenicichla sedentaria		x	x		x							x		x	x		x	x		x
	Cichlasoma amazonarum	x	x	x	x				x		x	x							x		x
	Heros appendiculatus		x			x													x		
	Hypselacara temporalis														x				x		
	Oreochromis niloticus	**x**	**x**	**x**			**x**	**x**	**x**	**x**		**x**					**x**				
SILURIFORMES																					
Aspredinidae	*Bunocephalus* sp.					x					x										
Astroblepidae	*Astroblepus* spp.								x	x											
Auchenipteridae	*Auchenipterus nuchalis*									x											
	Tatia perugiae		x	x						x											
Callichthyidae	*Callichthys callichthys*						x					x						x			
Loricariidae	*Ancistrus* spp.	x	x										x			x			x	x	
	Aphanaotorulus unicolor				x	x				x	x			x				x			
	Brochiloricaria sp.			x																	
	Chaetostoma spp.	x	x	x		x				x			x			x					
	Cocliodon sp.																		x		
	Farlowella spp.		x			x					x		x			x		x			
	Hypostomus emarginatus	x	x			x	x			x					x	x	x	x		x	x
	Lasiancistrus sp.									x											
	Loricaria sp.			x		x				x						x					x
	Panaque gnomus									x											
	Panaque nocturnus					x				x											
	Rineloricaria sp.	x			x	x					x							x	x		
	Sturisoma nigrirostrum					x								x							x
Pimelodidae	*Hemisorubin platyrhynchos*					x															
	Heptapterus sp.						x			x											
	Hypophthalmus edentatus									x											

(*Continued*)

Table 3. Fish species recorded in different water bodies of the lower Huallaga River basin, 1997 and 1998. Alien species are highlighted in bold print. R. = River, Str. = Stream, Re. = Reservoir—cont'd.

ORDER family	Species	Ahuashiyacu Str.	Cumbaza R.	Gera R.	Huallabamba R.	Huallaga R.	Indoche R.	Limón Laboon	Mashuyacu Re.	Mayo R.	Mishquiyacu Str.	Potochico Str.	Pucayacu R.	Sacanche Str.	San Pablo Re.	Saposoa R.	Sauce Lagoon	Shanusi R.	Sisa R.	Tonchima R.	Yuracyala R.
	Microglanis sp.																				x
	Pimelodella gracilis									x								x			
	Pimelodella spp.			x		x				x	x			x				x			
	Pimelodus blochii					x												x			x
	Pimelodus pictus					x															
	Pseudoplatystoma fasciatum					x															
	Rhamdia quelen	x	x						x	x			x	x					x		
	Sorubim lima					x															
Trichomycteridae	*Henonemus taxistigmus*			x		x					x							x			
	Trichomycterus sp.																				
	Vandellia cirrhosa			x		x					x							x			
SYNBRANCHIFORMES																					
Synbranchidae	*Synbranchus marmoratus*				x	x						x							x		
TOTAL		18	32	22	10	56	11	4	10	32	22	12	18	16	16	18	6	32	18	9	20

rivers of the central coast (Departments of Ancash, Lima, and Ica), according to Sifuentes (1992). We collected 11 species—9 native and 2 alien—in the Santa River. These were distributed zonally. *Astroblepus simonsü*, *Oncorhynchus mykiss*, and *Orestias agassii* were found in the upper area; *Basilichthys semotilus* and *O. mykiss* were found in the middle area; and *Aequidens rivulatus*, *Brycon atrocaudatus*, *Bryconamericus peruanus*, *Lebiasina bimaculata*, *Poecilia reticulata*, and *Trichomycterus punctulatus* were found in the lower area. In the Rio Grande, *Oreochromis niloticus* and *P. reticulata* were the only species present in the final 10 km of the river. The only native fish collected, *Trichomycterus punctulatus*, began to appear only around 50 km upstream from the outlet.

3.2. ALIEN FISHES IN PERU

Here, we list the known alien fishes in Peru. Species in several of these fish families (e.g., Cichlidae, Cyprinidae, Salmonidae) have been introduced in widespread areas throughout the world. We summarize the known history of these introductions into Peru and the known current status of the invasions by these species. The known general locations of these species are listed in Table 4. Half of these introduced species have been found in natural environments within one or more regions of Peru; seven have been introduced into reservoirs for various purposes, and nearly three-quarters have been introduced for various types of aquaculture.

1–3. *Aristichthys nobilis* (big-head carp), *Ctenopharyngodon idella* (grass carp), *Hypophthalmichthys molitrix* (silver carp) (all Cyprinidae). In the 1970s, these species were introduced from Israel and Panama for research purposes at La Molina University. Along with these species, considerable numbers of *Cyprinus carpio* (common carp) were also introduced from those locations.

4. *Carassius auratus* (pez dorado, goldfish; Cyprinidae). This ornamental species, native to Asia, was introduced more than 50 years ago. Although its distribution is principally contained because it is kept in aquaria, it has been found in natural environments such as the wetlands of the central coast; for example, the Humedales de Villa (Department of Lima) (Castro et al., 1998).
5. *Cichlasoma nigrofasciatum* (ciclasoma, convict cichlid; Cichlidae). This species, introduced in the late 1980s for the aquarium trade, is native to Central America. It, too, has adapted to the wetlands of Lima (e.g., Humedales de Villa) (Castro et al., 1998).
6. *Cyprinus carpio* (carpa comun, common carp; Cyprinidae). This species is native to Asia. It has been introduced from Japan and China since 1940 for aquaculture. In 1987, this species was introduced into rivers of Peruvian high-altitude forests as part of programs developed by the Native Communities Asociación de Estudios y Proyectos e Desarrollo (ASPRODE) for native communities such as the Ashaninkas, who live

Table 4. Alien freshwater species introduced and native freshwater fishes transferred to nonindigenous water masses in Peru. Altitudinal divisions follow Gentry, 1997. Numbers below subheadings are elevations above mean sea level, in meters. L.T.S. = Lake Titicaca System, A = present in aquaculture facilities, X = present in natural areas, R = present in reservoirs.

	River systems						
	Pacific Ocean system			L.T.S.	Amazon River system		
Fishes	Coast 0–1000	Western Andes >1000–3500	High-lands >3000–5000[1]	Altiplano >4000	High-lands >3500[1]	Eastern Andes high forest 1000–3500	Low forest 500–1000
Alien fishes							
Anabantidae							
Trichogaster leerii	A						X
Atherinidae							
Odonthestes bonariensis		A	A	X	A		
Cichlidae							
Cichlasoma nigrofasciatum	X						
Oreochromis aureus						A, R	
Oreochromis hornorum	A					A, R	A
Oreochromis mossambicus	A						
Oreochromis niloticus	X, R, A					X, R, A	R, A
Oreochromis urolepis	A						
Tilapia rendalli	A					A, R	A
Cyprinidae							
Aristichythys nobilis	A						
Carassius auratus	X, A						A
Ctenopharyngodon idella	A						
Cyprinus carpio	A					X, A	A
Hypophthalmichthys molitrix	A						
Poecilidae							
Gambusia cf. *affinis*	X, A						
Poecilia reticulata	X	X				X	X
Poecilia velifera	X						
Xiphophorus helleri	X						
X. maculatus	X						
Salmonidae							
Oncorhynchus mykiss		X	X	X	X		
Lowland forest native fishes							
Arapaima gigas	R						A
Astronotus ocellatus	R						A
Brycon cephalus						X	A
Cichla monoculus	R						A
Colossoma macropomum						X	A
Piaractus brachypomus						X	A
Prochilodus nigricans						X	A

[1] Highest point in the Peruvian Andes: 6,768 m above sea level (Nevado Huascarán).

along the Perené River in Junin. Presently, *C. carpio* is being successfully farmed in the Chanchamayo and Satipo valleys (Department of Junin) (Luna et al., 1999) and the species occurs in the Mashuyacu Stream.

7. *Gambusia* cf. *affinis* (gupi, mosquitofish; Poecilidae). This species is native to Central America, where is called the mosquito fish. It was introduced into Peru in 1940 to control malaria vectors by eating mosquito larvae and was established in natural water bodies for natural reproduction. Its ecological effects are unknown (FAO, 1998). In addition, at least 15 years ago, it was reintroduced accidentally into culture ponds and channels along the coast in the Department of Tumbes, mixed with shrimp larvae. Presently, this species also occurs in the Humedales de Villa (Castro et al., 1998).
8. *Odonthestes bonariensis* (pejerrey argentino; Atherinidae). This species is native to cold waters of southern Brazil and Argentina, where it is used as a food fish. In the early 1960s, it was accidentally introduced into Lake Titicaca through the Bolivian side from Poópo Lake (Treviño et al., 1991). In the 1970s, it was introduced into Pacucha Lagoon (Department of Apurímac). Presently, it is well adapted to Lake Titicaca and there is an active commercial fishery based on this species at Bahia Puno in Lake Titicaca, where abundant primary production stimulates high population levels of this species. This alien species also feeds on native fishes.
9. *Oncorhynchus mykiss* (rainbow trout; Salmonidae). This species, native to cold-water northwestern rivers of the USA, was introduced into cold-water rivers and lagoons of the Peruvian Andes for fish farming and sport fishing (FAO, 1998). It is the most widely introduced of the salmonids. The Peruvian Department of Fishing and Hunting, as well as private enterprises, introduced *O. mykiss* from Chile and the USA (FAO, 1998). The species was introduced into Lake Titicaca in 1940 (Treviño et al., 1991). The species currently exists not only in the PNRA but also in the Santa River basin in the high-altitude, colder portions of the river. Recently, the Ares Mining Company introduced only females of new strains into lagoons of the Department of Arequipa highlands (Ortega, personal observation).
10. *Oreochromis aureus* (tilapia dorada, blue tilapia; Cichlidae). This species' origin is uncertain, apparently it is a hybrid imported from Cuba in 1983 (FAO, 1998). Presently, it is used for fish culture in the Department of San Martin (e.g., in Moyobamba).

11–14. *Oreochromis hornorum* (wami tilapia), *O. mossambicus* (Mossambique tilapia), *O. niloticus* (Nile tilapia), and *O. urolepis* (rufigi tilapia) (all Cichlidae). These species, native to Africa, were introduced into Peru from Brazil and Panama between 1979 and 1983 for fish culture (FAO, 1998). They were used to implement hybridization experiments being conducted in Brazil. During the 1970s and 1980s, the Regional Direction of Fisheries in Moyobamba developed programs for fish farming of *O. niloticus* and *Tilapia rendalli* in the Special Project of the Alto Mayo (Guerra et al., 1999). Presently, only *O. niloticus* is found in natural environments, mainly in the Department of San Martin.

15. *Poecilia reticulata* (gupi, guppy; Poecilidae). This small, viviparous species is native to northern South America and Central America. It was introduced during the 1940s for public health to control malaria insect vectors (FAO, 1998). Presently, this species resides in most of the natural environments along the north and central Peruvian coast, as has been confirmed through fieldwork conducted by us near the coast (e.g., the Santa River basin) and by Sifuentes (1992), and in both high- and low-altitude rainforest water bodies of Ucayali and Loreto, and even in contaminated waters.
16. *Poecilia velifera* (moli, sailfin molly; Poecilidae). This viviparous, ornamental species was introduced from tropical waters of Central America in the 1980s. Presently, *P. velifera* is found in natural environments of the coastal region in the Department of Lima (e.g., Humedales de Villa).
17. *Tilapia rendalli* (tilapia del Congo, redbreast tilapia; Cichlidae). This omnivorous species, native to Africa, was introduced from Brazil in 1966 for aquaculture (FAO, 1998) (see *O. niloticus*, above). In 1968, this species was introduced as living food for the giant Amazonian species, *Arapaima gigas*, which had been transferred to Sauce Lagoon (Department of San Martin).
18. *Trichogaster leerii* (pearl gurami; Anabantidae). This species was introduced from its native southeastern Asian still-water habitat into Lima and Iquitos (Department of Loreto) during the 1970s for the aquarium trade. However, there is already a population adapted to the polluted waters of the Moronacocha Lagoon in Iquitos (Department of Loreto; 0340′ S, 7315′ W).

19–20. *Xiphophorus helleri* (green swordtail) and *X. maculates* (southern platyfish) (both peces espada; Poecilidae). According to Castro et al. (1998), these species, which are in the same family as *Poecilia velifera*, also occur in the natural waters of coastal Peru, although in a smaller scale.

3.3. Species Transfers

According to Guerra et al. (1996, 1999) and Barthem et al. (1995) a few native fishes have been transferred from the lowland forest to other water systems of Peru. During the late 1960s and 1970s, a number of fingerlings of various native species (listed below) from lowland tropical forest river systems and lagoons were transferred to highland forest river systems and lentic waters (e.g., Sauce Lagoon; Sandoval Lagoon, Department of Madre de Dios) by the Fishery

Station of Loreto (Department of Iquitos). Transfers have also occurred from the Amazon River basin to the Pacific Ocean basin. Most are used for aquaculture.

1. *Arapaima gigas* (paiche; Arapaimatidae). This giant, carnivorous fish (2.4-m total length) from Amazonia inhabits quite waters, is ichthyophagous, and breeds after the fifth year of its life. It was introduced into lagoons in the highland forest (Sauce Lagoon) and, along with *Cichla monoculus*, reservoirs along the coast (San Lorenzo, Poechos [Department of Piura]); it has successfully established in the coastal reservoirs (Barthem et al., 1995). There are also well-established populations in lagoons in the lowland forest of southeastern Peru in the Madre de Dios River basin. Some populations are also found in Bolivia.

2–3. *Astronotus ocellatus* (acarahuasú, oscar) and *Cichla monoculus* (tucunaré) (both Cichlidae). These are Amazonian fishes of lowland forest lagoons. They were introduced together into reservoirs along the coast and into other basins during the 1970s, but with little success (see 1, above).

4. *Brycon cephalus* (sábalo cola roja; Characidae). This species is well adapted to fish farming, due to its fast growth. Adults of this species, as well as of *Colossoma macropomum* and *Piaractus brachypomus*, are induced to breed by hypophization and/or through the use of synthetic hormones.

5–6. *Colossoma macropomum* (gamitana, tambaqui) and *Piaractus brachypomus* (paco, pirapitinga) (both Characidae). These are micro- and macrophytophagous fishes. Their fingerlings, obtained annually in Iquitos, are transferred to other Amazonian river basins (e.g., the Huallaga, Perené, and Ucayali) for fish farming. These species, *Prochilodus nigricans*, and the alien *Cyprinus carpio* were introduced into the water bodies of Satipo (Department of Junin) in 1987 as part of the Native Community ASPROPE program.

7. *Prochilodus nigricans* (boquichico, black prochilodus; Prochilodontidae). This species is widely distributed (see 5–6, above). Its high-density populations and relatively large size make it an important fishery species; it constitutes one third of the commercial fishery of Peruvian Amazonia. It is also an important species for aquaculture because it could be readily reproduced in laboratory conditions and easily adapts to fishponds.

4. DISCUSSION

4.1. Ecological Aspects of Species Introductions

4.1.1. Natural influences

Biological pollution caused by the introduction and assimilation of alien species may alter aquatic ecosystems by directly or indirectly affecting the existence of native species (e.g., by competition, predation) and by alternating their habitats

(Primack, 1993; Simberloff, 2000). In the continental waters of Peru, alien fishes are adapted to both cold waters (e.g., *Oncorhynchus mykiss*) and warm waters (e.g., *Oreochromis niloticus*) (Ortega and Chang, 1998) and, thus, alien species are distributed in the Amazon River system, Pacific Ocean coastal river system, and Lake Titicaca system. In some cases, alien species have (possibly seriously) reduced native species distributions and abundances, principally through displacement and predation. For example, *O. mykiss* is an opportunist-predator species. It adapts easily to the availability and abundance of the prey organisms and is a predator of the native species of the both PNRA and Lake Titicaca.

Many biotic and abiotic factors may contribute to the ability of an introduced species to successfully colonize an area. In Peru, the uneven distribution of the fish species richness seems to affect the establishment of introduced species. Some alien species well settled in some natural environments do not yet predominate everywhere that they exist. Their abundances are inversely related to the fish species richness of the area involved. For example, in the cold-water rivers of PNRA, 4 native species occurred but the alien *O. mykiss* predominated. On the contrary, in the Huallaga River, at Juanjui, 34 species were recorded and the introduced tilapia was not among the predominant species. Tropical aquatic areas in particular typically contain more species than the numbers of possible available ecological niches. Thus, some activities (feeding for example) overlap in the niche spaces of native sympatric species (Machado-Allison, 1987). Under such conditions, the ecological web becomes dense and complex, hindering the successful establishment of exotic species.

Abiotic characteristics of ecosystems, such as current speed, bottom quality, and water chemistry (Welcomme, 1983), are also important factors that influence the establishment of alien species. For example, river and stream bottoms can be deepened or otherwise altered by high current speeds during short but intense seasonal floods, destroying nests and other reproductive habitats of species. This can prevent the establishment of introduced species that are not adapted to these types of environments. The hard and stony bottoms of most lotic water bodies in our study area might also adversely affect the establishment of nesting species that must build nests in sandy or slimy bottoms to spawn. These characteristics may have deterred the installation of tilapias in that type of fluvial system. Water flow, which is associated with current speed, is also important in the establishment of the alien species. In most lotic water bodies that we surveyed, it varied from quick to very quick (e.g., 1.52 m/s in the Huallabamba River). For example, high current speeds, irregular flow rates, and stony bottoms characterize most of the aquatic environments of the Huallaga River basin. Even in low-altitude rivers (e.g., the lower Sisa River, which had a current speed of 0.12 m/s), water flow may not allow establishment of fishes adapted to lentic environments (e.g., the tilapias). In sharp contrast, native species are well adapted to local current and water-flow conditions.

4.1.2. Human influences

Peruvian aquatic ecosystems have faced threats due to pollution and habitat destruction, which are products of human activities such as deforestation, mining, oil extraction, and drug trafficking (Ortega and Chang, 1998). Urban development and aquaculture have also taken a toll on Peru's freshwater environments. All of these alterations and other modifications to natural water bodies (e.g., for watering, energy generation, food consumption) can generate environmental conditions that can favor exotic species. For example, *Trichogaster leerii* has adapted to the small, blackwater, almost polluted Moronacocha Lagoon in the Amazonian plain. However, not all alien species have an adaptive advantage to polluted waters. In the polluted Santa River basin, *Oncorhynchus mykiss* was restricted to small tributaries with optimal conditions, and was not found in the polluted waters of the main channel.

Since the 1940s, various forms of aquaculture (ornamental fish culture, "ranching" of species in natural environments, intensive aquaculture) have continuously increased in importance as sources of food production and economic benefit in Peru. Consequently, the release or escape of nonnative species from aquaculture operations have increased in frequency and scope within the country. The coastal region has a long tradition of seafood consumption that dates back to the first Peruvian settlements (Lanning, 1965). In recent times, tilapia aquaculture has been encouraged in that region. However, this activity is debatable as an economic alternative because marine fishes are still cheaper and the ecological effects of the aquaculture have been negative. For example, in the coastal region of the Rio Grande, the native fishes were completely displaced by *Oreochromis niloticus* and *Poecilia reticulata*, at least during the dry season near the river's outlet.

Of all introductions of alien species, the introduction of tilapias should be of greatest concern. In general, tilapias are either escaping or being released from aquaculture operations near towns where aquaculture facilities exist; for example, near towns of the central forest (Departments of Junin and Pasco), where *Oreochromis niloticus* farming has been promoted since the 1970s by the Pichis-Palcazú Special Project (Luna et al., 1999). Tilapias have already apparently escaped or been released from fish farms into warm-water bodies of the high Amazon River system. Although the percentages of occurrence of *O. niloticus* in our sampling locations did not differ significantly between 1997 and 1998 (*G*-test [Sokal and Rohlf, 1995]), we recorded that species in more natural lotic water bodies (i.e., the Ahuashiyacu Stream and the Gera, Indoche, and Mayo rivers) and at more locations along the Cumbaza River (Juan Guerra and at the mouth of the Mayo River) in 1998. In 1997, we recorded that species from only two lotic streams (Cumbaza River at Juan Guerra and Potochico Stream) and three human-influenced lentic water bodies (Limón Lagoon, Mashuyacu Reservoir, Sauce Lagoon).

Despite the buffer presented by the numerous species present and complexity of the ecosystem, the lowland forest river systems are jeopardized by aquaculture. Tropical aquatic ecosystems of the lowland rain forest ultimately could be more adversely affected by aquaculture than the water systems of the highland forest because most aquaculture is being developed in low-altitude waters. For example, most important fish-farm activities for *Oreochromis niloticus* are located in areas around 200 m.a.s.l. (e.g., Yurimaguas and Iquitos, Pucallpa [Department of Ucayali], and Puerto Maldonado [Department of Madre de Dios]), in proximity of several fluvial lagoons. There, this alien species could have a high probability of finding good conditions for its establishment. It has already adapted to local conditions in the Department of San Martin.

Lentic water conditions, no predators, and low species diversity can favor some alien species. *O. niloticus* was introduced into the lentic waters of Sauce Lagoon and the Mashuyacu Reservoir, where it established. Its establishment may have been facilitated by the sandy bottoms (favorable for the construction of breeding nests), quite waters, and low native-species diversities of these water bodies. *O. niloticus*, like other cichlids, prefers slower currents or shallow still waters with plenty of refuges such as shore banks, submerged logs and branches, heaped rocks, and dense vegetation (Zaret, 1980). In addition, the absence of high numbers of species in these water bodies could reduce niche competition.

The problems affecting introductions of alien species into lentic water systems can be complex. For example, the problems affecting the Lake Titicaca water system are indeed complicated. Eutrophic processes have increased phytoplankton productivity, which, in turn decreased zooplankton production. This generated a competition for zooplankton between the introduced *Odonthestes bonariensis* and several native fishes in the genus *Orestias*. The biological impact on several of the 30 *Orestias* species has been direct and irreversible; some of them even seem to be on the road to extinction. In addition to competition for food or habitats, severe predation on *Orestias* species has reduced their populations. The introductions of both *Oncorhynchus mykiss* and *Odonthestes bonariensis* may have already driven to extinction at least two species—the endemic *Orestias cuvieri* and a catfish, *Trichomycterus rivulatus* (suche), the largest species in the family Trichomycteridae (Treviño et al., 1991). Finally, these alterations have impacted native human populations, with mixed results. Although these species reduced the *O. cuvieri* population through competition and predation, they became important species for commercial fisheries (Treviño et al., 1991).

Native species transfers are apparently not common in Peru, but some spectacular consequences have arisen in a few cases. In at least one situation, the transfer of one species led to the introduction of more alien species. After *Arapaima gigas* was transferred into Sauce Lagoon in 1962, the alien *Poecilia reticulata* was introduced in 1965 because the native fish fauna was insufficient to meet the feeding demands of *A. gigas*. Then, another alien species, *Tilapia rendalli*, was successfully introduced in 1968 because even the population of *P. reticulata* was insufficient to meet the food demands of the *A. gigas* population. Interestingly, the *T. rendalli* population proliferated to the extent that a fishery for this species became an important economic activity (Fukushima et al., 1975). However, in 1978, *O. niloticus* was also introduced into Sauce Lagoon and apparently has completely displaced *T. rendalli*. The tilapia of the Congo seems to have driven the tilapia of the Nile to local extinction; *O. niloticus* subsequently became an important fishery species in Sauce Lagoon.

It is important to note that the impacts of species introductions and transplantations are not all negative. For example, polyculture systems that at least partially "self-clean," thus reducing water pollution (see Section Four, this volume), have been successfully developed using carps, native *Hemibrycon* fish species, and ducks (Luna et al., 1999). Several introduced species have served as the bases for economical enterprises. *Trichogaster leerii*, which has established in the almost polluted Moronacocha Lagoon, was incorporated into the ornamental aquarium-fish trade in Iquitos and, until its local extinction, *Tilapia rendalli* supported a commercial fishery in Sauce Lagoon. Finally, not all cultured introduced species escape; *Cyprinus carpio* apparently remains confined to cultivation ponds. In almost 20 years of collecting fish in rivers and lagoons of the highland or lowland forest, we have never found this species (H. Ortega, personal observation).

4.2. Social and Economic Aspects of Exotic Fish Introductions

In Peru, the introduction of alien species has been motivated by several factors (Guerra et al., 1999), including the hope for economic gain through aquaculture by improving the economic condition of the rural people. For example, during the 1980s, programs were implemented to develop aquaculture technologies for tilapia. As a result, production of tilapia increased to levels that made the industry competitive with other production activities. During that time, the yield increased from 2,500 kg/ha/year to 8,500 kg/ha/year (Ascon, 1998). The culture of *Oreochromis niloticus* is particularly promising. In countries where this aquaculture activity is performed on a large scale, the results are impressive. For example, in public reservoirs in northeastern Brazil, annual production averaged 17,000 t between 1979 and 1983 (Jurgel, 1986).

In the Department of San Martin, fish production increased from 10 t in 1979 to 220 t in 1993. The production of tilapia in Sauce Lagoon alone has maintained at approximately 100 t per year, which translates into a yield of approximately 200 kg/ha/year and compares quite favorably with the maximum production of tropical environments (150 kg/ha/year [Bayley, 1981]). Currently, exotic species contribute 71% of the Department of San Martin's annual aquatic fish production and aquaculture activities generate approximately US$4 million per year. In addition, employment is increased due to the expansion of aquaculture and other related commercial activities.

However, not all aquaculture ventures enjoy long-term success or clearly benefit the local human community. In Lake Titicaca, *Oncorhynchus mykiss* was successfully cultured and harvested during 1960–1965, and a canning industry based on harvest of this species was developed. Unfortunately, at the beginning of the 1970s, these activities collapsed, possibly due to overfishing, environmental variations, or complex interactions between the several introduced species in the lake. Since that time, the *O. mykiss* population has not recovered (Everet, 1973). *Odonthestes bonariensis*, which was also introduced into Lake Titicaca, became established and is presently harvested for both commercial and subsistence use in Peru and Bolivia. In the case of Lake Titicaca, these culture and harvest activities are not without a cost. These introduced fishes displaced several native *Orestias* species that were the traditional protein resources used by the native Uros people (Treviño et al., 1991).

5. RECOMMENDATIONS

The control of species introductions in Peru is not an easy task. Actually, the problem is a paradox, a complex situation. On one hand, aquaculture can generate products that contribute to the protein needs of rural populations; on the other hand, aquaculture can cause problems to natural ecosystems. To reduce the negative impacts, programs for aquaculture using native species have already been initiated (MIPE, 1994; Guerra et al., 1996). Because the implementation of these sound practices on a large scale will take some time, the practice of aquaculture using alien species with little control will continue for a while. Therefore, it is necessary to alert institutions about the problems associated with culturing alien species. The Commission on Continental (Inland) Fishing in Latin America (COPESCAL), of which Peru is a member, has approved the Code of Practices for Introduction of Exotic Species for Aquaculture and is recommending that governments apply it through political regulations and that they require authorization of all new introductions into their countries (COPESCAL, 1986). We here present some suggestions for implementation of various control mechanisms to reduce the frequency of nonindigenous species introductions from aquaculture facilities into open waters and for promulgation of the problems associated with the culture of nonindigenous species.

5.1. Rainbow Trout in the Parque Nacional Río Abiseo

1. A management plan for *Onchorrhynchus mykiss* should be implemented. It should include periodic experimental fishing to control the populations in the northern area of the PNRA, for the following reasons: (1) to avoid further propagation of this exotic species, (2) to improve the survival and preservation of natural population sizes of the native species, and (3) to provide the local rural people with work and protein of good quality, which should help to increase their standard of living.

2. Periodic experimental fishing areas at the heads of the Montecristo, La Playa, and Las Palmas rivers should be established. Cast nets, gillnets, and hook-and-line gear should be allowed because those gear types can be selective for larger fishes without affecting other biological resources.
3. Periodic biological monitoring should be conducted in the experimental fishing areas to evaluate both the current state and level of recovery of the native fish species.

5.2. Tilapia in the Lower Rio Huallaga River Basin

1. A management plan for tilapia aquaculture should be implemented. Tilapia aquaculture continues to be practiced, sometimes in inadequate conditions and in spite of the 1992 governmental prohibition for the cultivation of tilapia species in Peruvian Amazonia (Guerra et al., 1999).
2. A monitoring program for the presence and abundance of tilapia should be implemented in natural areas of higher risk, such as Sauce Lagoon, the Cumbaza-Huallaga river section between Juan Guerra and Shapaja, the upper Mayo River between Cocha Governador and Puerto Tahuishco, and the lower Sisa River between San Cristóbal and the river's outlet.
3. Research programs to define ecologically, economically, and socially viable technologies that would facilitate the transformation of aquaculture activities into viable alternatives for regional development should be initiated. The Fishery Station of Ahuashiyacu should become the focal point of the program.
4. The introduction of alien species, as well as the transferring of fishes from one system to other within the country should not be allowed unless the Code of Practice for the Introduction of Exotic Species for Aquaculture is strictly followed and the activity is approved by COPESCAL. The rules for other international agreements to which Peru subscribes should also be considered.

5.2.1. Infrastructure control

To reduce the frequency of escape of tilapias from fishponds into natural systems, the following advice should be considered:

1. aquaculture ponds should be built considering the water resource to be used; they should be designed with controlled effluents;
2. aquaculture ponds should have traps in their drainage channels, immediately after the dikes, to allow the recovery or recapture of fish that could escape;
3. the drainage channels of tilapia fish farms should not drain directly to natural water courses (flowing waters) or other natural aquatic environments.

5.2.2. Monitoring the control measures

To ensure that aquaculture operations are adhering to governmental requirements and practicing environmentally safe aquaculture, the following precautionary monitoring should be implemented:

1. periodic monitoring of fingerling production, which should be done at adequate centers, to verify the efficiency of the method and the quality of the fingerlings;
2. periodic monitoring of production ponds, especially the drainage systems, including entrance channels and exits to natural water bodies;
3. periodic monitoring of all lotic and lentic water bodies bordering fish farms, to verify the presence or absence of tilapia;
4. periodic monitoring of the aquaculture operation for the introduction of unusual pests, parasites, or aquatic species.

5.2.3. Natural environments

To facilitate the protection of natural environments in the vicinities of aquaculture operations, the following steps should be taken:

1. The objectives of aquaculture programs should be well defined, regarding both the use of the introduced species and the conservation of native species.
2. To supplement the specific requirements of the MIPE, environmental impact studies that include the participation of all people involved is necessary, as is consultation with, and the advice of, public or private organizations (MIPE, 1999).
3. Environmental education programs that include information on the importance of monitoring natural ecosystems and the safeguards that should be taken when initiating and maintaining aquaculture operations should be developed, principally in areas where aquaculture is being conducted.
4. Plans for environmental monitoring of the water bodies potentially or already affected by the range expansions of escaped exotic species should be developed and implemented. Both the protection and the maintenance of the diversity of native fishes should be a principal goal because native species diversity and the presence or absence of particular native species can be important indicators of the health of the environment.

To ameliorate or control the impact of the escaped alien species already present in Sauce Lagoon, that lagoon should be a focal area for the implementation of these suggested management measures. The fisheries in the lagoon (fishing effort, capture volumes, size composition of the captures), the whole fish community, and selected abiotic conditions (precipitation, flow rates of the main tributaries, limnological conditions) should be regularly monitored.

5.3. CONTROL MEASURES FOR EXOTIC SPECIES THROUGH MALE PRODUCTION

Aquaculture activities conducted under controlled conditions should not be a problem to natural environments. However, the experience of several decades of that practice, especially with *Oreochromis niloticus*, has shown that restrictions to avoid the escape or release of cultured alien fishes have not been efficient. One way to control and reduce the problem is through the production of only males. Technologies to produce all-male broods of *O. niloticus* have already been developed and are being applied outside of Peru (Little, 1998). The methods used follow:

1. Sex selection. Quite simply, males, which have two ventral apertures (anal and urogenital) are maintained alive whereas females, which possess three ventral apertures (anus, oviduct, and urinal) are sacrificed. This is the simplest and most common method; it has been and is being used in our study area. This method is useful only when low numbers of fingerlings are needed because it is tedious and requires much practice.
2. Hybridization. The hybrid offspring of female *O. niloticus* or *O. mossambicus* mated with male *O. hornorum* or *O. aureus* are only males. To be successful, this method requires that the progenitors are genetically pure.
3. Mating normal females with supermales. In this method XX female eggs are fertilized by YY male sperma, through genetic manipulation. The offspring will be only normal XY males.
4. Sexual reversion. Females in their first week of life are maintained using a diet containing hormones that cause them to revert to male individuals.

Implementation of any of the approaches mentioned above will advance the regulation of aquaculture. With proper monitoring and control, aquaculture, particularly of native species, could become an important source of economic benefit and food production without seriously impacting Peru's rich and diverse native fish fauna.

Editor's note: Peru's PNRA has been declared a United Nations Education, Scientific, and Cultural Organization (UNESCO) World Heritage Site (O'Neill, 2002). Accompanying UNESCO World Heritage status is a commitment by the home nation to protect the designated location and by other member nations to assist the home nation in the preservation of such an international treasure. The World Heritage designation of the PNRA makes the preservation of its native fish fauna a world-class responsibility. Thus, the recommendations made in this chapter by Ortega et al. are even more important.

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CHAPTER 15

INTRODUCTION OF EXOTIC SPECIES AND TRANSPLANTATION OF NATIVE SPECIES ACROSS RIVER BASINS IN VENEZUELA

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Abstract: The intentional introduction of biological organisms from their native environments into new areas is expanding, partially to satisfy an increased need for protein for human consumption. These alien species introductions, often promoted aggressively by international interests, have the potential to cause significant and increasing adverse impacts on native species and ecosystems, and on national economies. They may also pose risks to human health. Although these invasions have been of interest to ecologists for a long time, the attention that the effects of introduced species draws today is of unprecedented proportions. Understanding how introduced species influence natural communities is one of the most important challenges linking ecology and conservation today. In Venezuela, the introduction of exotic species dates back to the 1930s, when several species of trout (including *Oncorhynchus mykiss*) were introduced into Andean streams. To date, 10 species of fishes and 4 species of shrimps have been introduced. More recently, frogs and algae have joined the list of exotic cultured species. Extensive culture of native species is also common. Several authors have called attention to the various effects that aquaculture of alien species may have on the environment, especially when the cultured organisms are genetically altered. Another less-publicized mode of exotic introduction has been taking place in several countries: the transportation of native species across river basins. Although our knowledge of how that activity may affect ecosystems is very limited, these transplantations, which are often conducted without regard for biotic or biogeographic criteria, rivals the introduction of exotics in its potential danger, especially in countries where there is little knowledge of the autochthonous fauna. Establishing regulatory controls, providing incentives for research on the aquaculture of indigenous species, and creating awareness about the particular biotic situation of each country could increase fish supplies, rural employment, and income while preserving the biological integrity of the environment.

Theresa M. Bert (ed.), Ecological and Genetic Implications of Aquaculture Activities, 279–289.

Key words: algae, alien species, aquaculture, environment, exotic species, fish, impact assessment, invertebrates, South America, Venezuela

1. INTRODUCTION

The intentional introduction of biological organisms from their native ranges into new areas is increasing as a consequence of intense human activities and trade. Many species introduced for aquaculture and harvest cause little harm and provide much-needed protein sources for human consumption in underdeveloped countries. However, a growing number of these species and their pathogens have established free-living populations, some of which have become invasive and threatening to native species. These exotic species, whose culture is often promoted aggressively by international interests, are causing a significant and increasing impact on native species, aquatic ecosystems, and national economies, and they may pose increasing risks to human health. Invasive species have been of interest to ecologists for a long time. However, the attention that the effects of introduced species draw today is of unprecedented proportions. Understanding how introduced species influence natural communities is one of the most important challenges linking ecology and conservation today (Vitousek, 1996).

In South America, fish cultivation during colonial times was almost nonexistent. However, also during those times, numerous South American species were mistaken for similar European species, which caused some people to consider fish culture as a possibility in the colonies. Artificial propagation of fishes for human consumption or for commerce started in earnest in the early nineteenth century. However, initially only a few people attempted to culture fishes. Thus, very few data are available to validate the actual species used. One of the few existing examples of nineteenth century fish cultivation is a report from Ecuador, where a pimelodid catfish (*Pimelodus cyclopum*) was cultivated. Villagers collected this species in its natural habitat and subsequently transferred it to either culture ponds or clay containers. Later reports mention carps (*Cyprinus carpio*) and several species of trout and tilapias as the preferred species for cultivation in several countries in the Americas (Patiño, 1970). Today, aquaculture is practiced throughout Latin America and a number of fish, invertebrate, and plant species are cultured. Inadvertent or purposeful release of cultured species has led to widespread colonization of native habitats by alien species and the establishment of native species outside of their normal ranges.

2. AQUACULTURE IN VENEZUELA

A rich assemblage of fish species inhabits Venezuela's rivers, lakes, and ponds. Approximately 1200 species have been reported for Venezuela (Mago-Leccia, 1970; Chernoff et al., 1996) and many more may still be undescribed. The freshwater fishes of Venezuela include several commercially important species as well as many others that have been identified as having potential for aquaculture.

Although, in 1887, goldfish (*Carassius auratus*) were imported for display in aquariums in Caracas, modern aquaculture activities were initiated in Venezuela later (in 1937), with the introduction of several trout species (*Salmo trutta*, *Oncorhynchus mykiss*, and *Salvelinus fontinalis*) in Andean rivers that had temperatures low enough to allow acclimation of these species. The introduction of carp (*Cyprinus carpio*) into Venezuela followed shortly thereafter, in 1940. In 1959, the first specimens of tilapia (*Oreochromis mossambicus*) were brought from Trinidad and introduced into the Lake Valencia area and in littoral lagoons around the Cumaná River. In the 1960s, commercial cultivation of mussels (*Perna perna*) and oysters (*Crassostrea rhizophorae*) began in eastern Venezuela, following technical and scientific criteria established for that purpose. By the 1970s, aquaculture had further diversified and many more species were included in projects developed by universities and governmental agencies (Cervigón, 1983; MAC, 1995). From that period to the present, most efforts have been centered on cultivating tilapia hybrids and shrimp. Both private and public funding have been incorporated for projects and research in these directions. In general, some aquaculture efforts have failed (e.g., sturgeon in the Andean piedmont, carp) and others have become flourishing industries (e.g., trout in the Venezuelan Andes).

Since fishes and most introduced species are not considered to be wildlife under Venezuelan conservation laws, their management and preservation are taken up by several government agencies that often have conflicting agendas. As far as we know, no Venezuelan fishes are endangered or have recently become extinct, but many local extinction events have occurred due to the catastrophic alteration of areas by habitat destruction, urbanization, and pollution from various sources. In this respect, López-Rojas and Bonilla-Rivero (2000) reported a 65% reduction in the fish faunal diversity of Lake Valencia and attributed this decline to anthropogenic activities.

An overview of recent work in the field of aquaculture in South America was presented at Aquacultura ’99, a symposium on aquaculture held in Venezuela (Cabrera et al., 1999). In this symposium, research performed in Latin American countries other than Venezuela was presented on the aquaculture of 20 species of freshwater fishes, 10 species of marine/estuarine fishes, and 8 species of exotic fishes; 3 reptiles; 5 crustaceans; and 12 mollusks (Table 1A). Additionally, 15 marine or estuarine species were suggested as possible candidates for culturing. Of the presentations in which aquaculture in Venezuela was addressed, 13 concerned native freshwater fishes, one concerned an estuarine fish, 5 concerned exotic fishes, and 15 concerned mollusks, shrimps, and algae (Table 1B).

Table 1. Species currently or potentially cultivated in South America

A. Countries other than Venezuela[1]

Freshwater fishes
Arapaima gigas
Astronotus ocellatus
Brycon cephalus
Brycon siebenthaiae
Cheirodon axelroldii
Cichla sp.
Colossoma macropomum
Corydoras sp.
Hoplosternum littorale
Metynnis argenterus
Panaque nigrolineatus
Papillochromis ramirezi
Piaractus mesopotamicus
Pimelodus pictus
Prochilodus nigricans
Pseudoplatystoma corruscans
Schizodon fasciatus
Semaprochilodus insignis
Sorubim lima
Symphysodon sp.

Exotic fishes
Clarias gariepinus
Ctenopharyngodon idellus
Cyprinus carpio
Lithopenaeus vannamei
Onchorhynchus mykiss
Oncorhynchus kisutch
Oreochromis niloticus
Salmo trutta

Marine/estuarine fishes
Carangidae
Centrolophidae
Galaxias maculatus
Micropogonias furnieri
Oncophterus darwini
Paralichthys microps
Paralichthys orbygnyanus
Scophthalmus sp.
Serranidae
Urophycis brasiliensis

Mollusks
Anadara sp.
Argopecten purpuratus
Choncholepas choncholepas
Chorus giganteus
Crassostrea gigas
Fisurella sp.
Haliotis sp.
Octopus sp.
Plicopurpura pansa
Strombus pugilis
Tagellus dombeii
Tiostrea chilensis

Crustaceans
Artemia sp.
Panulirus sp.
Farfantepenaeus paulensis
Pleoticus muelleri

Reptiles
Podocnemis expansa
Podocnemis sextuberculata
Podocnemis unifilis

Algae
Gracilariopsis sp.

Suggested species
Caranx spp.
Centropomus spp.
Coryphaena hippurus
Cynoscion spp.
Epinephelus spp.
Lutjanus sp.
Menticirrus spp.
Micropogonias spp.
Mugil spp.
Paralichthys spp.
Pogonias cromis
Sciaenops spp.
Seriola spp.
Thunnus sp.
Trachinotus spp.

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[1] Partial listing; not intended to be comprehensive.

(*Continued*)

Table 1. Species currently or potentially cultivated in South America—cont'd.

B. Venezuela

Freshwater fishes (native)
Astronotus ocellatus
Astyanax bimaculatus
Colossoma macropomum
Mylossoma acanthogaster
Pimelodus blochii
Pseudoplatystoma fasciatum
Pseudoplatystoma tigrinum
Serrasalmus rhombeus

Hybrid freshwater fishes (native)
Callophysus macropterus × *Leiarius marmoratus*
Colossoma sp. ×*Piaractus* sp.
Perrunihthys perruno × *Leiarius marmoratus*
Pseudoplatystoma fasciatum × *Leiarius marmortatus*
Pseudoplatystoma fasciatum × *Pimelodus blochii*

Exotic freshwater fishes
Oreochromis spp.
Carassius auratus
Tilapia hybrids
Oncorhynchus mykiss
Sturgeon

Estuarine fishes
Mugil curema

Crustaceans
Artemia sp.
Farfantepenaeus brasiliensis
Farfantepenaeus notialis
Farfantepenaeus subtilis
Lithopenaeus vannamei
Thamnocephalus venezuelensis

Mollusks
Crassostrea rhizophorae
Euvola (Pecten) ziczac
Nodipecten (Lyropecten) nodosus
Pinctada imbricata
Pinna carnea
Polimesoda solida

Exotic marine algae
Eucheuma denticulatum
Kappaphycus alvarezi

3. EXOTIC INTRODUCTIONS AND SPECIES TRANSPLANTATIONS IN THE FRESHWATER ECOSYSTEMS OF VENEZUELA

An analysis of the biogeographical relationships of Venezuela's numerous river basins is clearly beyond the scope of this work. However, a brief word on the issue is important to understand the potential negative impact that introductions and transplantations can have on the Venezuelan freshwater ichthyofauna. The principal river/lake systems of Venezuela are shown in Figure 1. The great Orinoco River drainage system, which occupies almost 70% of eastern and central Venezuela, shares many species and species affinities with Colombian river systems east of the Andes Mountains. In northwest Venezuela, the Lake Maracaibo basin has more affinities with the Colombian Magdalena River basin than with the rest of Venezuela because these two basins were connected prior to the uplifting of the Sierra de Perijà in Venezuela and the Sierra de Santa Marta in Colombia approximately 11 million years ago (Diaz de Gamero, 1996). Isolation of the many small, isolated rivers that drain into the Caribbean (which are collectively called the Caribbean basin system) from other drainage systems in northern Venezuela dates to the uplifting of the Cordillera de la Costa approximately 12–13 million years ago (Mencher et al., 1953; Vila, 1969). These streams constitute an experiment in evolution (at least

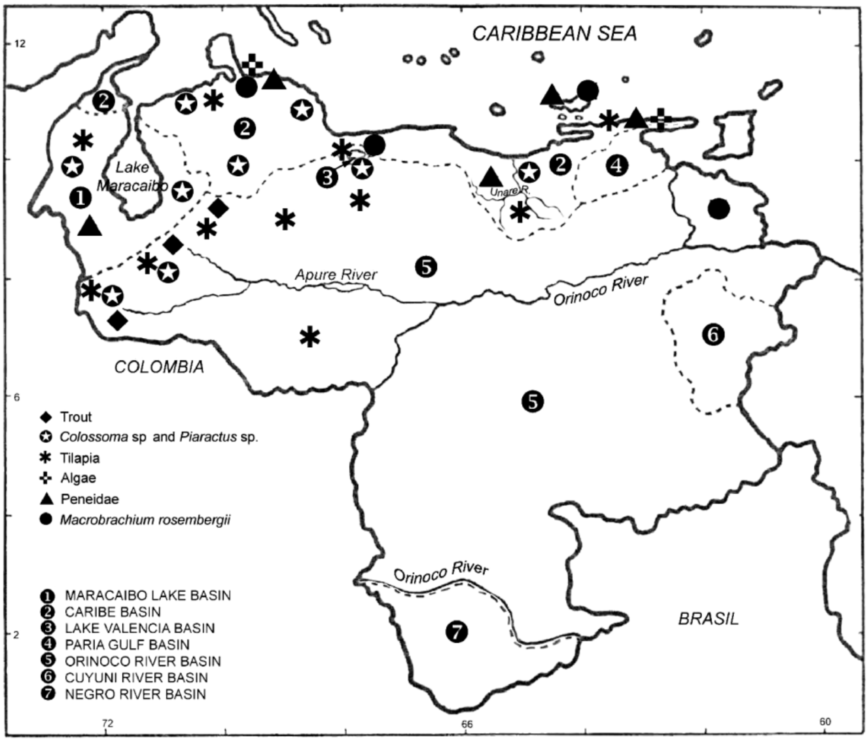

Figure 1. Distribution of the main exotic freshwater species in Venezuela. *Colossoma* and *Piaractus* are native species that were transplanted from the Orinoco River basin to the Lake Maracaibo basin. Numbers 1–7 indicate main river basins proposed by Mago-Leccia (1970)

for secondary freshwater fishes [those derived from marine ancestors]) that is poorly known and begs to be studied. In central Venezuela, the Lake Valencia basin is an endorrheic basin that has been isolated from the Caribbean basin system for one million years. However, until recently (300–400 years before the present), Lake Valencia was connected to the Orinoco River (Peeters, 1968). In eastern Venezuela, the Cuyuní River basin, which is isolated from the Orinoco River basin, shares many ichthyofaunal elements with Guyana's Essequibo River. The smaller basins of the Río Negro (a subbasin of the Amazon River that connects the Orinoco River to the Amazon River via the Casiquiare River), Gulf of Paria (a basin in northeastern Venezuela that connects with the Orinoco River delta), and other freshwater systems have been little studied (Mago-Leccia, 1970). Thus, their ichthyofaunal relationships and affinities are poorly known.

To illustrate the extent of the distribution of exotics and transplanted species in Venezuela, we have mapped the most common species used in aquaculture in Figure 1. Of the alien species, aquaculturists have farmed *Tilapia niloticus* throughout the country and now the species' distribution reflects this fact.

In 1980, *Macrobrachium rosembergii*, an icon of cultivation worldwide, was introduced illegally into Margarita Island, which is offshore from northeastern Venezuela. That species has since been cultured in the Orinoco River delta and has established feral, reproductive populations there (Pereira et al., 1996). Other penaeids have also been cultured (Table 1B) and escaped. Feral populations of alien aquacultured trouts are restricted to cold-water, fast-flowing Andean streams due to their habitat requirements, but their impacts on local fishes have not yet been evaluated. Two exotic algal species (Table 1B) are now established at two localities along the coast.

For aquaculture in the form of "ranching" (allowing feral populations of the introduced species to expand and then harvesting from them), several fish species have been transplanted into river or lake systems in which they are not native. The principal route of expansion is from the Lake Maracaibo basin to more easterly regions of Venezuela; however, transplantation from eastern Venezuela to western Venezuela also occurs (Figure 2). *Colossoma* spp. and *Piaractus* spp. have been hybridized and transplanted from the Orinoco River basin, which is the only river system in which they occur, into the Lake

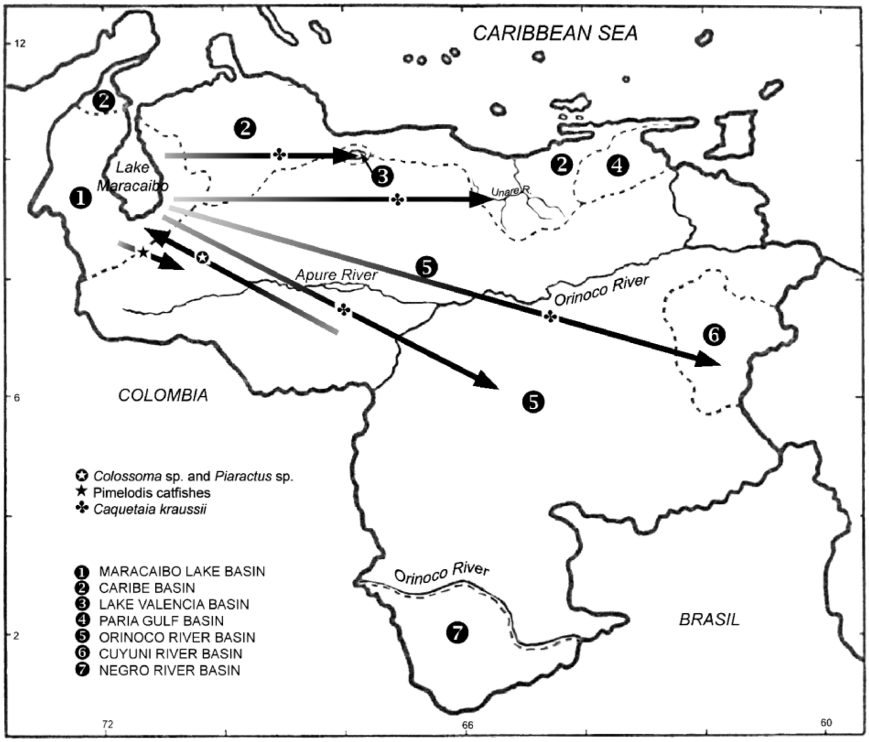

Figure 2. Transplantation routes of native freshwater fish species across river and lake basins in Venezuela. Numbers 1–7 indicate main river basins proposed by Mago-Leccia (1970)

Maracaibo basin, for cultivation (Figure 1). *Perrunichthys perruno* (endemic to the Lake Maracaibo basin) and *Leiarius marmoratu* (endemic to the Orinoco River basin), two pimelodid catfishes native to Venezuela but from very different drainage systems, have been hybridized and transplanted for open-water aquaculture. The transplantation of the native *Caquetaia kraussii* (Cichlidae) has been well documented. The original distribution of this species is the Magdalena River basin and the Lake Maracaibo basin (Mago-Leccia, 1970), although a report of *C. kraussii* in the Unare River basin (Mago-Leccia, 1965) seems to some researchers to confirm the presence of this species in the Caribbean basin as well. Introduced approximately 40 years ago from its original areas of distribution into several bodies of water for cultivation, *C. kraussii* occurs now in almost all Venezuelan freshwater aquatic systems (Figure 2) (Royero and Lasso, 1992). These hybridizations and transplantations have changed scientists' vision of the natural distribution of species and of their relationships.

A similar case can be made for *Pipa parva* (Anura: Pipidae), a frog endemic to the Maracaibo Lake Basin which was introduced in natural and man-made lagoons in central Venezuela (Lake Valencia). *P. parva* feeds on juveniles and small fish, amphibian larvae and juveniles, mollusks and several aquatic insects (Royero and Hernández, 1995), so its impact on aquatic ecosystems needs to be evaluated.

Aquaculture has undoubtedly brought benefits, in the form of improved access to food, to those communities that lack the resources to sustainably exploit them in their natural environments. However, cultivation methods have undergone drastic changes in recent years. Initially, aquaculture practices were restricted to incrementing the production of organisms taken directly from their natural habitats. However, current aquaculture practices not only seek a cost-effective increase in production, but also production, by means of genetic manipulation, genetically and morphologically attractive organisms to meet an increasingly demanding market. Because these modified individuals can only be obtained by diverse techniques of genetic manipulation that are used worldwide, special attention should be given to the impact that genetically altered species can cause to native species. Hybrids or transgenic species could cause erosion of genetic variability through founder effects and/or inbreeding.

In addition to the problems associated with the application of genetic techniques in Venezuela, a variety of problems associated with aquaculture facilities need to be resolved. Among them we can mention: habitat alteration or destruction (mangroves, for instance), pollution by discharges of pond or tank effluents into other bodies of water, and land-use conflicts, as well as the genetic and ecological impacts of escaped exotics (Sebastiani et al., 1994; Pérez, 1996a, b).

4. LOOKING AHEAD

Numerous potential or actual solutions to the many problems caused by the introduction of exotic species and the transplantation of Venezuelan species among basins were presented at Aquacultura '99 (Cabrera et al., 1999).

In Venezuela and other South American countries, researchers have already started investigations on several topics related to cultivating native species. For example, natural diets, nutritional requirements, and the feasibility of feeding alternative foods are being evaluated for several native species. Other biological and physiological aspects of culture being investigated include larval survival and cultivation, post-larval quality, pathology, substitute hormonal promoters, reproductive performance, and semen preservation. Increasing use of genetic manipulation has led to research on sex reversions and genetic improvements of native fishes. The increasing emphasis on methods for successfully culturing tropical species (principally mollusks) and criteria for site selection (developed as part of the FAO [Food and Agricultural Organization of the United Nations] Fisheries Development Program) has led to research on contamination control, bacteriological examination, cage culture, and closed circulating systems.

In Venezuela and other South American countries, problems affecting aquatic ecosystems have received very little attention in the past. The principal limitation in evaluating the impacts of aquaculture activities not only in Venezuelan freshwater environments but also in the freshwater environments of most regions of South America is a lack of knowledge of the species composition of the regions and of information on the distributions, ecologies, and life histories of the native species.

At least two international groups have recognized the general absence of this critical information. (1) Scientists from several Latin American countries and the USA have joined efforts in the Aquatic Rapid Assessment Program (AquaRAP), which is designed to address major environmental problems associated with biodiversity reduction and habitat degradation, including the impacts of aquaculture (Chernoff et al., 1996). (2) At the Summit on Sustainable Development held in Santa Cruz, Bolivia, in December 1996, leaders of participating governments acknowledged the importance of having adequate information on the biodiversity residing within their respective countries and the need for cooperation among countries to obtain that information. They established the Inter-American Biodiversity Information Network (IABIN), to promote the collection, exchange, and distribution of information on biodiversity conservation. As a continuation of this meeting, in October 1998 a small group of experts representing several countries, governmental agencies, museums, nongovernmental organizations, and universities met in Santa Barbara, California, USA, to assess the existing information, identify the information gaps, and identify the users of information on invasive species in the Western Hemisphere. Among the results of deliberations in this meeting, a need to develop education material and to educate users on the potential consequences of exotic introductions was identified. To promote awareness of the problem and to stimulate research on alternatives to the introduction nonindigenous species, this group of experts agreed to encourage the participation of the relevant industries (including the aquaculture industry) and the public and to advocate the presentation of papers at appropriate forums (IABIN, 1999).

In any species-rich fauna, most species are rare in abundance, and this is the case in most South American countries. In this type of ecosystem, the introduction or transplantation of species can alter ecosystem-level processes in a shorter period of time and with a much greater intensity than normal disturbances usually can. Coupled with environmental stresses in the form of pollution or habitat destruction, the effects may be even more dramatic (Sousa, 1984; Sheldon, 1987; Pickect et al., 1989; Sparks et al., 1990). To simultaneously alleviate food problems through modern aquaculture methods and maintain ecosystem integrity, we should focus on a holistic view of river basins and their associated components in our assessments of these impacts. Fortunately, this perspective is increasingly recognized in Venezuela and in other South American countries. Governments and researchers are working in several ways to identify the impacts of aquatically based industries such as aquaculture and to seek alternative solutions to those impacts so that these industries can operate and expand sustainably.

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CHAPTER 16

IMPACTS OF NON-NATIVE FISH SPECIES IN MINAS GERAIS, BRAZIL: PRESENT SITUATION AND PROSPECTS

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Abstract: For some time, the rate of non-native fish introductions has been increasing in South America. There are many reasons for introductions: reservoir stocking programs, aquaculture, sport fishing, control of disease vectors, and the pet trade. Accidental escapes also contribute significantly. In Brazil, despite federal and state regulations, there are misunderstandings about such concepts as native, exotic, allochthonous, or autochthonous fishes and introductions, translocations, reintroductions, and transfers of fishes. Known impacts of exotic fishes include native species extinction, changes in competition and predation rates, limnological perturbations, introduction of diseases and parasites, hybridization with native species, and changes in fisheries composition. The few recorded benefits of non-native species introductions are restricted to the improvement of fish production and sport fisheries. In Minas Gerais, Brazil, records of exotic species have increased over the past seven years. In some of the most important river basins of that state, alien fish species might represent up to 40% of the fish fauna. Congeneric species, such as *Hyphessobrycon bifasciatus* and the exotic *H. eques*, can be captured from the same water body and the non-native species can be much more abundant than the native species. The recent introduction of *Leporinus macrocephalus* from the Pantanal may cause the same impact to the native *L. copelandii*. The widespread introduction of the peacock bass and other piscivorous species is the cause of local extinctions in the central lake of Lagoa Santa and in the

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Rio Doce valley lakes. Genetic problems can also be foreseen with the release of hybrids of *Pseudoplatystoma corruscans* and *P. fasciatum* in areas where only the first species naturally occurs. Tilapine species, the most widely distributed exotics within the state, have had negative impacts on fisheries and on fish species compositions in reservoirs. Solution to these problems must involve the following: (1) better enforcement of legislation governing the sale and transport of live organisms, (2) development of native-species aquaculture, and (3) public awareness programs on the adverse impacts of exotic species to the native fish fauna.

Key words: aquaculture, Brazil, environment, exotic species, fish introduction, fishery, Minas Gerais, ornamental fishes, stocking

1. INTRODUCTION

Although the introduction of non-native freshwater fish species is an ancient practice, it has become frequent on a global scale since the end of the 1800s. There are many reasons for introductions. Purposeful introductions can be for stocking reservoirs, improving aquaculture, controlling undesirable disease vectors, enhancing sport fishing, stocking ornamental fish, or increasing angler catches (Welcomme, 1984; Crivelli, 1995; Lever, 1998). In addition, fish confined for various reasons often escape. After habitat alterations, the introduction of alien species is the second main cause of fish species extinctions (Miller et al., 1989; Moyle and Leidy, 1992). Crivelli (1995) showed that, in the Mediterranean Sea, more than 80% of endemic freshwater fishes coexist with one or more exotic or transferred species, and many examples can be found in Cowx (1998).

The rate of introductions is still increasing in South America. This trend have been noticed in late 1980s (Welcomme, 1988). In Brazil, introductions did not begin until the early 20th century, coincident along with the growth of aquaculture activities. At that time, the federal government promoted the use of fish as an animal protein source for human consumption in the poor and arid Northeastern region of the country. Several Brazilian fishes, as well as species from other countries, were placed in reservoirs, and many became established. Escapes from fish-culture farms and from reservoir stocking programs in the Northeastern region were the initial sources of fish introductions in Brazil. Some purposeful introductions were also carried out in rivers during this time. Carps, tilapias, and Brazilian species such as the pirarucu (*Arapaima gigas*), peacock basses (*Cichla* spp.), croakers (*Plagioscion* spp. and *Pachyurus* spp.), curimbatá (*Prochilodus argenteus* = *P. marggravii*), and piaus (*Leporinus* spp.) are believed to be the first exotics released outside of their natural ranges (Menezes, 1953a, b).

A second period of introductions occurred in the middle 20th century, when hydroelectric power companies built hatcheries to mitigate the impacts negative of large dams on the reproductive migrations of native fish species. To minimize the impacts of their dams to migratory species, these energy companies invested in the development of fish production technology for those species. Although they made mistakes (e.g., the production and release of non-native species), they contributed significantly to native fish production technology, particularly of migratory species.

A third period of introductions is now in progress, fueled by an increased demand for fish production, the aquarium trade, and "pay-to-fish" (fee-fishing) farms. These activities have stimulated the transfer of Brazilian species among basins, as well as the introduction of additional non-Brazilian fish species, such as the very aggressive walking catfish *Clarias gariepinus* (Alves et al., 1999) and the rainbow trout, *Oncorhynchus mykiss* (Magalhães et al., 2002a).

Few studies report the impacts of alien fish species on the Brazilian native fish fauna, but such concerns are increasing. Here, we describe the fish species introductions in the state of Minas Gerais, southeastern Brazil (Figure 1). We outline the history of legislation involving introductions, describe the pathways for introductions and the actual or possible impacts of introductions, and provide recommendations for minimizing further introductions in the future. We use English common names, and scientific names from the Fishbase Project (www.fishbase.org; Froese and Pauly, 2003). For unlisted species, the Brazilian or translated names are used.

2. LEGAL ASPECTS OF INTRODUCTIONS IN BRAZIL

In Brazil, there are conflicts in interpreting the laws that deal with non-native species. The misunderstandings began with confusion over concepts and terms. Even with specific federal and state laws, there are misunderstandings about concepts such as native, exotic, allochthonous, or autochthonous species and introduction, translocation, reintroduction, or transfer of species.

In a Federal Decree (#145/98-1998), these categories of aquatic species are defined as follows:

1. native: species with origin and natural occurrence in Brazil;
2. exotic: species of foreign origin and natural occurrence only in other countries, even if already introduced to Brazil;
3. autochthonous: species of origin and natural occurrence within the Brazilian watershed in question;
4. allochthonous: native species of origin and natural occurrence in Brazil but outside the Brazilian watershed in question.

However, these definitions may create inappropriate loopholes in the laws or in the interpretations of the law. Here, we do not distinguish biological differences between the introduction of an exotic species or an allochthonous species. If a peacock bass (*Cichla* spp., from Amazonia) or a walking catfish (*Clarias* spp., from Africa) is introduced into a river outside of its natural range, either is a non-native species to the host community. The deleterious effects of both on the native fauna could be the same. Therefore, we assume that the terms exotic, alien, non-indigenous, and non-native have the same meaning and use only the

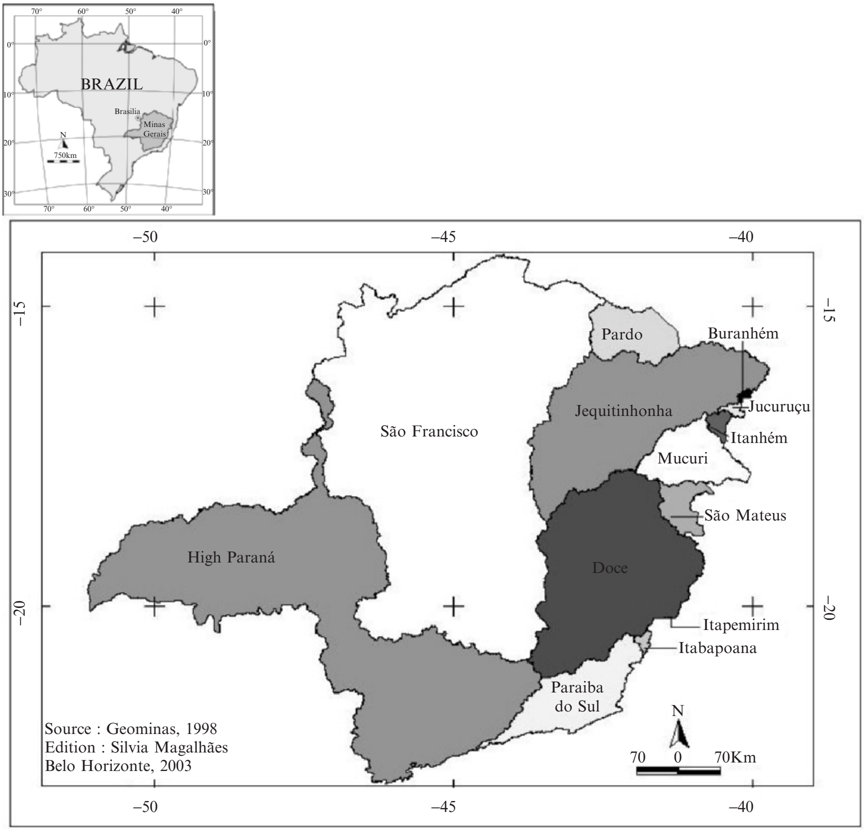

Figure 1. Location and river basins of Minas Gerais, Brazil

term non-native. Legislation should consider all of these terms equally; all imply that the species under consideration is not from the river basin in question.

Activities associated with the movements of these species are also defined by Brazilian law, as follows:

1. introduction: import of a non-native species, or a hybrid, into an area where it did not occur before;
2. translocation: any process of moving a species between river basins, from inside or outside the country;
3. reintroduction: import of a non-native species, or a hybrid, into an area where it occurred before;
4. transfer: translocation of a given species from one river basin to another, where it is considered to be allochthonous.

Especially in a nation with the size and geographic complexity of Brazil, where river basins and states are larger than some other nations, it matters little from an ecological perspective whether a non-native species comes from a different country, continent, or Brazilian river basin, when that species is released into the natural environment. From an ecological perspective, the laws must consider any species as non-native when it is located outside of its natural range of distribution. The historical geographic range of the species is also important when you are questioning whether a species is non-native.

In Brazil, there are good federal and state laws on introducing non-native species. For example, Federal Law # 9.605-1998 states the following:

1. introduction is prohibited and considered a crime;
2. transfer, translocation, and reintroduction must be licensed.

In addition, in Minas Gerais, State Law # 12.265-1996 and Decree-Law # 38.744-1997 state the following:

1. introduction is considered damaging to the native fauna and is prohibited without government permission;
2. the culture and transport of live fishes must be licensed.

However, such laws are frequently controlled, repressed, not followed, or, with the assistance of ambiguous terminology, manipulated.

Misunderstanding and misinterpretation of laws can lead to mismanagement of native species or inappropriate mitigation of environmental damage. For example, because regulations for both native and exotic species have restrictions on the sizes of fish that can be legally caught and kept, a fisherman may be prohibited from catching a non-native species at a size smaller than the legal length, but may be allowed to fish for an officially endangered species (e.g., the jaú, *Zungaro jahu* = *Paulicea luetkeni* [Machado et al., 1998]) within the permitted size range. There are many examples in which prosecutors require an environmental aggressor or polluter to stock fishes in order to mitigate damage, often a fish kill. Because as the accused generally have little knowledge of local species or access to fry of appropriate native species, such judgments can lead to the release of non-native species that further harm the native species.

Local environmental or sports-fishing interests may also cause the creation of inappropriate measures. For example, the Itamonte local government, by means of decree number 001-1997, created a sport fishing area at the Rio Aiuruoca headwaters to stimulate a rainbow trout fishery supported by the National Sport Fishing Development Program (PNDPA, 2000).

In summary, although laws governing non-native fish species exist, in practice, fish introductions are of little concern. In fact, any citizen can buy cultured fish from any Brazilian river basin or from another country and release them into privately owned water bodies. The owners and managers of many privately operated hatcheries state in magazine advertisements that their fishes can be delivered to anywhere in Brazil.

3. THE SITUATION IN MINAS GERAIS

3.1. General Overview

Minas Gerais, which is slightly larger than France, is one of the biggest Brazilian states. It has an area of 586,528.3 km^2 and a growing population, currently of approximately 18 million people (IBGE, 2002). It is drained by 13 different river basins (Figure 1); the São Francisco and High Paraná are among the largest hydrographic basins in Brazil. A total of around 400 fish species, including 63 non-natives, have been recorded in the state. These numbers could be underestimates because some river systems have not yet been thoroughly investigated.

For each basin, the total number of known species, number of known non-native species, and change in the number of non-native species in the past six years are shown in Figure 2A. To obtain a perspective on the proportions of non-native species to the total number of species in each river basin, we used an index of contamination, as calculated by the following equation:

$$\mathrm{CI} = \frac{\mathrm{E}}{\mathrm{N} + \mathrm{E}}$$

where CI = contamination Index, E = number of exotic species, and N = number of native species. The CI varies from 0 in pure assemblages, with no non-natives, to 1 in totally contaminated communities, with only non-native species.

In Figure 2B, we illustrate the relationship between the total number of species and the proportional level of non-native species contamination in each of these river basins. Fortunately, the two largest river basins in Minas Gerais, the High Paraná and São Francisco, contain relatively low proportions of non-native species (Figure 2B). In contrast, most of the less diverse, smaller river basins contain relatively high numbers and proportions of non-native species, particularly the Paraíba do Sul and Doce (Figure 2). (We acknowledge that the number of species may not be a good indicator of the total number of non-native individuals in a river basin and that the thoroughness of sampling is not equal among river basins.)

The Neotropical biogeographic area is the world's richest in fish species (around 8000 species [Schaefer, 1998]), but is also one of the least known (Menezes, 1996). In Minas Gerais, non-native species records have increased over the past seven years, compared with available data through 1996 (Alves and Vieira, 1996). Relatively large numbers of new records have been documented for some areas. Those are areas where few past studies were conducted or where field research is currently occurring. Nevertheless, the number of non-native species introductions into Minas Gerais may be underestimated.

Tilapine species (i.e., *Oreochromis* spp. and *Tilapia* spp.) are the most widespread non-native species in Minas Gerais, and they are present in almost all river basins. In reservoirs, aspects of their biology (omnivorous feeding habit, reproductive strategy with parental care, resistance to pollution, adaptations

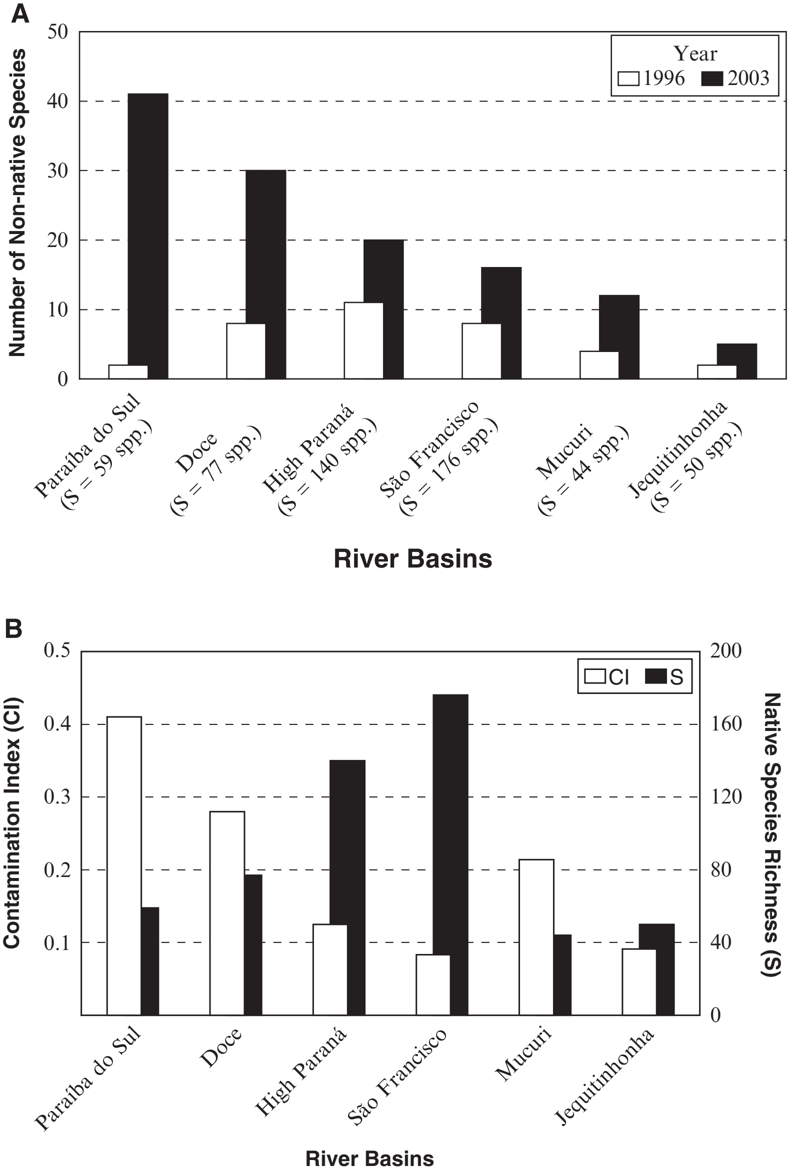

Figure 2. Characterization of fish species in Minas Gerais, Brazil main river basins. Values are based on estimates from Alves et al. (1998), Costa et al. (1998), and V. Vono, Universidade Federal de Minas Gerais (personal communication). A. Number of exotic fish species, 1996 and 2003. In brackets: the total species richness (S) in each river basin. B. Total number of species (black bars; includes both native and non-native fishes; and level of contamination with non-native fish species (white bars). Index used to calculate level of contamination is presented and defined in the text (Section 3.1)

to still waters, fast growth) are advantages in competition with native species. In most reservoirs, they have large populations and are commercially fished. In other regions of the country, the negative impacts of these species have changed not only fisheries but also fish species compositions in reservoirs (Menescal and Attayde, 2001).

3.2. Purposes and Known Impacts of Introductions

The purposes of fish introductions in Minas Gerais are well known, as they are in the rest of the world. Some factors that contribute to the number of introductions are proximity of hatcheries to rivers, river alterations (dams, canals, and water transfers), stocking programs, deliberate releases, use of live bait, or habitat disturbances in the natural environment, which also may increase the chances of non-native species establishment (Moyle and Light, 1996; Gido and Brown, 1999). However, the establishment of non-native species can be inhibited by the isolation of drainages; by inadequate habitat for successful reproduction of the non-native species; by interactions with native species; when the number of introduced individuals is small; or when environmental conditions such as water levels, salinity, or temperature are adverse (Ross, 1991; Baltz and Moyle, 1993; Crivelli, 1995; Gido and Brown, 1999).

The principal reasons for non-native species introductions into the natural environment and some examples of the genera introduced into Minas Gerais are listed in Table 1. Over 90% of Brazilian electricity is hydropower (Kohlhepp, 1999), and Minas Gerais is one of the states with great hydroelectric energy production potential in Brazil. That state has more than 2000 small, medium-sized, and large reservoirs. The population of Minas Gerais is growing and the increasing number of inhabitants leads to increasing energy demands. Many new dams are already under construction or are under study for their viability. Because reservoir stocking programs are among the main causes of non-native fish introductions in Brazil (Agostinho and Júlio, Jr., 1996; Vieira and Pompeu, 2001), this pathway for introductions must be an increasing concern. The creation of artificial reservoirs alters local ecosystems and the chance of invasion success can be augmented in altered ecosystems (Ross, 1991; Moyle and Light, 1996), especially when lotic environments are changed into lentic ones.

Stocking for sport fishing also occurs directly in river systems. In southern Minas Gerais, which has high-altitude (above 1300 m), cold, clear, well-oxygenated waters, trout can easily become established. There, an intense local culture linked with rainbow trout exists; it includes a sport fishery, aquaculture, and culinary art in which trout have been used in traditional dishes for almost 50 years. All trout species are non-native to Brazilian waters. Escapes of rainbow trout from fish ponds are frequent and may increase the probability that this species will definitively establish in local waters and impact the unique natural fish fauna of that region.

Table 1. Known purposes and examples of non-native fish genera introduced into Minas Gerais, Brazil (**X**). Dash = no information or not applicable

Purpose of introduction	Genus																							
	Astronotus	*Cichla*	*Carassius*	*Clarias*	*Colossoma*	*Cyprinus*	*Hoplias*	*Gymnocorymbus*	*Hyphessobrycon*	*Lepomis*	*Lophiosilurus*	*Micropterus*	*Mikrogeophagus*	*Oncorhynchus*	*Oreochromis*	*Piaractus*	*Plagioscion*	*Poecilia*	*Pseudoplatystoma*	*Pterophyllum*	*Pygocentrus*	*Salminus*	*Tilapia*	*Xiphophorus*
Accidental	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–
Aquaculture	–	–	–	–	X	X	–	–	–	–	–	–	–	–	X	–	–	–	X	–	–	–	X	–
Deliberate (aquarium release)	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	X
Fishery improvement	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	X	–	–	–	–	X	–	–
Forage	–	–	–	–	X	–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ornamental	–	–	–	–	–	–	–	X	X	–	–	–	X	–	–	–	–	–	–	X	–	–	–	–
Pay-to-fish ponds	–	–	–	X	X	X	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	X	–
Reservoir stocking	–	–	–	–	–	–	X	–	–	–	–	X	–	–	–	–	X	–	–	–	–	–	X	–
Sport fisheries	–	X	–	–	–	–	–	–	–	–	–	X	–	X	–	–	–	–	–	–	X	X	–	–
Undesirable organisms control	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–

Known impacts of non-native species introductions are as follows (Kabata, 1970; Courtenay and Stauffer, 1984; Welcomme, 1988; Miller, 1989; Ross, 1991; Rosenfeld and Mann, 1992; Scribner and Avise, 1993; Hickley, 1994; Lever, 1998; Trexler et al., 2000; Tapia and Zambrano, 2003):

1. extinction of native species;
2. perturbations of limnological conditions;
3. introduction of diseases, pathogens, and parasites;
4. hybridization between native and non-native species, with the possibility of genetic introgression;
5. changes in fish assemblage structure, with altered competition and predation rates;
6. changes in fisheries composition;
7. damage to low-fecundity native species;
8. adverse effects to local or regional social–economic structure.

Many of these have already occurred in Minas Gerais.

The few benefits of non-native species introductions are restricted to the improvement of fish production and sport fisheries (Pullin et al., 1997; Bartley and Casal, 1998). These benefits are mainly related to the monetary return that non-native species can provide to human populations through the commercialization of fish as food, ornamental species, or sport fish. Environmentally, no introduction can be considered positive.

3.3. Case Studies

3.3.1. Changes in lower Rio Doce fisheries

The Rio Doce drains 82,000 km^2 in Minas Gerais and Espírito Santo (86% of the river system is in Minas Gerais). The great majority of its area is heavily altered by a variety of human activities, with negative consequences on the ichthyofauna. At present, anglers dominate fishery activities because low productivity precludes commercial utilization. Professional fishermen concentrate their activities on the middle and lower reaches of the main stem. Before 1970, many diadromous species in the genera *Centropomus*, *Mugil*, *Caranx*, and *Eugerres* were regularly captured by commercial fishermen in this region. They constituted a fishery of considerable value. After 1974, construction of the Mascarenhas Hydropower plant limited the distribution of such species to the stretch below the dam, i.e., outside of Minas Gerais. This change in the river channel led to a less productive fishery above the dam; however, approximately 50 fishermen continue to utilize this resource. To reduce the consequences of the dam, a fish passage has been recommended, but has not yet been constructed.

As a result of the change in fish composition and reduction in size of the commercial fishery in this portion of the Rio Doce, non-native species were stocked to increase fish availability. No official records of stocking in the Rio Doce exist except for the dourado (*Salminus brasiliensis*) (Ruschi, 1965) and the walking catfish (Alves et al., 1999). The black armored catfish (*Pogonopoma* *wertheimeri*), the last non-native species introduced, was brought into the area by local people after 1997. In Aimorés County, studies in 1997 and from 2002 to 2003 produced 50 fish species, 14 of them non-native (F. Vieira, personal observations). In the past, the local fishery was based on native catfishes and characins. Few native species are currently of commercial importance. Two native species formerly important to the local commercial fishery, the piabanha (*Brycon* cf.devillei.) and the "surubim-do-Rio-Doce" (*Steindachneridion doceanum*), are now "commercially extinct." Only the armored catfishes (Loricariidae), which are highly appreciated and demand good prices, remain in the local fishery market. The importance of the introduced species to the local fishery varies considerably among species (Table 2); most introduced species became established and now are components of the commercial catches. Four non-native species (*Hoplias lacerdae*, *Lophiosilurus alexandri*, *Oreochromis niloticus*, *Prochilodus costatus*) make up the bulk of the current fishery. The fisheries production of walking catfish is also high, but its commercial value is low. Among the exotics, the red piranha (*Pygocentrus nattereri*) is the only introduced species avoided by fishermen due to the destruction of fishing gear and handling accidents. Other introduced species are of less fisheries importance or do not contribute to fisheries. Although the composition of the species commercially fished in the Rio Doce has changed, the non-native species provide commercial fishes to professional fishermen. However, this new situation has eliminated focus on the problems caused by environmental degradation associated with construction of the dam—changes in water flow, silting, water pollution, and clearing of vegetation.

Table 2. Relevance to professional fishing of exotic fish species in the Aimorés region, Rio Doce basin, Minas Gerais, Brazil

Species	Abundance	Professional fishing relationship	Local importance to fishermen's gains
Astronotus ocellatus	Low	Positive	No importance
Cichla spp.	Medium	Positive	Low
Clarias gariepinus	Low	Positive	Low
Hoplias lacerdae	High	Positive	High
Hoplosternum littorale	Medium	Neutral	No importance
Lophiosilurus alexandri	High	Positive	Very high
Oreochromis niloticus	High	Positive	Very high
Pimelodus maculatus	Low	Positive	Low
Pogonopoma wertheimeri	Low	Neutral	No importance
Prochilodus costatus	High	Positive	High
Pseudoplatystoma sp.	Low	Positive	Low
Pygocentrus nattereri	High	Negative	No importance
Salminus brasiliensis	Low	Positive	Low
Tilapia rendalli	Low	Positive	Low

3.3.2. The ornamental fish trade and the introduction of non-native species

In Muriaé County, the Rio Glória, which flows into the Rio Muriaé (Rio Paraíba do Sul basin), is the most important aquarium fish production area in South America (Vidal, Jr. and Costa, 2000). The substantial ornamental fish-culture industry there has resulted in a fish assemblage that is composed of up to 50% non-native species, and recent studies show an increasing rate of new records for aquarium species in the environment (Magalhães et al., 2002b). Non-native aquarium species are continuously escaping into the wild from the high concentration of small ornamental fish farms (more than 250 farmers and about 3000 production ponds; Vidal, Jr. and Costa, 2000) located on or near the river. Through international and intercontinental shipping and movement of living organisms, including fish, into the area, the ornamental fish trade could threaten the native fauna (Andrews, 1990). For example, in this river, there are two species of tetras—the native yellow tetra (*Hyphessobrycon bifasciatus*) and the non-native common serpa tetra (*H. eques*), which has a natural range in the Rio Paraguay basin. These species have the same body size, feed on the same items, share the same habitat, and probably have the same reproductive strategy. The non-native species is now more abundant than the native species. At Itamuri, a small district of Muriaé County, the livelihoods of at least ten families are maintained by fishing only the common serpa tetra, using fish traps. They can catch more than 2000 specimens in a few days. The fish are sold in São Paulo and Rio de Janeiro ornamental fish markets. Experimental fishing has shown that *H. eques* occurs in high numbers whereas *H. bifasciatus* occurs in low numbers (LIMIAR, 2004; C.B.M. Alves, personal observation), but abundance studies in areas without *H. eques* are needed to determine if *H. bifasciatus* naturally occurs at low densities and if *H. eques* is displacing *H. bifasciatus*.

In the same river, the red piau (*Leporinus copelandii*), an attractive native fish species that can attain a weight of up to 4 kg, is one of the most important species in commercial and angler catches. Recently, another anostomid, the piauçu (*Leporinus macrocephalus*) was introduced into the region by a local sport fishermen's association. This species, which is native to the Pantanal (West-central Brazil), is bigger than the native species. Both species are migratory and have the same feeding habits and habitat requirements. Thus, they could compete for space, food, and shelter. Similarly, in the Córrego Santo Antônio and Córrego Boa Vista, tributaries of Rio Glória, both native (*Phalloceros caudimaculatus*, *Poecilia vivipara*) and non-native (*Poecilia reticulata*, *P. sphenops*, *Xiphophorus hellerii*, *X. maculatus*, *X. variatus*) poeciliids co-occur and have similar reproductive strategies, feeding habits, and habitat requirements. These species could compete, with unknown consequences.

3.3.3. Local extinctions in lakes

Local fish species extinctions in Minas Gerais have been documented. In a Rio Doce valley lake, 50% of the native fish species disappeared after introduction of a piscivorous peacock bass (*Cichla ocellaris*) and the red piranha (*Pygocentrus nattereri*) (Godinho et al., 1994). Data provided by Sunaga and Verani (1991), who studied the lakes (biannually) from 1983 to 1987, were the basis for such comparisons. The effects of these introductions were not restricted to reduced species richness. In lakes with peacock bass and red piranha, small-sized individuals of native species are absent and the piscivorous native trahira (*Hoplias malabaricus*) switched its diet of principally small fishes to a higher component of macroinvertebrates and insects, probably to avoid competition (Pompeu and Godinho, 2001).

Damages caused by *C. ocellaris* introductions are well known in other tropical lakes, such as Gatun Lake, Panama (Zaret and Paine, 1973). This species radically changed the fish composition of the lake by eliminating six of the eight most common native species. Molina et al. (1996) reported the extinction of a native species of pacu (*Metynnis* cf. *roosevelti*) caused by introduced peacock bass in Northeastern Brazil.

The fish fauna of the central lake of Lagoa Santa was originally evaluated between 1850 and 1856 (Lütken, 2001). Approximately 70% of the original fish fauna was extirpated by 2002 (Pompeu and Alves, 2003). Although other environmental impacts affected the fish assemblage of Lagoa Santa, one cause of this drastic fish diversity loss was the introduction of four non-native species: a peacock bass (*Cichla* cf. *monoculus*), the trairão (*Hoplias lacerdae*), a tilapia (*Tilapia rendalli*), and a calichtid armored catfish—the hassar (*Hoplosternum littorale*). The first two species are piscivorous and attain larger sizes than other picivorous fishes originally present in the lake. The locally extinct species included two small native piscivorous species—the dog fish (*Acestrorhynchus lacustris*) and the white piranha (*Serrasalmus brandtii*)—and *Characidium lagosantense*, which is one of three officially endangered species in Minas Gerais freshwaters (Machado et al., 1998).

3.3.4. Introductions of piscivores

Special attention must be given to the introduction of piscivores. They are commonly introduced because they have great appeal as sport fish. They tend to be very successful colonizers because they have advantages over native species that lack adaptations to avoid their predatory behavior. This is a common mechanism that leads to the extinction of fishes (Moyle and Light, 1996).

A number of Brazilian piscivores have been introduced and become established in regions of the country where they are not native. For example, the peacock basses (*Cichla* spp.), which are native to the Amazon region, caused problems in the central lake of Lagoa Santa (Pompeu and Alves, 2003), in the Rio Doce main stem and its lakes (Godinho and Formagio, 1992), and, together with the South American silver croaker (*Plagioscion squamosissimus*), in the Rio Grande (Santos et al., 1994; Santos and Formagio, 2000). *Cichla* spp. are becoming very widespread. They are stimulating changes in native fish assemblages and fisheries, such as in the Rio Piquiri in the Pantanal (Nascimento et al., 2001), Três Marias reservoir in the São Francisco basin (Magalhães et al., 1996) and Itumbiara reservoir in the Rio Paranaíba (Santos, 1999), where they are important for both commercial fishing and sport fishing. The dourado (*Salminus maxillosus*), a ferocious piscivore originally absent from the Rio Paraíba do Sul basin, was introduced in 1884, 1931, and 1945 (Moraes-Filho and Schubart, 1955) but was not present in local fish markets until 1948. The same species also was introduced and became established in the Rio Doce basin.

Piscivorous fish introductions are also likely to impact other native species in the near future. We foresee a problem with *Steindachneridion* species. In Minas Gerais, four species of this large native catfish, endemic to Eastern Brazilian river basins, are considered endangered (Lins et al., 1997). The most recent evaluation of endangered native species, to be ratified by the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA), includes four *Steindachneridion* species. Based on our observations of more than ten years, we believe that these species are almost extinct throughout their natural range in the basins of Rio Doce (*S. doceanum*) and Rio Paraíba do Sul (*S. parahybae*) due to environmental disturbances, including the introduction of other piscivores in the genera *Cichla*, *Clarias*, *Hoplias*, *Lophiosilurus, Pseudoplatystoma*, and *Salminus*. Many of the non-natives are larger than the native species. They are establishing where they have been introduced and are increasing the competition for food. *Steindachneridion* spp. have natural low densities, but although increased pollution and the elimination of migratory routes through the fragmentation of the main river stem by hydropower dams (Bizerril and Primo, 2001) also impact these species, their recent extremely low captures rates (they are essentially commercially extinct) could be partially attributed to the impacts of the introductions.

3.3.5. Hybridization, genetic introgression, and stocking

Hybridization is another consequence of the introductions of non-native species that are closely related to native species (Crivelli, 1995). The closely related *Hyphessobrycon*, *Leporinus*, and poeciliid species mentioned above could hybridize, particularly if they share the same reproductive niches and timing. In addition, two of the three recognized species of the commercially valuable *Pseudoplatystoma* catfishes have been artificially hybridized (*P. corruscans* × *P. fasciatum*; Figure 3). The first species occurs naturally in the São Francisco and Paraná basins and the latter in the Paraná and Amazon basins. As the hybrid spreads to many Southeastern river-basin areas for aquaculture, there is a danger of genetic introgression and reduced fitness of the mixed stock (Scribner and Avise, 1993) or displacement of the native species (Simberloff, 1996) if reproduction between the hybrid and either parental species is possible. There are no studies yet on the reproductive capacity of these hybrids.

Genetic problems associated with non-native species introductions have not received the required attention. Even when native species have been used for

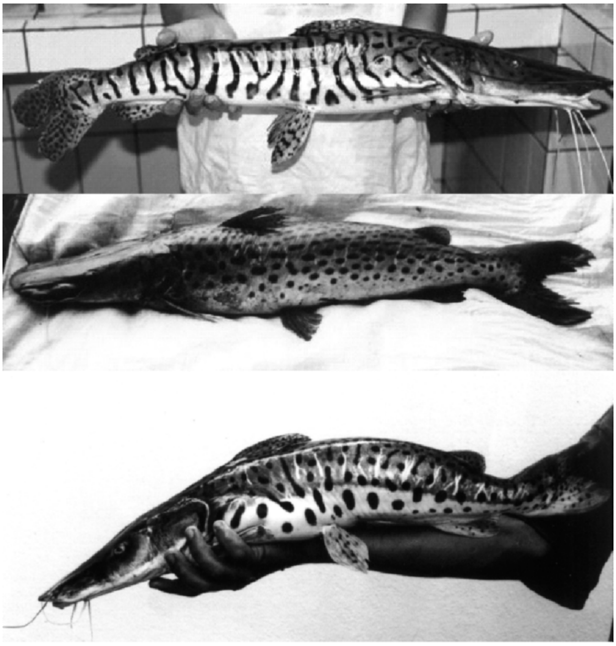

Figure 3. From the top, *Pseudoplatystoma fasciatum, Pseudoplatystoma corruscans* and the hybrid between them

stocking, there has been no evaluation of the successes or failures of stocking programs. Broodstocks in hatcheries always contain fish from a variety of different populations and the genetic composition of the broods reared for release is not examined. In addition, there are no monitoring studies to determine if introduced individuals reach reproductive age and disseminate their genetic characteristics. The possibility of genetic introgression is real because all government hatchery stations release millions of fry, alevins, and juveniles annually into existing wild populations.

4. PROSPECTS AND CONCLUSIONS

In the long term, as species spread to basins out of their natural ranges, there is a risk of fish faunal homogenization. The non-native species composition will be the same in many Brazilian river basins whereas on a broad scale, local native species could become less numerous and less abundant over time. Thus, waterways should be monitored for changes in species composition, density of native versus non-native individuals, and the appearance of hybrids.

In some important river basins of Minas Gerais, non-native fish species represent up to 40% of the total species richness (Figure 2). Certainly, many factors determine the susceptibility of an assemblage to invasions, but it is difficult to know which factors lead to the success of introduced species (Gido and Brown, 1999). Clearly the best approach is to reduce introductions altogether and to utilize the native species in the best way possible. Reducing the introduction of new species can be approached in a number of ways:

1. Consider improving regulations for the sale and transport of live organisms and clarify and enforce existing legislation. If the present laws, decrees, and rules were followed and respected, the spread of non-native fish species could be slowed or halted.
2. Publicize the adverse impacts of non-native species on the native fish fauna in audience-specific manners to politicians, legislators, decision makers, researchers, university staffs, school children, water-side communities, pet shop owners, sport fishers, etc. As an example of public misconception of the issue, many stocking programs are justified purely as environmental education instruments instead of being assessed for appropriateness and monitored for effectiveness.
3. Develop the aquaculture of native species. This could slow the spread of non-native species by providing alternatives to their culture. Although Brazil has the world's greatest freshwater fish biodiversity, fish ponds in hatcheries are dominated by exotic species. This development of native-species aquaculture would, of course, need to include the use of appropriate broodstock to reduce genetic impacts of escapes on local populations. Each river basin should have its own native cultivated stock of each species. Special concern must be given to raise public awareness regarding the non-native ornamental (Andrews, 1990) and commercial fish trades.

The aim of these proposed solutions is to stop or slow the spread of non-native species. Otherwise, Brazil will be another country with a large number of well-established, non-native species (currently, N =104 [Gurgel and Oliveira, 1987; Welcomme, 1988; Orsi and Agostinho, 1999; Bizerril and Lima, 2001; Magalhães et al., 2002b; Paiva et al., 2002]). The dramatic examples of impacts observed in Africa (Barel et al., 1985; Lowe-McConnell, 1993) and Florida (Trexler et al., 2000) could thus be readily replicated in Brazil if the people do not act soon.

Minas Gerais already has a large number of non-native fish species (Table 3) compared with other Brazilian states or regions such as the northeast (N = 39 [Gurgel and Oliveira, 1987]), Rio de Janeiro state (N = 37 [Bizerril and Lima, 2001]), and Paraná state (N = 13 [Orsi and Agostinho, 1999]), and elsewhere in the world (Table 4). Removal of non-native species is practically impossible. The problems created by introduced species are difficult or impossible to solve, but can be prevented by limiting their spread, as well as avoiding new introductions. Thus, it is more critical to prevent new non-native fish introductions than to attempt to remove established non-native fishes. At the present rate of introductions, Minas Gerais and Brazil, as a state and country, will soon

Table 3. Introduced species in Minas Gerais State (Brazil)

	Hydrographic basin (native species richness)					
Non-native species	Paraíba do Sul (59)	Doce (77)	High Paraná (140)	São Francisco (176)	Mucuri (44)	Jequitinhonha (50)
Aristichthys nobilis	–	X	X	–	–	–
Astronotus ocellatus	–	X	X	X	–	–
Callichthys callichthys	X	–	–	–	–	–
Carassius auratus	X	–	–	–	–	–
Cichla monoculus	X	–	X	X	–	–
Cichla ocellaris	–	X	–	–	–	–
Cichla temensis	–	–	–	X	X	–
Clarias gariepinus	X	X	X	X	X	X
Colisa lalia	X	–	–	–	–	–
Colossoma macropomum	X	X	X	X	X	–
Corydoras sp.	X	–	–	–	–	–
Ctenopharyngodon idella	–	X	–	–	–	–
Cyprinus carpio	X	X	X	X	X	–
Danio frankei	X	–	–	–	–	–
Danio malabaricus	X	–	–	–	–	–
Danio rerio	X	–	–	–	–	–
Gymnocorymbus ternetzi	X	–	–	–	–	–
Hemichromis bimaculatus	X	–	–	–	–	–
Hoplias lacerdae	X	X	X	X	X	X
Hoplosternum littorale	X	X	X	X	–	–
Hyphessobrycon eques	X	X	X	–	–	–
Hypophthalmichthys molitrix	–	X	–	–	–	X
Ictalurus punctatus	–	X	–	–	–	–
Laetacara curviceps	X	–	–	–	–	–
Lepidosiren paradoxa	–	–	–	X	–	–
Lepomis gibbosus	–	X	–	–	–	–
Leporinus macrocephalus	X	X	X	–	X	–
Lophiosilurus alexandri	–	X	–	–	–	–
Macropodus opercularis	X	–	–	–	–	–
Metynnis maculatus	X	X	X	–	–	–
Micropterus salmoides	–	X	X	–	–	–
Mikrogeophagus ramirezi	X	–	–	–	–	–
Misgurnus anguillicaudatus	X	–	–	–	–	–
Odonthestes bonariensis	–	–	X	–	–	–
Oncorhynchus mykiss	–	–	X	–	–	–
Oreochromis niloticus	X	X	X	X	X	–
Piaractus mesopotamicus	–	X	X	X	–	–
Pimelodus maculatus	X	X	–	–	–	–
Plagioscion squamosissimus	–	–	X	X	–	–
Poecilia reticulata	X	X	X	X	X	–
Poecilia sphenops	X	–	–	–	–	–
Pogonopoma wertheimeri	–	X	–	–	–	–
Polycentrus schomburgkii	X	–	–	–	–	–

(*Continued*)

Table 3. Introduced species in Minas Gerais State (Brazil)—cont'd.

Non-native species	Hydrographic basin (native species richness)					
	Paraíba do Sul (59)	Doce (77)	High Paraná (140)	São Francisco (176)	Mucuri (44)	Jequitinhonha (50)
Prochilodus argenteus	–	X	–	–	–	–
Prochilodus costatus	–	X	–	–	X	X
Prochilodus lineatus	–	–	–	X	–	–
Pseudoplatystoma hybrid[1]	X	X	–	–	X	–
Pterophyllum scalare	X	–	–	–	–	–
Puntius conchonius	X	–	–	–	–	–
Puntius nigrofasciatus	X	–	–	–	–	–
Puntius semifasciolatus	X	–	–	–	–	–
Puntius tetrazona	X	–	–	–	–	–
Pygocentrus nattereri	–	X	–	–	–	–
Salminus brasiliensis	X	X	–	–	X	–
Satanoperca pappaterra	–	–	X	–	–	–
Tambacu[2]	–	X	–	–	–	–
Tanichthys albonubes	X	–	–	–	–	–
Tilapia rendalli	X	X	X	X	X	X
Trichogaster chuna	X	–	–	–	–	–
Trichogaster trichopterus	X	–	–	–	–	–
Xiphophorus hellerii	X	X	–	–	–	–
Xiphophorus maculatus	X	–	–	–	–	–
Xiphophorus variatus	X	–	–	X	–	–

[1] Hybrid of *P. corruscans* × *P. fasciatum*.
[2] Hybrid of *C. macropomum* × *P. mesopotamicus*.

have the largest numbers of non-native species in the world, many of them will be well-established and reproducing in the wild.

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Table 4. Number of known introduced species in selected states, countries, or regions of the world

State, country, or region	Number of species	References
Australia	22	McKay, 1984
Brazil (all)	104	Gurgel and Oliveira, 1987; Welcomme, 1988; Orsi and Agostinho, 1999; Bizerril and Lima, 2001; Magalhães et al., 2002b; Paiva et al., 2002
Brazil (Minas Gerais)	**63**	**This paper**
Brazil (northeast)	39	Gurgel and Oliveira, 1987
Brazil (Paraná)	13	Agostinho and Júlio, 1996
Brazil (Rio de Janeiro state)	37	Bizerril and Lima, 2001
Canada	18	Crossman, 1984
Chile	21	Welcomme, 1988
Cuba	10	Wotzkow, 1998
Dominican Republic	16	Chakalall, 1993
France	26	Keith and Allardi, 1998
Greece	23	Economidis et al., 2000
Hawaii	50	Yamamoto and Tagawa, 2000
India	19	Seraji et al., 2000
Iraq	7	FAO, 1997
Israel	18	Golani and Mires, 2000
Italy	25	Bianco, 1998
Jamaica	9	Chakalall, 1993
Japan	34	Chiba et al., 1989
Madagascar	31	Stiassny and Raminosa, 1994
Mexico	55	Contreras and Escalante, 1984
Morocco	24	Azeroual et al., 2000
New Zealand	25	McDowall, 1984
Pacific islands (all)	56	Maciolek, 1984
Portugal	11	Almaça, 1995
Puerto Rico	32	Erdman, 1984
Singapore	38	Ng et al., 1993
Spain	25	Elvira and Almodóvar, 2001
Sri Lanka	15	Fernando, 1971
USA (California)	162	Fuller et al., 1999
USA (Colorado)	106	Fuller et al., 1999
USA (Florida)	127	Fuller et al., 1999
USA (Nevada)	93	Fuller et al., 1999
USA (Texas)	105	Fuller et al., 1999

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CHAPTER 17

SALMONID INTRODUCTIONS IN PATAGONIA: A MIXED BLESSING

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Abstract: The fish communities of Argentine Patagonian basins are characterized by low species diversity. Their fish community structure and underlying intra- and interspecific dynamic relationships have been and are still poorly understood. Around 1904, 10 species from Northern Hemisphere hatcheries were introduced for sportfishing. Following the original introductions, unplanned stocking was widely practiced. Of all introduced species, *Oncorhynchus mykiss*, *Salmo trutta*, and *Salvelinus fontinalis* thrived; they colonized almost any available water body in Andean Patagonia. In addition, *Salmo salar* and *Salvelinus namaycush* established self-sustaining populations at a few locations. The various populations that inhabit different water bodies seem to have diverged and given rise to what are believed to be particular stocks. Some of these became world-class sportfisheries and attained importance as generators of economic improvement. Simultaneously, and although no detailed studies exist, it has been thought that salmonids have a tremendous negative impact on the native biota. Thus, in less than 100 years, salmonids have been perceived as trophy sportfish, ecological nemeses, and promoters of social well-being through sportfisheries-associated economic development. In addition, the Chilean salmonid aquaculture boom led people to believe that this could be replicated in Argentine Patagonia and fostered the establishment of mostly *O. mykiss* caged-fish farming facilities. This raised concerns about a possible decrease in the quality of Argentine wild-salmonid (those salmonids that have successfully colonized and adapted to local waterways) sportfisheries due to negative effects associated with escapement of aquacultured fish. This scenario may be realized because escaped individuals of *Salmo salar*, *O. gorbuscha*, *O. keta*, *O. kisutch*, *O. nerka*, and *O. tshawytscha*, all introduced in Chile, may be finding their way into Argentine rivers that drain into the Pacific Ocean. These complexities have generated three interest groups: (1) people concerned with possible ecological damage upon the native biota, (2) promoters of sportfisheries as generators

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of economic revenue and development, and (3) promoters of salmonid aquaculture. Ironically, after almost 100 years, little is known about fish communities in Patagonia and the interactions that govern them. These communities may continue to change due to uncontrolled stocking, new arrivals of nonindigenous fishes from Chile, and escapes from aquaculture facilities. Salmonid introductions have thus become a mixed blessing—culprits of an ecological impact that may never be quantified or completely understood and promoters of economic development that would otherwise be impossible. The challenge for the future is to develop a consensus among Patagonian provinces regarding the leading policy for the introduced-salmonid resource and to establish the steps needed to generate information for its sound management.

Key words: aquaculture, Argentina, introduction, Patagonia, salmonids, sport fishing, stocking

1. INTRODUCTION

1.1. Past History

Argentine Patagonia extends over 800,508 sq km, from the Andes in the west to the Atlantic Ocean in the east, and has scarcely 0.8 inhabitants per square kilometer. Its numerous major watersheds (Figure 1), fed mostly by thawing winter snows in the Andes, provide a series of unique environments for freshwater fishes. However, native fish communities are characterized by low species diversity (Table 1); only 19 native species have been reported (Bello, 2002). Most of the native species are scarce. Only four of them—pejerrey patagónico (*Odontesthes hatcheri*), perca bocona *(Percichthys colhuapiensi*), and perca de boca chica (*P. trucha* and *P. vinciguerrai*)—are caught in significant numbers at reservoirs and lakes, through the use of gillnets (Vigliano et al., 1999). Two species of puyen, *Galaxias maculatus* and *G. platei*, are also present in these water bodies but are not harvested because they are small in the littoral zone; larger sizes occur in deeper water (Alonso et al., 1997; Milano and Vigliano, 1997).

Only partial records of the whole stocking history exist. Members of the family Salmonidae were introduced at the beginning of the century for sportfishing. Brook trout (*Salvelinus fontinalis*), lake trout (*Salvelinus namaycush*), Atlantic salmon (*Salmo salar*), landlocked Atlantic salmon (*Salmo salar sebago*), brown trout *(Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), sockeye salmon (*Oncorhynchus nerka*), coho salmon (*Oncorhynchus kisutch*), chinook salmon (*Oncorhynchus tshawytscha*), and whitefish (*Coregonus clupeaformis*) were introduced between 1904 and 1906 from Northern Hemisphere hatcheries (Baigún and Quirós, 1985). During this period, four major shipments, coming principally from the USA but also from England, arrived in Patagonia. From 1906 until 1910, three more imports added individuals of species and stocks already introduced and also rainbow trout from Germany. Then all imports stopped until 1931, when brown trout, originally from European stocks, were introduced from Chile (Marini, 1936). Fish were released into the Limay and Santa Cruz river basins (Figure 1). Subsequently, “local” (introduced, resident) salmonids were spread throughout Patagonia and the

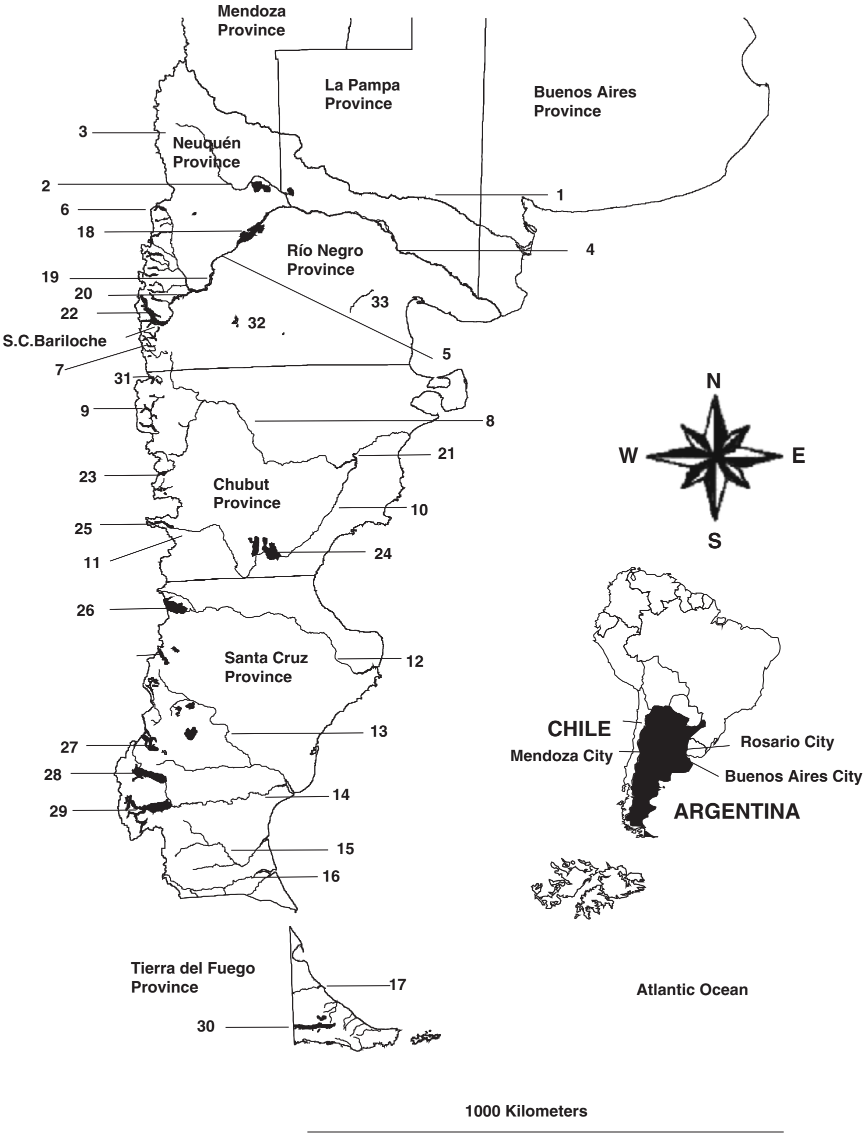

Figure 1. Principal Patagonian water masses. Rivers: 1 = Colorado; 2 = Neuquén; 3 = Agrio; 4 = Negro; 5 = Limay; 6 = Alumine; 7 = Manso; 8 = Chubut; 9 = Futaleufu; 10 = Chico; 11 = Senguer; 12 = Deseado; 13 = Chico; 14 = Santa Cruz; 15 = Coig; 16 = Gallegos; 17 = Grande. Reservoirs: 18 = Ramos Mexia; 19 = Piedra del Aguila; 20 = Alicura; 21 = Florentino Ameghino. Lakes: 22 = Nahuel Huapi; 23 = Vinter; 24 = Muster/Colhue Huapi; 25 = La Plata/Fontana; 26 = Buenos Aires; 27 = San Martin; 28 = Viedma; 29 = Argentino; 30 = Fagnano; 31 = Puelo; 32 = Carrilafquen Grande; 33 = Arroyo Valcheta

Table 1. Known fish species of Patagonia

Species	Common name	Character
Native		
Aplochiton taeniatus	Peladilla	Resident
Aplochiton zebra	Peladilla	Resident
Astyanax eigenmanniorum	Mojarra	Resident
Cheirodon interruptus	Mojarra	Resident
Cnesterodon decenmaculatus	madrecita	Resident
Diplomystes mesembrinus	Bagre aterciopelado	Resident
Diplomystes viedmensis	Bagre aterciopelado	Resident
Galaxias maculatus	Puyen chico	Resident/Catadromous
Galaxias platei	Puyen grande	Resident
Geotria australis	Lamprea	Anadromous
Gymnocharacynus bergii	Mojarra desnuda	Resident
Hatcheria macraei	Bagre del torrente	Resident
Jenynsia multidentata	madrecita	Resident
Odontesthes hatcheri	Pejerrey patagónico	Resident
Percichthys altispinnis	Perca espinuda	Resident
Percichthys colhuapiensis	Perca bocona	Resident
Percichthys trucha	Perca de boca chica	Resident
Percichthys vinciguerrai	Perca de boca chica	Resident
Trichomycterus areolatus	Bagre pintado	Resident
Introduced		
Cyprinus carpio	Carp	Resident
Odontesthes bonariensis	Pejerrey bonaerense	Resident
Oncorhynchus mykiss	Rainbow trout	Resident/Anadromous
Oncorhynchus tshawyscha	Chinook salmon	Anadromous
Salmo salar	Landlocked Atlantic salmon	Resident
Salmo trutta	Brown trout	Resident/Anadromous
Salvelinus fontinalis	Brook trout	Resident
Salvelinus namaycush	Lake trout	Resident

rest of Argentina. In Figure 2, we present our best estimate of the numbers of fish stocked from 1938 to the present. In 1938, brook trout was the species most widely utilized. A hatchery built around 1904 to handle the arrivals at Bariloche (Río Negro Province) became the center of widely practiced, unplanned stocking for sportfishing. The predominant policy was to stock any available water body. Fish for the new stockings were procured by fishing previously stocked water bodies and artificially spawning the fish obtained. Apparently no hatchery selection process was involved and young fish were released into the environment at ages ranging from a few months to several years. This procedure changed during the 1970s and 1980s, when the reproductive stock became a mixture of local wild and commercial hatchery strains. However, between 1979 and 1988, no detailed official records seem to exist. Although the records are incomplete between 1989 and 1999, partial records show that stocking was relatively high and that the rainbow trout was the

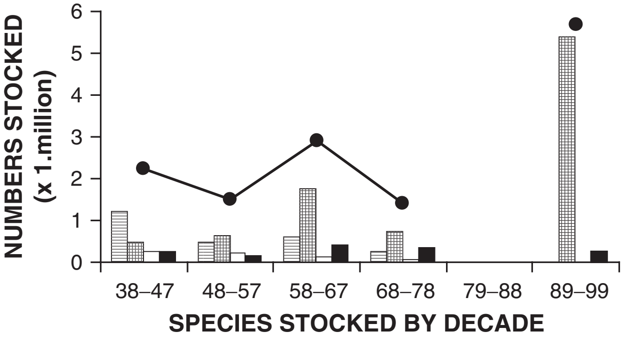

Figure 2. Estimated species-specific salmonid stocking history in Patagonia. The solid dots show total number stocked. Horizontal axis legend shows years (1900s). Species represented by bars: horizontal lines = *Salvelinus fontinalis*; grid = *Oncorhynchus mykiss*; white = *Salmo salar*; black = *Salmo trutta* (data from MIRI, 2003)

species most widely used (Figure 2). Within the last decade, provincial authorities established a policy to "intensify sportfishing opportunities far beyond natural capacities" (Cavanna, 1994); thus, rainbow trout and brown trout are stocked into the lakes created by huge hydroelectric dams in Patagonia. Within the past five years, stocking practices have changed toward stocking egg stages and juveniles several months old. Because commercial aquaculture has increased since 1993 and, in parallel, private citizens and fishermen's organizations continuously stock water bodies but leave no records, the number of fish that escape or are released into the environment may be several times greater than what has been historically recorded.

In addition to the stocking of deep glacial lakes and other Andean basins and hydroelectric reservoirs, the large Patagonian steppe is dotted with numerous ponds, creeks, and rivers, many of which have been stocked with rainbow trout since the 1940s, for sportfishing. This practice was maintained and many of the originally stocked water bodies were restocked, mostly because their environments have limited abilities to maintain self-supporting populations. Again, no detailed records exist, however the extent of this practice gave rise to numerous small local fishing organizations, which implies that stocking was common and extensive.

1.2. The Situation Today

The creation of communicating waterways and human dispersal into closed basins ensured that salmonids would be dispersed throughout Patagonia (Figure 3). Rainbow trout and brown trout have reached the Atlantic Ocean; several anadromous runs of these species have been established (Pascual et al., 2001, 2002) and have given rise to relatively recent world-class sportfisheries.

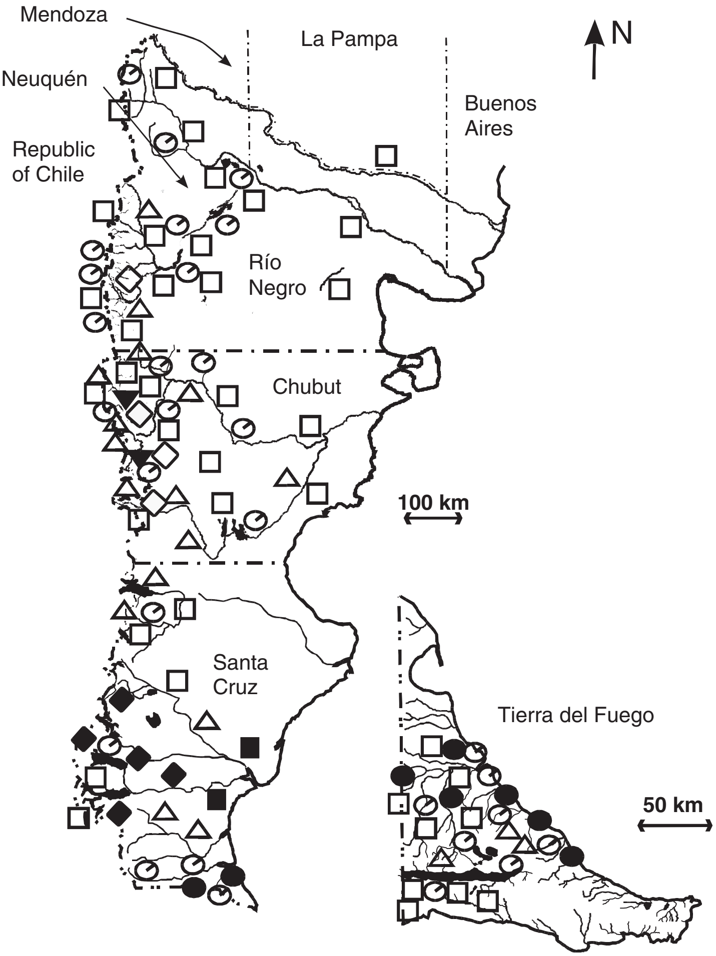

Figure 3. Actual salmonid distributions. Black areas show lakes and reservoirs. White squares = resident *Oncorhynchus mykiss* (rainbow trout); black squares = sea-run *Oncorhynchus mykiss*; inverted black triangles = *Oncorhynchus tschawyscha* (Chinook salmon); white diamonds = *Salmo salar* (Atlantic salmon); white circles = resident *Salmo trutta* (brown trout); black circles = sea-run *Salmo trutta*; white triangles = *Salvelinus fontinalis* (brook trout); black diamonds = *Salvelinus namaycush* (lake trout). Data sources: Baigún and Quirós (1985), Pascual et al. (2002), MIRI (2003)

Among these are sea-run rainbow trout in the Santa Cruz River and sea-run brown trout in Gallegos River, both in Santa Cruz province, and sea-run brown trout in the Río Grande in Tierra del Fuego province. More recently, chinook salmon have been reported to spawn in great numbers in the Corcovado and Futaleufu river basins (Chubut Province), which drain into the Pacific Ocean.

Of all introduced species, rainbow trout, brook trout, and brown trout thrived and colonized almost any available water body of the Andean Patagonic range

Table 2. Average overall and species-specific gillnetting catch per unit of effort in different water bodies of Patagonia according to the methodology of Vigliano et al. (1999). Catch per unit of effort in numbers (CPUN) and in weight (CPUW in kg) is expressed as catch per 24 h per 100 m^2 of gill-net surface. Province: RN = Río Negro, NQ = Neuquén, CH = Chubut; species: *G.p.* = *Galania platei*, *O.h.* = *Odontesthes hatcheri*, *O.m.* = *Oncorhynchus mykiss*, *P.t.* = *Percichthys trucha*, *S.f.* = *Salvelinus fontinalis*, *S.t.* = *Salmo trutta*, Prv. = province; * = native species; *n* = numbers of gill-net sets used. Data from Alonso et al. (1997), Vigliano et al. (1999), and Vigliano et al. (unpublished data)

Drainage/water body (n samples)	Prv.	CPUN	CPUW	Species-specific CPUN					
				*G.p.**	*O.h.**	*P.t.**	*S.f.**	*O.m*	*S.t.*
Pacific									
Fonck (10)	RN	6.95	5.07	1.18	–	–	3.21	1.60	0.96
Hess (10)	RN	2.21	2.36	–	–	–	0.18	1.01	1.01
J. A. Roca (10)	RN	3.11	2.47	–	–	–	1.95	0.93	0.23
Los Moscos (10)	RN	3.08	1.26	0.32	–	–	0.74	1.27	0.74
Martin (27)	RN	15.98	5.76	1.98	–	–	1.69	5.05	7.26
Mascardi (30)	RN	3.81	2.00	0.39	–	–	1.04	0.96	1.43
Steffen (20)	RN	5.86	1.90	0.15	–	–	0.24	0.95	4.52
Atlantic									
Correntoso (5)	NQ	3.24	2.77	–	–	1.25	0.12	1.62	0.25
Espejo (5)	NQ	3.61	2.72	0.37	–	1.49	0.50	1.25	–
Falkner (5)	NQ	2.12	0.93	0.12	–	0.75	0.12	1.00	0.12
Gutierrez (20)	RN	2.88	1.04	0.16	–	–	0.38	1.99	0.35
Moreno (20)	RN	6.66	4.02	0.39	0.03	3.96	0.81	1.40	0.07
Quillen (5)	NQ	11.50	5.17	–	–	8.15	0.48	1.92	0.96
Ruca Choroi (5)	NQ	4.32	2.16	0.19	0.10	1.44	1.06	1.53	–
Rivadavia (26)	CH	12.50	5.47	0.42	2.03	3.89	1.00	5.10	0.06
Villarino (5)	NQ	2.66	1.80	–	–	1.25	0.94	0.47	–

and the Patagonic steppe. Generally, the most numerically abundant salmonid species is the rainbow trout (Table 2, *O.m.*). In the Manso River basin, which drains into the Pacific, brown trout predominant, whereas in the Limay and Neuquén rivers, which drain into the Atlantic, rainbow trout predominate. Landlocked Atlantic salmon and lake trout managed to establish self-sustaining populations in only a few locations. Three species—rainbow trout, brown trout, and chinook salmon—have recently developed anadromous populations (Figure 3, sea-run *O. mykiss*, sea-run *S. trutta*, *O. tshawyscha*), whereas sockeye salmon, coho salmon, whitefish, and Atlantic salmon completely failed to establish.

2. THE BRIGHT SIDE

2.1. Sportfisheries Economics: An Unexpected Benefit

As time passed, the outcomes of the original introductions varied. In some cases, recreational anglers believed that some salmonid populations developed characteristics that differed from one another such that, currently, the populations are generally believed to be particular stocks. For example, the landlocked

Table 3. Values (in $US) of specific sportfisheries in Patagonia. Values with asterisks are unconfirmed projections

Area, province	Estimate	Type of evaluation	Source
Chimehuin River, Neuquén	Annually: $7,500,000	Travel cost method	Urbanski and Sanguinetti (1996)
75 km of Middle Limay River, Neuquén	Annually: $6,000,000	Travel cost method	J. Urbanski and M. Demicheli (personal communication)
Bariloche, Río Negro	Annually: $8,000,000	Global per capita expenses and licenses sold	Vigliano and Grosman (1997) and Vigliano and Alonso (2000)
Puelo Basin, Chubut	1990: $82,080	Visitor projection and per capita fishing cost	Urzúa Vergara (1992)
	1995: $224,000*		
	2000: $321,000*		
	2005: $512,000*		
	2010: $569,000*		
	2020: $595,000*		

Atlantic salmon introduced from the USA gave rise to a world-class sportfishery on the Traful River in the Limay River basin (Neuquén Province). There, these fish attain weights of up to 12 kg. In contrast, in most other environments this species failed completely or attains only smaller sizes; for example in the Carrileufu River (Chubut Province), fish attain weights of only up to 3 kg. Despite the fact that salmonids were introduced with sportfishing in mind, they were not viewed as an economic resource, but rather as a resource for the entertainment of a small group of elite people. Only recently has their potential as a resource for economic development at the local and regional levels been realized. Thus, only five studies related to some aspect of their economic importance exist (Table 3).

Although regional economic evaluations do not exist, unpublished data show that the overall economic value of sportfishing in Patagonia has been far greater than suspected. In 2000, around 50,000 fishing permits, costing $20 U$D each, were sold annually in all Patagonian provinces. On average, $160 U$D per fisherman is spent on tackle alone during the fishing season (Urzúa Vergara, 1992). Thus, the minimum total estimated value of sportfishing in Patagonia is $9,000,000 U$D. Because this value does not include other expenses related directly to sportfishing, such as transportation, food, lodging, fishing gear, permits, and fishing guides, the actual gross economic value of this industry must be much higher.

The development of world-class fisheries in Patagonia has attracted fishermen from all over the world. What was once a relatively small sportfishing industry promulgated by oral communication among fly fishermen has become a growing business in which travel packages are offered by international outfitters and fishing organizations. A good example of this development is the industry on the Río Grande, where brown trout introduced between 1930 and 1937 gave rise to a sea-run strain. In 1985, only one Lodge (Kau Tapen) existed on a 40-km stretch of the river. The fishery was catch-and-release and access was restricted. In that year, fishermen caught 207 fish that weighed an average of 5.5 kg; the record for that year was 10 kg (Leitch, 1991). In the 1996–1997 fishing season, 4224 fish, which averaged 5 kg each, were caught and released on the same stretch of river, and some weighed 12 kg. Today, five lodges cover approximately 150 km of the river. Access to the water is limited to only their clients, who are charged between $3500 U$D and $6000 U$D per week. Services include lodging and meals, fishing guides, and transport to and from the fishing sites, but not airfare. This example of growth in the sportfishing industry is not an isolated case; sportfishing lodges and services are rapidly extending throughout Patagonia. By 1994, 14 lodges that operate principally on 6 river systems offered world-class quality fishing. Their estimated capacity was 8730 bed nights during the 90 days of the high fishing season; this capacity has increased at least 15% annually. Alternative "new" high-quality fishing sites are actively sought out and an unknown number of guides offer their services to clients that do not use the fishing lodges. This type of development has raised new issues and conflicts. Demands to introduce other species because they supposedly have tremendous potential for sportfishing or to implement stocking programs or enhancement measures are common. In most cases, baseline information to consider the applicability of the demands does not exist.

Free access to water bodies has become a new and controversial issue. Traditionally, the vast expanse of Patagonia allowed anyone to fish wherever he or she liked. On private lands, sheep-ranch administrators granted permission to fish without reservations. However, as profits from wool production started to decline in Patagonia due to low international prices, salmonid fishing became a new ranch activity that earned hard currency. Thus, access is becoming increasingly restricted and the right to fish more expensive. As a consequence, the public feels that private landowners have taken away the right to fish, which was inherited from father to son through generations. The explosive development of the Río Grande fishery near a city of 40,000 inhabitants in Tierra del Fuego Province is a good example of this new type of conflict, which exists throughout Patagonia. There, sportfishing lodges are viewed both as revenue generators and as intruders that have deprived local people of their historical fishing grounds.

2.2. Commercial Aquaculture: A Relatively New Economic Development

Among other factors, the Chilean salmonid aquaculture boom led people to believe that open-water aquaculture could be developed in Argentine Patagonia and that caged-fish (mostly *O. mykiss*) aquaculture facilities could become established. The rearing of salmonids in Argentina started at a significant level in the 1980s. In the 1990s, fish-culture facilities designed to fulfill supply needs linked to tourist demands started to serve big population centers such as Buenos Aires, Cordoba, Mendoza, and Rosario. This brought about the need to increase production volumes and to offer a constant supply of more diversified products.

At this time, salmonid production reached the commercial or semi-industrial level. Initially, culture was in open, terrestrially located containers; it slowly changed to caged-fish farming in lentic water bodies. Only recently have land-based, enclosed, running-sea-water systems or open-ocean fish cages been utilized. Wicki and Luchini (1996), in their technical report about the aquaculture potential of northern Patagonia, estimate maximum sustainable production at approximately 17,000 metric tons (t) per year in reservoirs and rivers. These authors also mention that Patagonian environments are suitable for Atlantic salmon presmolt production and possible posterior development in land-based running-sea-water systems and sea cages. They further projected that salmonid production on the littoral coast of Tierra del Fuego province could reach 110,000 t per year; however, at this time, only pilot experiments have been undertaken.

To date, salmonid culture in Argentina has not surpassed 2000 t per year. Argentine aquaculturists must compete with imports from neighboring countries (for example, Atlantic salmon from Chile and rainbow trout from Peru) and endure disadvantages in exportation on the international market due to relatively high production costs (Luchini, 1999). Because of these problems, low levels of fish consumption by Argentineans, and high market prices, production volume is not expected to increase in the near future.

Aquaculture development in Patagonia is concentrated principally in the Alicura hydroelectric power reservoir, where the yearly production of five fish-cage farming facilities is nearly 1000 t of fish that range in weight from approximately 0.3 to 2 kg. Most of the production is sold in local markets; exports are small in quantity and low in frequency. All other fish-culture facilities are smaller, and some are experimental or academic facilities. Recently, Patagonian steppe ponds have been stocked to establish extensive aquaculture operations rather than to facilitate sportfishing. Wicki and Luchini (1996) estimated that 2500 ha of available ponds in Río Negro province could produce 150 t of 1-kg rainbow trout every 1.5 years. However, this estimate still needs to be confirmed.

3. THE DARK SIDE

3.1. Ecological Impact of Salmonid Introductions, How Big is the Problem?

Salmonids are thought to have a tremendous negative impact on the autochthonous biota of both the Pacific and Atlantic drainages of Patagonia. Possible negative impacts to native organisms include predation, competition, changes in habitat structure, and disease introductions. These factors must involve not only interactions between the introduced salmonids and native species but also interactions among the various introduced salmonid species. No detailed studies exist on the extent of the impacts due to salmonid/native fish interactions. Lack of information prior to the introductions and the absence of any deep glacial lakes or major rivers without introduced salmonids makes it very difficult to determine how the native species may have reacted to the introduced salmonids and the long-term impacts on those species. Furthermore, until recently, lakes were studied on a nonsystematic basis and biased sampling designs were used to establish fish community components and characteristics (Vigliano et al., 1999).

Preliminary data on fish communities, obtained from extensive, depth-stratified studies (Alonso et al., 1997; Vigliano et al., unpublished data) in lakes and in the littoral zones of Patagonian reservoirs, have shown that native species are still present and can, in some cases, be more common than salmonids (usually brown trout; Table 2). A recent study of predator–prey relationships between salmonids and native fish in two lakes and two reservoirs in northern Patagonia (Macchi et al., 1999) has shown that piscivory existed prior to the introduction of salmonids. Specifically, large specimens of *Percichthys* spp. almost exclusively eat fish. Thus, it is probable that some native species had behavioral mechanisms that reduced the negative impact of salmonids as predators. If this is true, the degree of impact and extent of possible interactions may depend on the composition of the original fish community in each particular water body. In addition, salmonids apparently do not feed actively upon the planktonic community as they do in some Northern Hemisphere temperate lakes (Macchi et al., 1999). In Patagonian lakes, brown trout are principally piscivorous whereas rainbow trout and brook trout are more opportunistic feeders (P.J. Macchi, personal communication). Fluctuation between benthic feeding and piscivory seems to be a major distinctive trait of salmonids in Patagonian lakes (Macchi et al., 1999).

Another issue to be considered is the timescale of the introductions. Although the initial introductions occurred between 1904 and 1906, extensive nonplanned stocking continues to the present. Thus, fish community history may vary among water bodies throughout Patagonia, and it is not known if equilibrium among fish community components has been reached in any of these water bodies. No common dominance pattern or fish community structure can be defined for all lakes that have been studied. This variation may be due not only to natural history, but also to man's influence through habitat modifications, stocking practices, and fishing history. Nevertheless, salmonid introductions have not extinguished native species, but the types of ecological relations that exist in stocked water bodies are not well known. Their understanding will require both laboratory and field experiments.

3.2. Problems Associated with Aquaculture Development

The development of the aquaculture industry has raised concerns about the possibility of the impacts of declining water quality on wild-salmonid sport-fisheries. It is well known that aquaculture facilities may have a detrimental effect on local water quality, biota, and the genetics of wild conspecifics and, sometimes, closely related species (see, e.g., Phillips et al., 1985; Hindar et al., 1991; Hutchings, 1991; Mork, 1991; Thorpe, 1991; Johnsson et al., 1993). In Patagonia, at least in the Alicura Reservoir, excess feed, faeces, and excretion from aquaculture facilities have produced local changes in water quality, bottom sediments, and biotic components. Temporetti (1998) suspects that an increase in production beyond the planned 4,000 t per year could induce trophic-level changes in the reservoir. He discusses the use of an under-cage waste collector system, which, in experimental conditions, allowed the removal of up to 22% of the total phosphorus input from faeces. Laos et al. (1998) evaluated the use of such waste products to produce a high-quality organic fertilizer.

In the Alicura Reservoir, escapes from fish cages also may be responsible for changes in the biota (Temporetti et al., 2001). Experimental catches using gillnets to monitor species composition indicated that the rate of escape is high. Escaped rainbow trout, recognizable by their damaged fins, became a predominant component of the reservoir by 1994, only two years after aquaculture facilities were established in the reservoir. Since 1994, their relative abundance has increased from 21% to 53% of all individuals captured in the gillnets (Figure 4). This has been accompanied by a decrease in the relative abundance of wild salmonids, and variation in the relative abundances of the two native species (Figure 4). In contrast, in two other reservoirs in the area (Ramos Mexia and Piedra del Aguila) where only wild salmonids live, the relative abundance of salmonids decreased from 1994 through 1998, whereas that of the native species present increased (AIC, unpublished data). The decrease in wild salmonids in those lakes was attributed to lack of a suitable environment for salmonids in these reservoirs.

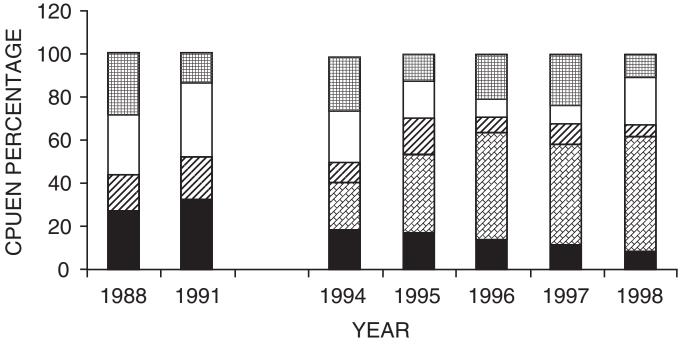

Figure 4. Fractional composition (CPUEN PERCENTAGE) of introduced and native species in the Alicura Reservoir, 1989–1998 according to HIDRONOR (1989; unpublished data), Freyre et al. (1991), and AIC (1993–1998; unpublished data). Black = wild *Oncorhynchus mykiss*; diagonal bricks = cultured, escaped *O. mykiss*; diagonal lines = *Salmo trutta* (introduced); white = *Percichthys trucha* (native); horizontal/vertical hatched = *Odontesthes hatcheri* (native)

The causes of these changes in species composition could be related to reservoir maturation processes, cyclical or random changes in fish abundance, direct or indirect effects of the fish farming facilities, or a combination of these factors. Nevertheless, escapes seem to be a major disturbing force in the Alicura Reservoir. Research on the causes of such catch variations should be undertaken to understand long-term fish community changes in these water bodies.

To protect the environment, in at least two Patagonian provinces (Neuquén and Río Negro), aquaculture facilities are required by law to be installed only in man-made environments such as hydroelectric reservoirs. However, although associated nutrients and chemical compounds (disinfectants, antibiotics, etc.) and possible trophic changes will remain principally within the reservoirs, escaped fish will eventually move through the connected waterways. Sportfishermen fear the mixing of escaped, cultured fish with wild conspecifics because of possible changes in fish quality due to interbreeding between escapees and wild salmonids (Vigliano et al., unpublished data). For example, in the upper Limay River, which flows into the Alicura Reservoir, sportfishermen report a noticeable decrease in the average size of rainbow trout but no decrease in catch rates. Although escapees from aquaculture facilities do not always have a negative impact upon wild strains (Skibinski, 1998), one possible effect is reduction in average size. Regardless of the actual situation, the perception of fishermen is that aquaculture operations in the Alicura Reservoir may be affecting the size of the fish upstream and that this negative effect may spread to other river basins within this river system. This perception led them to view aquaculture as a problem and to oppose aquaculture facilities.

Mixing of, and interbreeding between, cultured fish and wild fish may increase over time in Patagonia, in part because some Patagonian drainages flow through the Andes into the Pacific Ocean, where Chilean aquaculture facilities exist. Eventually, escaped individuals from different strains of Atlantic salmon (e.g., the varieties Mowi, Boulaks, and Fanat), rainbow trout (varieties Kamloops, Cofradex, Donaldson, and steelhead), sakura (*Oncorhynchus massou*), chinook salmon, and coho salmon may find their way into the Argentine side of rivers that drain into the Pacific. Chinook salmon have already been observed to spawn on the Futaleufu and Corcovado river basins in Chubut Province (Figures 1 and 3), where resident brook, brown, and rainbow trout populations exist. In addition, transgenic salmonids may be brought into Chile for aquaculture; they too could eventually escape and invade the Argentine rivers that drain into the Pacific.

The development of aquaculture in Patagonia has raised issues concerning the carrying capacity of aquatic systems, interrelationships between wild and escaped hatchery strains, ecological effects of hatchery escapees on the resident biota and local environments, changes that may occur in the various sportfish species, hatchery management tools that may be used to minimize escape of cultured fish, extent of the impact caused by escapees, and need to address the conflicts arising from the various uses of the sportfish resource. These issues must be solved in order to develop the different activities rationally and to utilize the resource wisely.

3.3. Legal Framework

National and provincial laws exist that regulate imports, introductions, and movement of living organisms; establish and maintain health standards for aquaculture operations; and manage sportfishing (Luchini and Wichi, 1996; Wicki and Luchini, 1996). However, federal, provincial, and municipal jurisdictions superimpose on one another, creating legal conflicts. Furthermore, the interjurisdictional nature of water basins and movement of fish across boundaries is generally not taken into account. However, some level of legal agreement exists in sportfishing regulations; both the National Park Administration and the provincial governments issue these regulations. Several provinces have created administrative and regulatory bodies for shared basins (for example, the Interjurisdictional Authority of the Limay, Neuquén, and Negro basins) and despite the fact that provinces retain a great deal of autonomy, when any action may harm the national interest, the federal government prevails.

4. TOWARD THE FUTURE

Policies regarding salmonids in Patagonia have not yet been clearly stated. Decisions on introduction, culture, stocking, and fishing are made *ad hoc*, and depend on prevailing circumstances and shifting pressures from the various interest groups. The result is rather a complex situation that contains neither clear, long-term goals nor exact definitions of appropriate priorities. Within this context, salmonid introductions in Patagonia are perceived as a mixed blessing—culprits of an ecological, ecosystem-level impact that may never be quantified nor completely understood, but, simultaneously, promoters of economic development. This situation generated the appearance of three distinct interest groups: (1) those concerned with the possible ecological damage upon autochthonous biota, (2) those who promote wild-salmonid-strain sportfisheries as generators of economic revenue and development at the local and regional level, and (3) those who promote salmonid aquaculture and have economic goals similar to those of sportfisheries supporters. Each of these groups is usually at odds with the others.

Ironically, after almost 100 years since the first salmonid introductions, little is yet known about Patagonian fish communities and the interactions that govern them. Whether a new dynamic equilibrium has been reached in many lentic water bodies and river basins is not known and, in many locations, the situation may still be changing due to uncontrolled stocking, new arrivals from Chile, and escapees from aquaculture facilities. Thus, conflicts that arise between interest groups are met with a lack of the information necessary to solve them.

Within Patagonia exists huge diversity of lentic and lotic water bodies and of socioeconomic situations that govern the people that control them. The sparse available published information about most of these water bodies suggests that a main goal of future research should be to generate information that would be the basis for establishing ecologically and economically sustainable development. Because scarcely a handful of research-and-development institutions exist in Patagonia, the task of gathering and analyzing the necessary information will require a long-term effort. Management areas should be defined according to relevant geographical, environmental, biotic, and socioeconomic characteristics so that areas suitable for conservation, aquaculture, sportfisheries, or a combination of these are appropriately defined. Then, for each management area defined, particular policies or projects could be developed according to the area's characteristics and the local, regional, or national priorities. Usually, proposed projects consider only the potential production or economic benefit associated with the projects themselves. They rarely focus on particular aspects outside of the projects' goals, which may be in conflict with other proposed uses of the area. Issues such as water quality, possible dispersal of hatchery strains, hatchery-induced diseases, alterations of wild-fish community structure, effects of excess fishing pressure, and restocking should be addressed in light of the relevant human socioeconomic context within each designated management area.

Because many basins cross provincial and international boundaries, an interprovincial commission should exist to establish policies and co-ordinate efforts. Following a standardized protocol, each province could act as a module responsible for gathering and maintaining the necessary information related to its jurisdiction. To make the data readily available, a comprehensive information network that includes standardized databases and Global Information System capabilities should be created. Over time, this management structure would increase the knowledge base necessary to resolve emerging conflicts and would enhance our capability to manage Patagonian aquatic resources.

In less than 100 years, introduced salmonids have been perceived as sportfisheries trophies, then as ecological nemeses, and finally as promoters of social well-being and economic benefits through sportfisheries and aquaculture. The challenge for the future is to develop a consensus among Patagonian provinces about the leading policies for this resource and to establish the steps to generate the necessary information for its sound management.

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CHAPTER 18

INTRODUCED ANADROMOUS SALMONIDS IN PATAGONIA: RISKS, USES, AND A CONSERVATION PARADOX

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Abstract: Because of their peculiar life cycle, introduced anadromous salmonids can have cascading effects on both marine and freshwater communities. From an ecological standpoint, there are three aspects of exotic salmonids that merit special attention: the factors that govern the establishment of wild populations, the impact of the introduced fish on the receiving communities, and their adaptations to the new environments. Here, we examine several case studies dealing with anadromous salmonids introduced in Patagonia, the southern region of Argentina, from these three viewpoints.

Key words: alien species, aquaculture, environment, exotic species, Patagonia, salmonids, stock enhancement, sport fishing, trout

1. INTRODUCTION

Patagonia, the southernmost region of Argentina and Chile (Figure 1), has today firmly established populations of trout, red deer, and wild roses, among many other exotic species. While many early introductions were driven by aesthetic or recreational reasons, a new wave of exotic imports is arriving into Patagonia. This time the driving force is development and economic progress—the introduction of exotic species for hatcheries and animal farms.

These new activities differ in several ways from the import of species by European immigrants, who took a favorite plant or animal when they immigrated to South America. The new introductions include freshwater, marine, and terrestrial species. New hatcheries and farms are commercial enterprises

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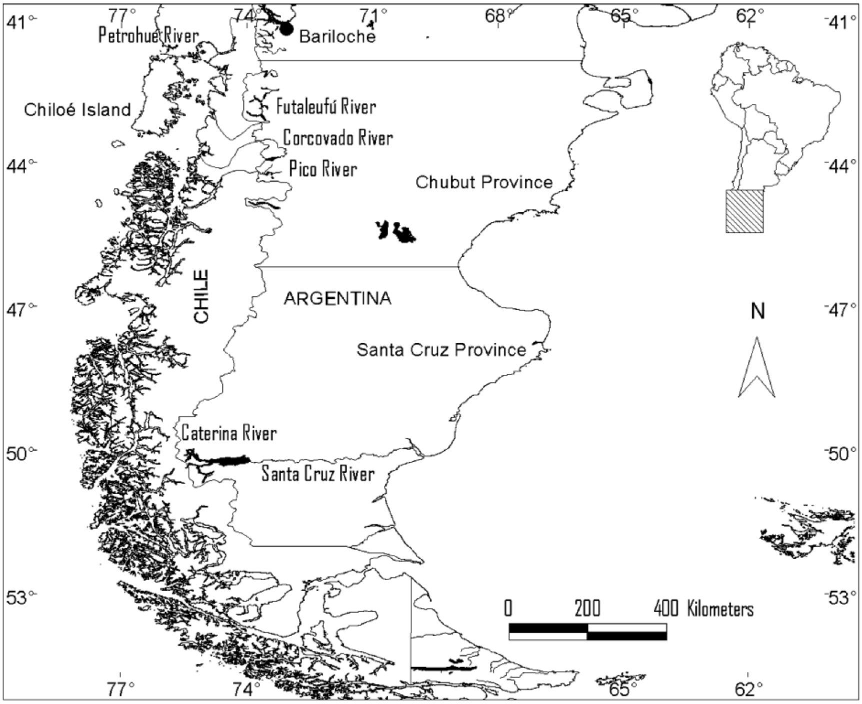

Figure 1. Location of Patagonia and the Argentinian locations mentioned in this paper

that handle large numbers of organisms over wide geographic regions. Once established, these facilities become the source of a persistent influx of exotic organisms, bettering the chances for successful colonization of neighboring communities. Typically, these enterprises are a part of economic development plans that are promoted by governments, funded privately, and highly regarded by society during the initial development stages. In the minds of politicians and the public, the promise for short-term economic progress dwarfs any specter of long-term environmental damage. For the same reasons, the import of species for culture in captivity is bound to increase significantly in coming years.

For creating fishing opportunities and for aquaculture, salmonids have been widely exported around the world from their native ranges in the Northern Hemisphere. In this trade, Argentina and Chile have been assiduous importers (Pascual et al., 2002b). Among salmonids, Pacific species of the genus *Oncorhynchus* are a major target for contemporary marine net-pen aquaculture efforts in Chile; they are actively colonizing coastal and freshwater environments in both Chile and Argentina. As a result, because of their peculiar life cycle, their introgression can have cascading effects on both marine and freshwater communities. Therefore, these fish offer opportunities for analyzing the environmental, economic, and scientific implications of exotic species in Patagonia.

From an ecological standpoint, there are three aspects of exotic salmonids that merit special attention: the factors that govern the establishment of wild populations, the impact of the introduced species on the receiving communities, and the adaptations of these fish to the new environments. In this paper, we examine different case studies dealing with anadromous *Oncorhynchus* species in the Patagonian region of Argentina from these three viewpoints and propose some avenues to answer the question: What can we scientists do to help mitigate the impact of these new species?

2. SALMONIDS IN ARGENTINA'S PATAGONIA

The three first consignments of salmonids that arrived in Argentina in 1904 and 1905 were ordered by the Argentinean Ministry of Agriculture and were destined to establish feral populations in lakes and rivers of northern Patagonia. They consisted of embryos of brook trout (*Salvelinus fontinalis*), lake trout (*S. namaycush*), rainbow trout and steelhead (*Oncorhynchus mykiss*), and landlocked salmon (*Salmo salar sebago*) (Tulian, 1908; Marini, 1936; Marini and Mastrarrigo, 1963).

With the goal of introducing salmonids in rivers of southern Patagonia, a fourth consignment was shipped to Santa Cruz Province in 1906. It consisted of embryos of chinook (*O. tshawytscha*), sockeye (*O. nerka*), coho (*O. kisutch*), and landlocked salmon, as well as lake, brook, and rainbow trout, all from the USA. The Santa Cruz Province received three more shipments of the same species from the USA between 1908 and 1910 (Pascual et al., 2001). Early shipments also contained sea trout (anadromous form of brown trout, *Salmo trutta*) and Atlantic salmon (*Salmo salar*) from England.

The *Oncorhynchus* species contained in these early shipments most likely came from the Baird Hatchery on the McCloud river in California (Scott et al., 1978; Riva Rossi et al., 2004), which distributed eggs all around the USA and to several other countries (Valette, 1924; Marini and Mastrarrigo, 1963; Pascual et al., 2001), but alternative locations in California and Oregon are possible sources as well (Behnke, 2002; Pascual et al., 2002a). The rainbow trout eggs in these early shipments presumably contained a mixture of anadromous and strictly resident stocks of rainbow trout; both varieties occurred at sites where hatcheries such as the Baird Station collected fish for its operations (Wales, 1939; Busack and Gall, 1980; Nielsen et al., 1997). The last imports of salmonids into Argentina occurred between 1950 and 1970, when most of the rainbow trout came from resident hatchery stocks from Denmark and Germany (Pascual et al., 2002b). In summary, rivers in northern and southern Patagonia received fish of typically anadromous species (chinook, coho, sockeye, and Atlantic salmon), facultative anadromous species (rainbow, brown, and brook and trout), and typically freshwater resident species (brook and lake trout).

By the 1930s, salmonid production in Argentina was centered at the Bariloche Hatchery in northern Patagonia, which then became the main center of propagation of salmonids in Argentina. Beginning in the 1980s, the marine net-pen culture of salmon in Chile grew dramatically, from a total of 53 metric tons (t) harvested in 1981 to well over 500,000 t today. As salmon production has increased, so have reports of fish escaping from net pens and straying into rivers in the Patagonia region of Chile and Argentina. Although these reports started as early as 1984, it was only recently that we started gathering proof that anadromous salmon are actually spawning in South American rivers. In March and April of 1996 we witnessed, for the first time on record, chinook salmon spawning in South American streams. At that time, one of us (M.P.) found groups of chinook salmon adults spawning in the Futaleufú River (Argentina; Figure 1). The following year, Doris Soto and Fernando Jara from the Universidad Austral in Chile found spawning chinooks in the Petrohué River (Chile). Both rivers drain into the Pacific Ocean. Chinook salmon are also present in significant numbers in two other river basins in the region, the Pico and Corcovado Rivers (Figure 1); spawning occurs regularly in those rivers (Soto et al., 2007). More recently, we found chinook salmon spawning in the Caterina River, Santa Cruz River Basin (Ciancio et al., 2005); these fish presumably recently colonized from water bodies used for ranching experiments in southern Chile (Becker et al., 2007). Interestingly, chinook salmon account for only a small fraction of Chile's salmon production (less than 5%), which is dominated by Atlantic salmon, coho salmon, and rainbow trout.

3. THE ESTABLISHMENT OF ANADROMOUS POPULATIONS

Although resident populations of rainbow, brook, and brown trout thrive in lakes and rivers throughout Patagonia, anadromous populations are rare and are limited to rainbow trout, brown trout, and chinook salmon. The same picture arises as we analyze the record of salmonid imports around the world: freshwater-resident species of trout have adapted very quickly to diverse environments (e.g., MacCrimmon and Campbell, 1969; MacCrimmon, 1971) but attempts to establish self-sustaining anadromous populations mostly have been failures (Withler, 1982). As coastal net-pen aquaculture based on exotic species expands in temperate waters of the world, understanding the factors that affect the establishment of anadromous species becomes of paramount importance for pondering the risks associated with these enterprises.

The results of a literature search for, worldwide, reports of attempts to establish anadromous populations of *Oncorhynchus* from North America serves to further illustrate how difficult it is to establish anadromous populations (Table 1). Several of the 61 cases recorded consist of multiyear projects in which huge numbers of eggs and juveniles are released. In several of these cases (11, 17–20, 29, 35, 41, 42, 49–54), the investment included the construction of costly facilities to incubate imported eggs or to breed the progeny of returning

Table 1. Details of 61 introduction attempts of *Oncorhynchus* species, worldwide. *N.* = case number

N.	Species	Origin	Destination	Years	Effort	Result	References
1	Sockeye (*O. nerka*)	Lake Baker, USA	Lake Washington, USA	1940–??	??	Successful establishment of sport and commercial fishery	Burgner (1991)
2	Sockeye	Neighboring rivers, USA	Dog Salmon River, Alaska, USA	1951–??	??	Successful establishment of commercial fishery	Kyle et al. (1988) and Burgner (1991)
3	Cherry (*O. masou*)	Hokkaido, Japan	Lake Westward, Canada	1966	5,500 Alevins	Failure	Christie (1970)
4	Coho (*O. kisutch*)	Washington, USA	South Korea	1970s	??	Failure	Sandercock (1991)
5	Coho	Washington and Oregon, USA	Hokkaido, Japan	1973–1978	??	Apparently successful	Sandercock (1991)
6	Chinook (*O. tshawytscha*)	California, USA	East coast, USA	1870–1880	30,000,000 Eggs	Failure	Harache (1992)
7	Coho	??	Lake Erie, USA	1873, 1878, 1933	"Thousands" of alevins	Failure	Sandercock (1991)
8	Coho	Oregon, USA	Maine, USA	1905–1915 (?)	1,300,000 Alevins	Failure	Harache (1992)
9	Pink (*O. gorbus-cha*)	Washington, USA	Maine, USA	1906–1908	992,000 Alevins	Failure	Lear (1980)
10	Pink	Washington and Alaska, USA	Maine, USA	1910–1925	29,165,000 Eggs	Initial success, without replacement	Lear (1980) and Harache (1992)
11	Chinook	California, USA	Maine and New Hampshire, USA	1920s	5,800,000 Eggs	Failure	Harache (1992)
12	Chinook	??	Maine, USA	1934–??	??	Failure	Harache (1992)
13	Coho	??	Maine, USA	1942–1953	??	Failure	Harache (1992)
14	Pink	Skeena River, British Columbia, Canada	Hudson Bay, Canada	1956	738,000 Eggs and alevins	Failure	Lear (1980)
15	Pink	Skeena River, British Columbia, Canada	Lake Superior, USA	1956	21,000 Alevins	Firmly established sport fishery	Kwain and Lawrie (1981), Bagdovitz et al. (1986), Kwain (1987), and Heard (1991)
16	Pink	British Columbia, Canada	Newfound-land, Canada	1959–1966	15,000,000 Eggs	Initially abundant returns, without natural replacement	Lear (1975), Lear (1980), and Harache (1992)

(*Continued*)

Table 1. Details of 61 introduction attempts of *Oncorhynchus* species, worldwide. *N.* = case number—cont'd.

N.	Species	Origin	Destination	Years	Effort	Result	References
17	Chinook	Washington and Oregon, USA	New Hampshire and Massachusetts, USA	1960s–1986	1,100,000 Alevins	Initially abundant returns, without natural replacement	Harache (1992)
18	Coho	Washington and Oregon, USA	New Hampshire and Massachusetts, USA	1960s–1986	3,400,000 Alevins	Initially abundant returns, without natural replacement	Harache (1992)
19	Chinook	??	Lake Superior, USA	1966–present	??	Sport fishery established	Healy (1991) and Harache (1992)
20	Coho	North Pacific	Lakes Michigan and Superior, USA	1966–1977	51,540,000 Alevins	Sport fishery established	Sandercock (1991) and Harache (1992)
21	Pink	Alaska, USA	Casco Bay, Maine, USA	1981–1982	3,000,000 Eggs	Failure	Harache (1992)
22	*Chum* (O. keta)	Washington, USA and Japan	Casco Bay, Maine, USA	1981–1986	5,000,000 Eggs	Failure	Harache (1992)
23	Chinook	North Pacific	France	1872–1910	1,053,000 Eggs	Failure	Harache (1992)
24	Chinook	North Pacific	Germany	1872–1910	955,000 Eggs	Failure	Harache (1992)
25	Chinook	North Pacific	Italy	1872–1910	100,000 Eggs	Failure	Harache (1992)
26	Chinook	North Pacific	Holland	1872–1930	900,000 Eggs	Failure	Harache (1992)
27	Chinook	North Pacific	England	1872–1890	150,000 Eggs	Failure	Harache (1992)
28	Chinook	North Pacific	Ireland	1891–1910	50,000 Eggs	Failure	Harache (1992)
29	Pink	Sakhalin Island, Russia	Kola Peninsula, Russia	1956–1980s	200,000,000 Alevins	Abundant initial returns, without natural replacement	Heard (1991) and Harache (1992)
30	Chum	Sakhalin Island, Russia	Kola Peninsula, Russia	1957–1964	50,000,000 Alevins	Failure	Harache (1992)
31	Pink	??	Baltic Sea	1973–1976	??	Failure	Harache (1992)
32	Chinook	??	North Island, New Zealand	1875–1878	More than 427,000 eggs	Failure	Waugh (1980) and Flain (1981)

33	Chinook	McCloud River, California, USA, and New Zealand	Tasmania, Australia	1876–1834	725,000 Eggs	Failure	Stewart (1980)
34	Sockeye	Fraser River, British Columbia, Canada	Waitaki River, New Zealand	1901–1904	95,000 Alevins, 18,000 juveniles	Establishment of landlocked population	Waugh (1980) and Flain (1981)
35	Chinook	Sacramento River, California, USA	Waitaki River, New Zealand	1902–1907	72,400 Juveniles; 1,000,000 eggs	Sport fishery established	Stewart (1980), Waugh (1980), and Flain (1981)
36	Sockeye	Canada	Tasmania, Australia	~1900	??	Failure	Stewart (1980)
37	Chinook, coho, sockeye	USA	Argentina	1905–1910	377,000 Eggs	Failure	Joyner (1980) and Sandercock (1991)
38	Chinook, sockeye	USA	Southern Chile	1905–1938	??	Failure	Joyner (1980)
39	Chinook	American River, California, USA	Jaquari River, Brazil	1958	??	Failure	Joyner (1980)
40	Coho	Washington and Oregon, USA	Ancud Gulf, Chile	1969	180,000 Eggs	Failure	Joyner (1980)
41	Cherry	Mena River, Japan	Río Claro River, Aysén fjord, Chile	1973	85,000 Juveniles	Failure	Joyner (1980)
42	Chum	Tokachi River, Japan	Fiordo Aysén, Coyaique, Chile	1974–1977 (?)	10,000,000 Eggs	Failure	Anonymous (1990), Joyner (1980)
43	Coho	Baker River, USA	Ancud, Chile	1977–1978	100,000 Juveniles	Failure	Joyner (1980)
44	Coho	?	Kerguelen Islands, Indian Ocean (France)	1980–??	??	Limited population, in fourth generation	Harache (1992)
45	Pink	Baran of Island, Alaska, USA	Santa María River, Chile	1982	600,000 Eggs	Failure	Heard (1991)
46	Pink	Japan	Aysén fjord, Chile	1982–??	1,350 Fry	Failure	Anonymous (1990)
47	Cherry	Hokkaido, Japan	Lake Carrera, Chile	1987	56,000 Fry	Some returns	Sakai et al. (1992)

(*Continued*)

Table 1. Details of 61 introduction attempts of *Oncorhynchus* species, worldwide. *N.* = case number—cont'd.

N.	Species	Origin	Destination	Years	Effort	Result	References
48	Chinook, coho	University of Washington, USA	Santa María River, Chile	1982	70,000 Coho, 200,000 chinook; alevins	Failure	Donaldson and Joyner (1984) and, Basulto (2003)
49	Chinook, coho	University of Washington, USA	Pratt River, Chile	1983–1989	670,000 Alevins	5% and 2% Coho and chinook returns	Basulto (2003)
50	Chinook	Paris, France	Quinta Normal, Chile University	1886	100 Alevins	Failure	Basulto (2003)
51	Chinook	Washington, USA	Chirri River, Chile	1969–1970	1,126,000 Eggs	??	Basulto (2003)
52	Coho	Washington, USA	San Pedro River?, Valdivia, Chile	1901–1910	225,040 Eggs	??	Basulto (2003)
53	Chinook, coho sockeye	USA	Chile	1921–1930	200,000 Chinook, 225,000 coho, 314,000 sockeye; eggs	??	Basulto (2003)
54	Cherry	Hokkaido, Japan	Claro River, Cohiaique, Chile	1973	85,000 Alevins	Failure	Basulto (2003)
55	Cherry	Hokkaido, Japan	Simpson River, Don Poli Lake, Chile	1982–1984	61,000 Alevins	Failure	Basulto (2003)
56	Chinook	USA	Cautín, Maullín, Cochamó, Puelo rivers, Chile	1924	200,000	Failure	Duffloqc (1981)
57	Sockeye coho	USA	Chile	1930	114,000 Sockeye, 225,000 coho	??	Duffloqc (1981)
58	Chinook	USA	Chirri River, Chile	1968–1971	355,850	??	Duffloqc (1981)
59	Coho	USA	Grisanche River, Kerguelen Islands	1978	5,000	??	Davaine and Beall (1997)
60	Coho	Washington, USA	Armor River, Kerguelen islands	1984–1990	275,506	??	Davaine and Beall (1997)
61	Chinook	University of Washington, USA	Armor River, Kerguelen islands	1987	80,000	Failure	Davaine and Beall (1997)

adults. Despite the magnitude of the efforts, the success rate has been dismal. Most attempts failed to produce returning adults. In some other cases (7, 11, 13, 21, 22, 47, 49), only isolated returns occurred, while in others (10, 16–18, 29) returns were abundant but insufficient to secure population replacement. Self-sustaining populations were established in only eight cases. Three of them (cases 1, 2, 5) were facilitated by the elimination of geographical barriers that were blocking salmon movements in regions where feral Pacific salmon occur. In four of the five remaining successful cases, the fish established freshwater-resident populations, developing what until then had been unrecorded land-locked life cycles (cases 15, 19, 20, 34).

The only successful acclimatization of anadromous populations of *Oncorhynchus* of significant size outside of the native range was that of chinook salmon introduced into New Zealand at the turn of the 20th century (case 35). A total population of around 50,000 spawners, established in several rivers of the southern island, today sustains an important sport fishery (McDowall, 1994). The success of this acclimatization project may be a result of the large scale of this effort, which involved millions of juvenile fish planted over several years. But in general the rate of success has not been related to planting efforts (Table 1), indicating that more complex processes determine the fate of anadromous imports. Two extreme cases exemplify the fortuitous nature of anadromous salmon acclimatization. Pink salmon (*Oncorhynchus gorbuscha*) populations in the Great Lakes (USA) originated from the unplanned dissemination of 21,000 alevins (case 15), but a large-scale plan to establish populations of the same species in the Kola Peninsula, Russia, by planting 200 million fish over several years, failed (case 29).

The establishment in Chile and Argentina of apparently self-sustaining populations of chinook salmon that originated from net-pen aquaculture and ranching in Chile constitute only the second case of migrating salmon runs in the Southern Hemisphere to date, underlying the extraordinary uniqueness of the establishment of self-sustaining populations of anadromous salmon. Given this record, it is pertinent to ask what is the reason for the frequent failure of anadromous varieties. The success of freshwater populations in the Southern Hemisphere indicates that rivers are appropriate for salmon. Marine environments in the southern oceans are rich in forage species (e.g., James and Unwin, 1996) similar to those upon which salmon prey in northern oceans (Brodeur, 1990). Moreover, oceanic temperature regimes, which have been proposed as a limitation for Pacific salmon introduced into the North Atlantic (Harache, 1992), are optimal for salmon in the South Atlantic and Pacific oceans. The explanation for failures, therefore, should not be sought in the simplicity of a limiting factor, but in a more complex mismatch between the highly elaborate marine migration of salmon and the conditions encountered by them in the southern oceans.

To explain the lack of success of Atlantic salmon in the Southern Hemisphere, Stewart (1980) proposed that the southern oceans lacked some dynamic oceanographic features characteristic of native oceans, specifically gyres or cyclic currents, that govern marine migration and ensure homing. This explanation, however, does not take into consideration the plasticity of salmon and their ability to adapt to new conditions, which has occurred in some instances of salmon introductions. Over 50 years ago, Ricker (1954) offered a lucid explanation for the difficulty of establishing new anadromous populations: "...homing of a sufficient number of newly-introduced stock to their adopted stream, or to any single stream, may be fraught with hazards. This would be especially true if the salmon's ability to home and become established in a new site depended partly on hereditary factors...If this hereditary component in homing ability exists, then the process of establishing a new run becomes an example of speeded-up adaptation by natural selection. The most obvious by-product of this selection is a poor rate of return during the first generations."

Today, we possess strong evidence for the existence of genetic components in migratory behavior, suggesting that a mismatch between genetically determined behaviors and the characteristics of the new environment, such as postulated in the hypothesis advanced by Ricker, could indeed be an impeding factor for the establishment of salmon populations. Different salmon stocks have characteristic migratory patterns in the ocean. Transplanted fish retain this ancestral migratory behavior (Nicholas and Hankin, 1988; Pascual and Quinn, 1994), suggesting that their oceanic movement patterns are largely determined by genetic factors (Figure 2). This "hard-wired" behavior could force the introduced fish to follow "inappropriate" patterns of ocean migrations, or they could simply be unable to adjust to new orientation cues and get lost in the ocean. Once in the rivers, olfactory imprinting by juveniles can help surviving fish return to their new home streams (Quinn, 1993; Pascual et al., 1995).

The record of salmon introductions also indicates that some species may be more able to colonize new environments than others. For instance, although several different species were introduced into Australasia and South America, only chinook salmon established anadromous populations on both continents. Chinook salmon are characterized by a high intra- and inter-populational variability in life-history characteristics (Healy, 1991), a plasticity that may have increased their chances for adapting to the conditions of their new environments. The other species that have developed anadromous runs in South America, rainbow trout and brown trout, also have highly plastic behaviors, particularly in the critically important anadromous behavior. Species with narrower life-history requirements, such as sockeye salmon and Atlantic salmon, which were imported into New Zealand (Quinn and Unwin, 1993) and South America without success, may be on the other end of the "invasiveness" spectrum. Nevertheless, ability of some salmonids to rapidly adapt to new environments indicates that this lack of success should not be considered permanent or immutable. The continuous flow of salmon provided through their escape from marine net pens increases the likelihood

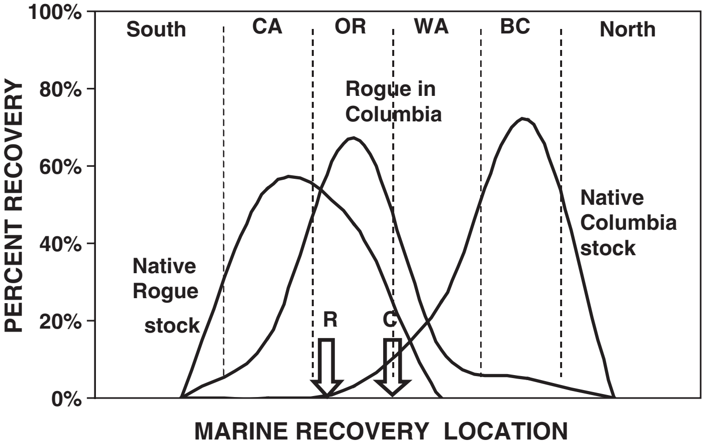

Figure 2. Marine recoveries of three different stocks of tagged chinook salmon released from two sites along the USA Pacific Coast (relative location indicated with arrows, **R**: Rogue River, **C**: Columbia River). "Native Rogue stock" is composed of native fish from the Rogue River in southern Oregon, reared and released locally at the Cole River Hatchery. "Native Columbia stock" is composed of native fish from the Columbia River, reared and released locally at the Big Creek Hatchery. "Rogue in Columbia" fish are descendants of Rogue River fish, reared and released from the Big Creek Hatchery in the Columbia River. Transplanted Oregon fish display the ancestral tendency to migrate southward in the ocean, which differs markedly from the northward migration characteristic of Columbia River fish. Modified from Pascual and Quinn (1994). CA = California, USA; OR = Oregon, USA; WA = Washington, USA; BC = British Columbia, Canada. Data source: Nicholas and Hankin (1988)

that critical masses of reproductive fish will be available to adjust to new environments.

After a critical number of fish develop a suitable migratory pattern at sea and reproductive populations are established, the plasticity characteristic of salmonid freshwater life history could allow them to rapidly colonize neighboring rivers. After attempts failed for years, this type of adaptation to a new environment occurred when chinook salmon rapidly colonized neighboring rivers in New Zealand after a population was established (McDowall, 1994). Chinook salmon in Chile and Argentina appear to be experiencing a similar phenomenon; the fish are already present in at least four different river basins (Soto et al., 2007).

Most of what we know about the colonization potential of salmon species comes from analyzing patterns of straying in established populations (Quinn, 1993). But only the colonization of new environments (Milner, 1987; Milner and Bailey, 1989) or the recolonization of habitats affected by environmental catastrophes (Leider, 1989) provides opportunities to evaluate the colonization potential of a species. Growing chinook salmon populations in South America presents a new opportunity to examine the colonization process in real time, as well as to evaluate the ecological impacts of the colonization.

4. EVALUATING POTENTIAL IMPACTS OF SALMON INTROGRESSION

Because anadromous salmon attain most of their growth at sea but return to spawn (and, in many species, also die) in freshwater, they may constitute an important agent for the transport of nutrients from the ocean to freshwater. Large increases in dissolved nutrients occur in streams following the die-off of salmon that have spawned (Kline et al., 1990, 1993) and trout occurring in sympatry with anadromous salmon are known to consume large numbers of salmon eggs and juveniles (Ruggerone and Rogers, 1984; Berejikian, 1992). The list of consumers of freshwater stages of salmon is not limited to fish, but encompasses a long list of wildlife species (Willson and Halupka, 1995). Yet, salmon can compete with local species for food and space during their early life stages and can also prey on those species (Fausch, 1988; Krueger and May, 1991). The complexities of the salmon life cycle indicate that interactions between salmon and sympatric species can propagate through the ecosystem in unforeseen ways.

A typical approach in impact assessment studies is to derive general rules from a retrospective analysis of case studies. Although historical analyses are informative, it is often puzzling to try to apply general rules when considering specific new cases. There is always a measure of uncertainty when extrapolating observations and results from one part of the world to new settings.

In 1997, the Santa Cruz Province fisheries administration in Argentina elaborated a plan to introduce chinook salmon into the Santa Cruz River. The final objective was to provide 200 t of fish per year for harvesting by a coastal fishery. One of us (M.P.) was asked to perform an impact assessment for scenarios in which salmon were successfully established. The general approach was to develop population models (similar to that of Hankin and Healey, 1986) coupled with a bioenergetic model (Hewett and Johnson, 1992) to predict potential consumption rates by hypothetical salmon populations. The models were then contrasted with the abundances of different candidate prey species or the consumption rates of competitor species that had diets similar to that postulated for chinook salmon that would inhabit the Santa Cruz River region. The demographic model was also used to evaluate the benefits of the proposed introductions in terms of sustainable yields, to calculate how long would it take to build up an exploitable stock, and to estimate how hard it would be to eradicate the introduced chinook salmon if they became a nuisance. With this approach, it was possible to evaluate some of the potential impacts and gains of the proposed introduction as an integrated cost–benefit analysis.

In the analysis, the team that I led considered the interaction of chinook salmon with both freshwater and marine species. We also calculated population standing stock, food consumption, and maximum sustainable yield for introduced populations of different sizes, varying life-history characteristics, and recruitment productivity. All of these factors were calculated for chinook salmon inhabiting waters of different temperatures. Figure 3 shows an illustration of the type of results obtained for a given set of parameters and settings.

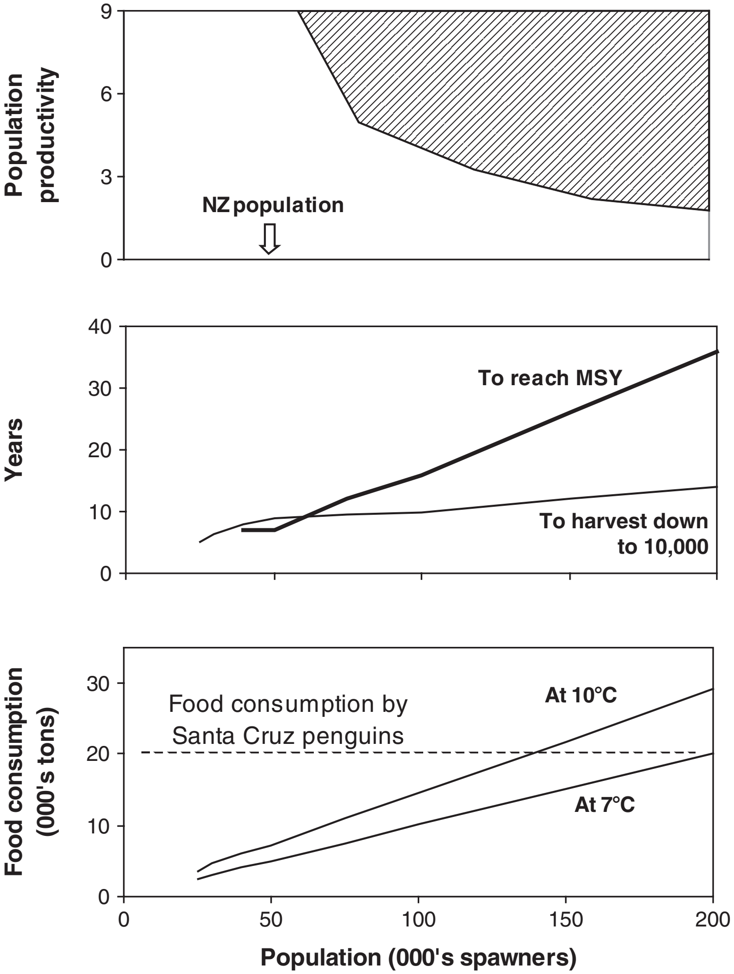

Figure 3. Risk analysis of introducing chinook salmon in the Santa Cruz River basin. Upper panel: the gray area represents combinations of population sizes (*X*-axis) and productivities (*Y*-axis, slope in stock-recruitment relationship) that produce sustainable yields of at least 200 t. Average productivity for salmon is about 3. The size of the New Zealand population is 50,000 spawners (indicated with the arrow). Middle panel: years required to arrive at the abundance that produces MSY and years needed to reduce population to 10,000 spawners by harvesting 90% of the run. Lower panel: marine food consumption of populations of different sizes estimated for temperatures of 7°C and 10°C. The horizontal line shows the food consumption estimated for the population of penguins of Santa Cruz (270,000 pairs, Gandini et al., 1996) during the breeding season

The results of our analysis indicated that large populations (as large as twice the New Zealand population) were needed to produce a harvest of 200 t per year. It also showed that it would take at least two decades to establish these populations and at least 10 years of very intensive harvest (removal of 90% of spawners every year) to reduce them down to an arbitrarily small number (10,000 individuals). The most likely freshwater species to be affected by competition with chinook salmon was the exotic brown trout, an important sport fishery resource in the Santa Cruz River system. In the ocean, likely competitors with salmon were two species with similar diets: the magellanic penguin (*Spheniscus magellanicus*; Frere et al., 1996) and the palometa (*Parona signata*). Susceptible preys included decapod larvae of the valuable southern king crab (*Lithodes santolla*). The estimated consumption of food by the population of breeding penguins in Santa Cruz (270,000 pairs) is comparable to the estimated food consumption of projected salmon populations (Figure 3). Given all this information, the provincial government decided not to proceed with the introduction and to apply the resources available to study and promote the exploitation of more traditional resources.

A particular case like this can help illustrate the complexities involved in using an alien species to establish a new fishery better than can a generic ecological discussion. The specific methods used could as well provide some general tools for forecasting the potential effects of planned and unplanned introductions. This analysis was admittedly crude in some aspects. For example, it reduced complex species interactions to ballpark figures of biomass and consumption. But on the other hand, it had the advantage of representing risks in a relatively unambiguous way, thanks to the development of a quantitative framework. More importantly, it considered costs and benefits within the same framework. If the analysis had been based on impact alone, the project might have proceeded, encouraged by groundless calculations.

5. A CONSERVATION PARADOX?

Perhaps paradoxically, the introduction of salmon in South America provides a chance to contribute to salmon conservation in North America. Because of their homing ability, salmon species are organized into local populations, each with a characteristic geographic distribution and some degree of reproductive isolation from other populations. As a result of this isolation, populations typically display local characteristics, and much of this variation among populations has a genetic basis (Ricker, 1972; Taylor, 1991). These local adaptations are evident at even very small geographical scales and include morphological traits, behavioral characteristics, developmental and physiological characteristics, disease resistance, and life-history traits (reviewed in Taylor, 1991).

Studies on the genetic bases of the geographical variation in salmon populations became the focus of considerable scrutiny as an increasing number of salmon stocks became endangered (Nehlsen et al., 1991). For example, conservation plans for salmonids under the Endangered Species Act rely on identifying "Evolutionarily Significant Units" (Waples, 1991) as the units to which rescue efforts are to be directed. Tracking the divergence of transplanted fish provides a direct means for assessing the genetic and environmental bases of life-history characteristics, as well as an opportunity to estimate the rates at which population characters evolve (Stearns, 1983; Reznick et al., 1990). These types of studies can aid decisions on what constitutes "significant" variation (NRC, 1996). The analytical value of contrasting biological characteristics of different introduced populations to one another and/or to their parental populations has been well demonstrated in recent years (see for example Quinn and Unwin, 1993; Kinnison et al., 1998). Opportunities for such research abound in Patagonia. We present here an example based on the development of anadromy in rainbow trout and discuss the research opportunities presented by the recent introgression of chinook salmon in Pacific basins of Patagonia.

As has occurred in many other rivers of Patagonia, the Santa Cruz River has established populations of rainbow trout of significant fishing value. What is peculiar about the Santa Cruz is the presence of an anadromous run (Pascual et al., 2001), an uncommon behavior in introduced rainbow trout. Anadromy is a pivotal trait in salmonids, not only because of the physiological and behavioral adaptations associated with this behavior (Hoar, 1976), but also because it results in an alteration of the growth and survival opportunities of individuals.

The value of this setting is enhanced by the fact that the Santa Cruz River received, separately and at different times, fish from both resident and anadromous stocks. Our first results suggest that microsatellite DNA analysis (Wright and Bentzen, 1994; Pascual et al., 2001), together with mitochondrial DNA analysis (Riva Rossi, et al. 2004), provides a powerful method to discriminate among the candidate parental stocks, the same stocks that have been extensively used throughout Patagonia as the origin of feral populations.

The new environment had an extraordinary effect on how anadromy is expressed in Santa Cruz River rainbow trout. Whereas freshwater residence time, growth patterns, and age-at-maturity do not differ dramatically from those of North American stocks, Santa Cruz fish live much longer and spawn significantly more times throughout their lives than any known Northern Hemisphere population (Pascual et al., 2001). The Santa Cruz population presents a fantastic natural experiment to evaluate the trade-offs and coevolution of life-history characteristics such as anadromy, longevity, and iteroparity.

The other ongoing unique natural experiment in South America that would allow researchers to study the genetic and environmental bases of life-history characteristics is associated with chinook salmon that colonize different Patagonian rivers that flow into the Pacific and Atlantic Oceans. The value of this experiment is heightened by the fact that a parallel setting has been studied for over 15 years in chinook salmon that were introduced into New Zealand at the turn of the 20th century (reviewed in Quinn et al., 2001). The New Zealand populations vary in several phenotypic traits, including growth in freshwater and at sea, age at maturity, dates of return to fresh water and reproduction, morphology, and reproductive allocation. Strong evidences of trait divergences with likely adaptive bases are found between populations, particularly in freshwater growth rate, date of return, and reproductive output. Since these salmon populations were all derived from a single source, these data show that considerable variability among populations developed in 90 years, or approximately 25–30 generations.

The colonization of a collection of rivers in Patagonia by the same species provides an opportunity not only to test for the development of local adaptations, but also to track the temporal progression of this phenomenon. Chinook salmon in New Zealand provide researchers with a fantastic opportunity to study the evolution of population characteristics in the time scale of several decades; chinook salmon in South America provide an opportunity to study the same process over a much shorter time scale.

6. CONCLUDING REMARKS

The record of intentional salmon introductions unambiguously shows that they more often than not end in failure. The adaptation of some components of the marine migratory behavior of salmon species to conditions in their native range may be responsible for rendering adaptation to new regions difficult. This should not, however, be used as an argument to disregard the risks of invasion posed by salmon net-pen aquaculture. Adaptation of exotic anadromous salmon has occurred and is likely to occur in the future as escapes continue to increase. In fact, southern South America is proving to be a place where anadromous salmonids were particularly successful, compared with the record elsewhere in the world.

But a strategy of crying wolf may not serve the environmental cause either. Ecologists tend to outright combat the use of exotic species, but opposition without supporting data can have a detrimental effect or be simply disregarded. In the eyes of the public and governments, blunt opposition is sometimes regarded as insensibility to the needs of society and obtuse interference with progress. This is particularly true in developing countries, where the pressure for new productive activities is higher. There is a need to have a proactive approach and to develop quantitative frameworks that include the concept of risk and make explicit economic considerations (cost–benefit analysis) such as those described above. This requires anticipating and evaluating long-term environmental costs.

Whereas refined analytical techniques can help us evaluate hypothetical scenarios, our great ignorance about the likely effects of introduced salmon can only be reduced with documentation of actual cases. There is an urgent need to document ongoing invasions such as those occurring in Patagonia and to monitor changes in the receiving communities as they occur. With time, the information produced will certainly prove precious. These initial stages of colonization also provide a unique opportunity to record the process of adaptation of salmon to new conditions and to evaluate how genetics and environment interplay in the expression of life-history characteristics.

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CHAPTER 19

ADDRESSING PROBLEMS ASSOCIATED WITH AQUACULTURE AND AQUACULTURE EFFLUENTS IN THE USA: A HISTORICAL ESSAY

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Key words: aquaculture, environment, USA, effluents, shrimp, Texas, sustainability

If a poll of the aquaculture community were to be conducted, there is high probability that the majority of those associated with the activity would consider themselves to be environmentally sensitive. Most would probably consider themselves to be environmentalists. Commercial producers and academics alike strive to maintain optimal environmental conditions in their culture systems (with the exception of scientists who may intentionally impose stress under experimental conditions). Degradation of the environment, and the consequences thereof, are constantly on the minds of aquaculturists.

In spite of the careful attention that aquaculturists were paying to establish and maintain healthy environments for the organisms being reared in their facilities, criticism of aquaculture began to become quite visible during the 1980s. Initially, the aquaculture community responded by ignoring the critics or charging them with dispensing fallacious information and smear tactics that were using environmental concerns as a smokescreen to hide some other agenda.

The level of criticism continued to increase, and those who questioned the environmental friendliness of aquaculture or who opposed aquaculture on other grounds began to gain credibility in the media and in the minds of at least a portion of the public. At a meeting of aquaculturists from around the world, held in Hawaii during 1988, the subject of environmental impacts that might result from aquaculture was discussed openly by a wide representation of

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the aquaculture community, perhaps for the first time. While it was generally agreed that many of the criticisms were based on misinformation or were developed by those who had agendas that were opposed to aquaculture on grounds other than those that they professed to regulators, the media, and the public, the aquacultural community did acknowledge that some of the criticism was valid.

Much of the criticism of aquaculture was aimed at activities occurring in coastal waters. Few objections, at least in the early years, were lodged against aquaculturists who had facilities on private land, particularly if that land was some distance from a seacoast. In some areas, such as Puget Sound, Washington, USA the first objections were lodged by upland landowners who protested the appearance of net pens in sight of their high-valued property. Citing "visual pollution," these landowners petitioned the regulators to halt the granting of permits for salmon farms. Judges finally ruled that upland landowners did not have a right to an unobstructed view, so the focus of the objections changed. The litany of objections that ultimately surfaced included the following:

1. Exotic species (such as Atlantic salmon on the west coast of the USA) will escape and out-compete native salmon species.
2. Captive fish will transmit diseases to wild fish.
3. Antibiotics employed to treat diseases in cultured fish will lead to development of resistant bacteria in nature and increase the incidence of disease in wild fish.
4. Uneaten feed and the feces leaving a net pen will decimate the benthos living under and adjacent to the pens.
5. Nutrients released from waste feed and feces will lead to increases in noxious phytoplankton blooms.
6. Marine mammals will be negatively impacted.
7. Excessive noise and odors will impair the quality of life for those living near aquaculture facilities.

Scientific studies demonstrated that at least some of the criticisms were valid (e.g., the bottom under some net pens could essentially be a dead zone because sufficient currents to carry waste products away from the site were lacking); however with proper siting, the real problem areas could be addressed. That did not serve to allay the criticism, however, and at least in the state of Washington, the opponents managed to largely curtail expansion of the salmon net-pen industry.

Opposition to the development of salmon net-pen culture also occurred in the state of Maine when a fledgling industry was under development in the 1980s. The situation changed during the 1990s, though, after the collapse of the cod fishery. The USA government provided loans and supported a retraining program for commercial fishermen if they would go into aquaculture, and many took advantage of the opportunity. Today, salmon culture continues to occur in Maine, though objections continue and the number of people employed by the industry is modest.

Another example of the development of opposition to aquaculture has been ongoing in the state of Texas, primarily with respect to the shrimp farming industry. Several years ago, permits were issued to some shrimp farms for virtually unlimited pumping of surface water for use in shrimp ponds. The resulting outrage by opponents, who believed that shrimp farm effluents were introducing excessive nutrient levels and causing sedimentation of receiving waters because of high turbidity loads, was intense. Because the state had also given permission for the farms to employ exotic shrimp, fears were expressed that exotic-species escapees would out-compete native species and destroy the commercial fishery. In addition, incidences of diseases, including Taura virus syndrome, plagued Texas shrimp farms and raised alarms that the diseases could spread to wild shrimp populations, leading to devastation of the commercial fishery.

While the situation may not have been as dire as that predicted by some opponents, there were clearly problems facing the Texas shrimp aquaculture industry. Texas shrimp farmers, faced with the threat of being regulated out of existence, took it upon themselves to address the problem. Stocking densities were reduced to help avoid the onset and spread of diseases; and on many farms, wetlands were constructed to intercept suspended solids and absorb nutrients. In some instances, after water passed through wetlands, it was recirculated back to the ponds rather than released from the facility. The use of recirculation, coupled with proper screening of pond drain structures, also greatly reduced the chance for escapement of exotic shrimp to the wild.

One of the other criticisms of aquaculture has been self-pollution caused by placing too many facilities in too limited an area. When wastes from one facility reduce the water quality in the local environment to unacceptable, or even lethal levels, this can seriously affect adjacent facilities. That has occurred when too many farms were placed in the same watershed or when too many net-pen facilities were placed in the same bay. Another criticism has been associated with the destruction of sensitive habitats, such as mangrove swamps, through the construction of pond facilities. Both types of activities have been destructive to aquacultural production as well as to the environment and are being curtailed or controlled in most parts of the world, including the USA.

One of the popular buzzwords of the 1990s has been "sustainability." There are many definitions of the term as it relates to aquaculture. The difficulties associated with defining and utilizing the term have, in part, led to the fact that it may be going out of vogue. Critics have seized upon such terms because they are useful for advancing their agendas. Focusing on sustainability, they have complained bitterly that aquaculture represents an unacceptable waste of natural resources. They claim that using energy to heat, cool, and move water is wasteful of petrochemical reserves and that the feeding of fish (in the form of fish meal or ground raw fish) to aquacultured animals is wasteful of living resources. It has been argued that the fish used for fishmeal could be more beneficially used to feed people directly.

Certain aquaculture activities do utilize large amounts of energy, but aquaculturists operate on slim margins and tend to be anything but extravagant in their utilization of electricity, natural gas, gasoline, and diesel fuel. As for the use of fishmeal, the majority of that product continues to be fed to terrestrial animals that have, in most cases, very poor food conversion ratios compared with aquatic animals.

Is aquaculture sustainable? Not if one defines sustainability as producing a crop without a net utilization of natural resources. But, what agricultural or commercial fisheries crop is sustainable under that definition? A more reasonable definition of sustainable is that it is the exploitation of natural resources without destroying the ecological balance.

Aquaculturists came a long way by first acknowledging that there are environmental consequences associated with their activities, and then instituting measures to deal with many of those consequences, often with dramatic results. This has not appeased the critics, however, and criticism of commercial aquaculture continues in many parts of the world, particularly in nations that do not depend upon aquaculture to either provide food that would not otherwise be available, or to provide export income and tax subsidies for governments.

Can the problems be addressed to the satisfaction of the critics, and can aquaculture reach the stature that has been predicted for it by those who feel it can fill the food gap caused by a continually expanding human population, static commercial fishery catches, and increases in the demand for seafood? The answers to those questions remain to be resolved.

In the USA, the approach that is being promoted for expansion of aquaculture in the coastal zone involves rearing aquatic animals in recirculating water systems, moving containment facilities offshore, and developing enhancement programs. The first two methods could produce fish of marketable size, while the later approach might employ onshore recirculating or flow-through technology to produce fingerlings of a size shown to have high survival probability after release into suitable environments.

Rearing of aquatic organisms to market size in either recirculating systems or in offshore systems is an expensive proposition. Few species currently being cultured bring sufficiently high profits to producers to allow those species to be reared in such systems. A notable exception is the use of recirculating systems where the cost of maintaining water at the proper temperature is not a significant factor (e.g., where geothermal water or some source of free or virtually free heated effluent is available for heat exchange with the water in the culture tanks or where heated water is not needed). To be successful, most recirculating systems and those developed offshore will have to produce high-value species that bring a premium at the market. This may require the use of species that are not now routinely under culture, such as tuna.

Enhancement has shown some success in Japan and the USA, for example. However, a great deal of additional research is required to determine the best sizes and locations for stocking, as well as the proper numbers of fishes to stock in order to achieve the desired results without placing too much burden on the food base or causing negative impacts on other species inhabiting the area that is stocked. An enhancement program might involve the development of onshore broodstock holding and spawning facilities along with a hatchery and early rearing system. After released fish recruit to the commercial or recreational fishery, access to that fishery could be restricted to those who pay a license fee to participate in that fishery. Most of this fee could be returned to the aquaculturists to pay the expenses of constructing and operating the production facilities.

Moving offshore, to recirculating systems, or to enhancement as alternatives to nearshore marine culture systems might not ameliorate the outcry that exists against aquaculture. There are critics of each of these types of approaches. Depending upon the system, genetic integrity problems might be predicted, escapement (particularly of exotics) might be viewed as ominous, and eutrophication, interference with navigation, and access to traditional fishing grounds might be thought to be intolerable.

Despite the best efforts of aquaculturists, whatever has been done in the past to right the real and perceived wrongs done by them is viewed as insufficient in some circles. Thus, aquaculturists continue to seek solutions to challenges. A shrimp farmer in the USA recently said that the legal fees associated with developing his facility exceeded its construction costs. Reducing the expenditure of financial resources for fighting legal battles can be achieved if aquaculturists can continue to develop scientifically valid information that convincingly demonstrates how aquaculture can be conducted in an environmentally sound manner. In addition, aquaculturists need to attempt to deal with their critics through conflict resolution, not through legal confrontations.

Aquaculture might be viewed more favorably if the developed world were facing a food crisis. Today, if those of us who are fortunate enough to live in developed nations have a desire for products grown by aquaculturists, we can often import them from other, not so well-to-do nations. In the USA, the balance-of-payments deficit associated with seafood imports versus exports (for wild and cultured products) is approximately US$8–9 billion annually; apparently, this is not considered by the opponents of aquaculture. Much of that deficit is associated with the importation of shrimp and salmon, yet the commercial shrimping industry in the USA is operated at historical levels and the shrimp and salmon aquaculture industries are growing slowly, if at all. Let us all hope that it will not take a crisis in seafood supplies in the developed world to reverse the current situation. Progress can surely be made if reasonable people will agree to work together to resolve the issues that face us.

Editor's note: In 2002, Dr. Stickney and Dr. James McVey published and coedited a comprehensive, informative book on marine aquaculture (Responsible Marine Aquaculture. CABI Publishing, Wallingford, United Kingdom. 391 pp.); many examples given in that book were from the USA and North America. Please refer to that book for a thorough treatment of marine and estuarine aquaculture in the USA.

CHAPTER 20

PRODUCTIVITY OF ALASKA'S SALMON HATCHERY OCEAN RANCHING PROGRAM AND MANAGEMENT OF BIOLOGICAL RISKS TO WILD PACIFIC SALMON

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Abstract: Modern salmon hatcheries in Alaska were established in five regions of the state in the 1970s, when wild runs of salmon were at record low levels. Initially conceived as a state-run system, the Alaska program has evolved in the private sector and is centered on private, non-profit, regional aquaculture associations run by fishermen and other stakeholders. Presently, Alaska has 33 production hatcheries (14 hatcheries have closed). Many release over 100 million young salmon annually; between 1.3 and 1.4 billion are released in total. In 1975, hatcheries produced fewer than 20,000 adult salmon. During the 1990s, the Alaska program produced 27–54 million adult salmon annually, which accounted for 14–37% of the annual common-property salmon harvest. It is second in size and productivity to the Japanese ocean ranching program (approximately 2 billion fry released annually, 50–70 million salmon harvested). Pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*), which are species released into the oceanic environment as postlarvae, comprise >80% of the hatchery production. Protection of wild-salmon fitness and rigorous evaluation of hatchery contribution to fisheries have been emphasized throughout the development of the Alaska ocean ranching program. Strict regulation by public-agency geneticists, pathologists, and fishery managers of hatchery siting, hatchery capacity, and transport of salmon between streams has reduced risks to wild-salmon fitness. Recent implementation of mass-marking technology has enabled harvest managers to protect wild salmon in mixed-stock fisheries from unsustainable fishing mortality. Both hatchery and wild stocks have experienced high marine survivals since the late 1970s, resulting in record salmon harvests through the 1990s.

Key words: aquaculture, ecological risk, environment, genetic risk, harvest risk, regional private non-profit fishery enhancement corporation, salmonids, stock enhancement, USA

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1. INTRODUCTION

Salmon runs in Alaska and throughout the North Pacific Ocean have fluctuated greatly between decadal periods of high and low abundances over the past century (Figure 1). These often dramatic shifts in numbers of returning fish, once thought to be primarily caused by variations in harvest intensity, number of salmon escaping the fisheries to spawn, and various survival factors in freshwater habitats, are now recognized also to reflect cyclic climatic and environmental fluctuations affecting survival during the marine life phases of salmon (e.g., reviewed by Heard, 1994; Hare et al., 1999).

After reaching record high harvest levels during the 1940s, when over 100 million salmon were caught annually, a long decline began that reached record low levels in the 1960s. This was shortly after Alaska attained statehood. Many observers held that a long period of pre-statehood federal mismanagement, characterized by the widespread use of fish traps, was responsible for chronic overharvest and shortages in spawning populations, and thus for the decline (Cooley, 1963). Runs began to recover briefly under management by the new State of Alaska, only to take a new downturn. By 1973 and 1974, only 22 million salmon were caught commercially (Figure 1). Entire regional fisheries were closed during about one year in five, despite more than a decade of careful harvest regulation. The lack of a sustainable harvest was attributed to the

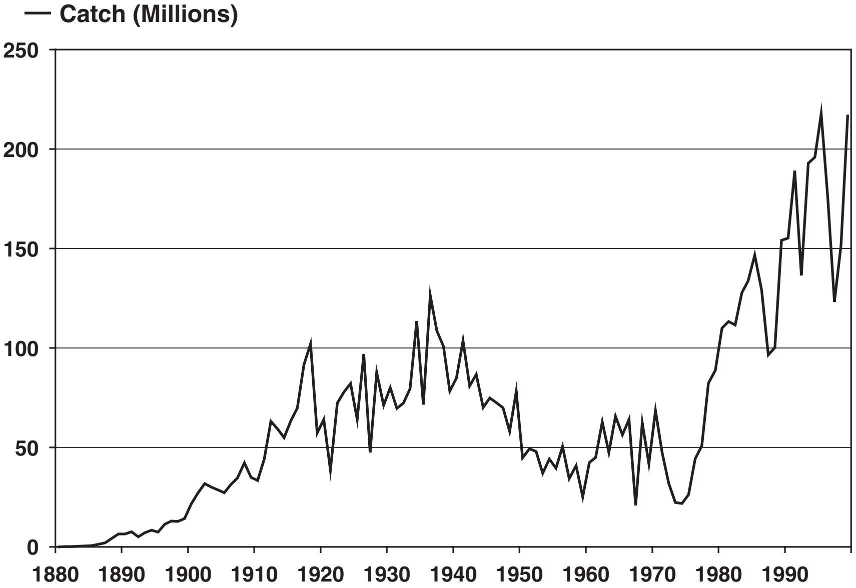

Figure 1. Alaska commercial salmon harvest, 1878–1999, in millions of fish. Data source: Alaska Department of Fish and Game, Juneau, Alaska, USA

frequent severity of winter weather and its destruction of embryonic and larval salmon (Koernig and Noerenberg, 1976; Smoker et al., 2000).

During this period of low returns, the Alaska legislature, in 1971, created the Division of Fisheries Rehabilitation, Enhancement, and Development (FRED) within the Alaska Department of Fish and Game (ADF&G; Alaska Statutes 16.05 *et seq.*). The primary responsibilities of the new division were as follows:

1. develop a comprehensive, coordinated state plan for the orderly rehabilitation, enhancement, and development of the state's fisheries;
2. encourage investment by private enterprise in the technological development and economic utilization of fisheries resources;
3. encourage, sponsor, and conduct research on the basic problems inhibiting the sound development of hatcheries.

In 1974, the Legislature enacted a program of salmon fishery enhancement in the private sector by enabling the creation of private non-profit corporations that would produce salmon that could be harvestable by common-property fisheries and supported by part of the annual salmon runs (Alaska Statutes 16.10 *et seq.*; reviewed by Smoker et al., 2000). In bare outline, these corporations were envisioned as being similar to the local fishing cooperatives that form the basis of salmon resource management, including salmon hatcheries, in Japan (Nasaka, 1988; Kaeriyama, 1999). The concept of "non-profit" grew out of concern for preventing large corporate entities from gaining control of public resources. Unlike salmon hatchery programs in other parts of North America, this program was designed to enhance the salmon fishery, not to mitigate for lost habitat or to compensate for excessive harvest. Unlike salmon hatchery programs in Japan, this program was designed to minimize effects on wild salmon and to give wild populations explicit protections in both policy and practice.

In this paper, we review elements of the Alaska salmon hatchery program that evolved from these beginnings. We focus on performance in different regions of Alaska, on interactions of salmon produced through the program with wild salmon, and on provisions in the program to avoid or minimize the effects of those interactions.

2. HISTORY: PUBLIC AND PRIVATE HATCHERY PROGRAM

During the late 1970s, the FRED Division assembled a team of fisheries professionals to help develop the present hatchery program in Alaska. Scientists from ADF&G and other agencies specializing in genetics, fish health, pathology, limnology, fish culture, and engineering developed statewide policies for these disciplines. These policies put into force Alaska law and regulation.

Two important policies were based on the results of the biological disciplines of genetics and pathology. The genetics policy prohibited both interstate transport of live salmonids, including gametes, into Alaska and interregional transport of salmonids within the state (GPRT, 1985; Davis and Burkett, 1989). The fish health management policy included guidelines for wild fish transplants, broodstock screening, approval of transfers of fish or eggs between hatcheries within regions, diagnostic procedures, review of the disease history of juveniles prior to release, and the general use of chemical disinfectants and therapeutic drugs (SPRC, 1988).

After creating a public-sector salmon fishery enhancement program through FRED in 1971, the Alaska Legislature passed a law authorizing the building and operation of private non-profit (PNP) salmon hatcheries in 1974. The PNP program is centered around five regional aquaculture associations modeled after the first to be formed, which was the Prince William Sound Aquaculture Corporation, established in Cordova in 1974 for enhancement of fisheries in that part of Alaska. The associations were comprised of commercial harvesters licensed in the region, fish processing companies located in the region, and other stakeholders. The other four regions encompass Northern and Southern Southeast Alaska (Southeast), Cook Inlet, and Kodiak. Not all PNP hatcheries in Alaska are required to be part of a regional association. Statutes allow for individuals or small non-profit corporations to build and operate hatcheries at specified sites and at approved production levels for particular species. Plans for these facilities are also reviewed and approved through the Regional Planning Team (RPT) process. The inception of the regional association PNPs, the non-associated PNPs, and FRED set into motion an intensive period of salmon resource planning and policy review throughout much of coastal Alaska. That planning effort formed the basis of the current hatchery program.

Following these new policies and guidelines, as many as 44 hatcheries were built and operated by FRED and the PNPs in Alaska in the 1970s and 1980s. Initially the state-built public hatcheries operated by FRED and the PNP hatcheries had similar and overlapping roles (Orth, 1978); by the early 1980s as many as 20 state-operated and 20 PNP-operated hatcheries were simultaneously permitted (Table 3 in McNair, 2000). Over a two-decade period, however, the hatchery system matured and simultaneously the catch of salmon increased. By 1993, the Alaska commercial salmon harvests had returned to record high levels; the Alaska Legislature closed the FRED Division and combined its duties with the Commercial Fisheries Management and Development Division within ADF&G (McNair and Holland, 1994). In succeeding years, public hatcheries have either ceased operation (4) or have been leased to PNPs (13). Under these arrangements, PNPs are responsible for annual costs of operating the hatcheries, which are principally funded from revenue generated by returning salmon and not from appropriations of public monies. Several PNP hatcheries have been decommissioned; there are now 30 salmon hatcheries permitted in Alaska (McNair, 2000).

2.1. Regional Planning and Investment

The RPTs broadly represent fishermen, scientists, and the general public. Beginning in the 1970s and under the direction of ADF&G, they developed comprehensive 20-year salmon plans for various regions of Alaska. These plans considered not only hatcheries but also a variety of other fishery enhancement tools, including spawning channels, lake stocking, lake fertilization, fish ladders over barrier falls, and various habitat improvement programs. A primary consideration during this planning process was protection of the fitness of wild stocks of salmon.

In 1976 and 1978, Alaska voters passed bond issues that authorized over US $50 million for the construction of major public salmon hatcheries. The plans for location, design, and operation of these facilities were governed by these long-range planning goals in each region. At the same time in the mid 1970s, the Alaska Legislature established a revolving fund from which the state loaned funds for construction of approved PNP hatcheries, which are also governed by the regional plans.

2.2. Operation and Productivity of Alaska Salmon Hatcheries

Under Alaska statutes, regional aquaculture associations in Alaska are allowed to do the following:

1. build and operate hatcheries;
2. assist ADF&G in developing and maintaining regional salmon plans;
3. authorize assessments (usually 2–3%) on common property, commercially caught salmon to support hatcheries;
4. provide for the sale of a portion of returning hatchery fish to help cover operational cost and repay state loans (McKean, 1991).

Non-associated PNP hatchery corporations do not have a direct voice in regional planning and do not derive revenue from assessments on the annual catch. This framework allowed the Alaska salmon hatchery program to evolve into a blend of public and private sector participation (Pinkerton, 1994).

Alaska hatcheries are required by law to benefit common-property harvesters in both commercial and recreational fisheries, for regional economic benefit. Regional aquaculture associations and non-associated PNP hatchery operators are, however, allowed to harvest and sell a portion of the hatchery salmon they produce. Special terminal area zones near the hatchery allow the harvest of hatchery salmon. Such terminal area harvests are meant to minimize impacts on wild stocks, on the supposition that relatively few wild salmon are taken in them. Because the main purpose of the hatcheries is for benefit of the common-property harvest, production from PNP hatcheries is commonly categorized as either common-property harvest or cost-recovery harvest.

Currently, there are eight regional aquaculture associations in Alaska. Five of these have either built hatcheries or are operating facilities initially built as public hatcheries (McNair and Holland, 1993; McNair, 2000). Ten non-associated PNP corporations operate hatcheries. The state operates only three hatcheries, primarily in support of recreational fishing. Regulation of and technical assistance for all hatcheries in Alaska remain responsibilities of the

Alaska Department of Fish and Game, which operates technical laboratories for fish health, genetics, limnology, and mark-and-tag processing (Koenings, 1993; McNair and Holland, 1994).

2.2.1. Southeast Alaska

Two associations in Southeast Alaska, the Southern Southeast Regional Aquaculture Association, headquartered in Ketchikan, and the Northern Southeast Regional Aquaculture Association, headquartered in Sitka, operate six major hatcheries in the region. In addition, two Federal experimental hatcheries, a Bureau of Indian Affairs hatchery on the Annette Island Indian Reservation, and ten non-association private hatcheries produce salmon in this region.

In 1999, 17 million hatchery salmon were caught in the common-property fishery or in support of cost recovery in Southeast Alaska (McNair, 2000). Chum salmon represented 68% of this harvest, followed by pink, coho (*Oncorhynchus kisutch*), and sockeye (*Oncorhynchus nerka*) salmon, which respectively represented 24%, 6%, and 1% of the catch. Although chinook salmon (*Oncorhynchus tshawytscha*) comprised only 1% of hatchery production in this region, they nevertheless are an important part of the Southeast Alaska hatchery program because of patterns in regional fisheries, biology of the species, and important elements of the U.S.A./Canada Salmon Treaty (Heard et al., 1995). Hatchery-produced chum salmon comprised 69% of those taken in the regional common-property fishery; for other species, hatchery-produced salmon were a minor component of the harvest.

In Southeast Alaska, 43% of all hatchery salmon produced were harvested for cost recovery by PNP operators. Chum salmon represented the largest part of the cost-recovery harvest; one third of the 11.4 million chum salmon harvested were sold by PNP corporations to pay for hatchery operations.

2.2.2. Prince William Sound (PWS)

The Prince William Sound Aquaculture Corporation (PWSAC), headquartered in Cordova, operates five hatcheries in the region. In addition, the Valdez Fishery Development Association operates one non-association hatchery in Valdez. Hatchery salmon harvested in PWS common-property fisheries in 1999 amounted to 26.7 million fish; pink salmon comprised 91% of the harvest. Chum and sockeye salmon respectively accounted for 4% and 3% of PWS hatchery production. In the PWS common-property fishery, of all salmon taken, hatchery-produced salmon comprised 78% of the pink salmon, 83% of the chum salmon, 29% of the coho, and 21% of the sockeye (McNair, 2000).

Hatchery production of sockeye salmon by PWSAC also occurs in interior Alaska at Gulkana in the upper reaches of the Copper River, which enters the Gulf of Alaska at the eastern edge of PWS. The Gulkana Project, one of many unique applications of hatchery technology in Alaska, involves a spring-fed sockeye salmon egg incubation system that allows fry to emerge naturally into otherwise fishless nursery lakes (Roberson and Holder, 1987).

Common-property fisheries that take both wild- and hatchery-produced salmon are regulated by the state, not only to prevent over-harvest of wild salmon but also to ensure that an adequate portion of hatchery-produced salmon is available for subsequent harvest by the hatchery corporations and for broodstock. This subsequent harvest is the cost-recovery harvest, which is sold to provide operating revenues to the hatchery corporations. In PWS, 35% of all hatchery salmon produced were harvested in support of hatchery cost recovery in 1999. The largest species component of cost recovery was pink salmon; 35% of the 35 million hatchery-produced fish were pink salmon and were harvested for that purpose (McNair, 2000).

2.2.3. Cook Inlet

Cook Inlet Aquaculture Association, headquartered in Soldotna, operates two hatcheries in the region. There are also two hatcheries operated by ADF&G for freshwater sport fishery enhancement and one non-association hatchery in Cook Inlet. In 1999, Cook Inlet hatcheries produced a harvest of 1.6 million salmon; pink salmon represent 38% of the total, sockeye salmon 60%, and coho salmon 3%. Hatchery-produced salmon represented 16% of the mixed-stock, common-property fishery and 35% of the total harvest. In Cook Inlet, 66% of all hatchery salmon were taken by PNP operators for recovery of operating cost; pink salmon accounted for the largest component (79%) of the 1.1 million salmon that were harvested for this purpose (McNair, 2000).

2.2.4. Kodiak

The Kodiak Regional Aquaculture Association, headquartered in Kodiak, operates two hatcheries in this region. A total of 5.2 million hatchery salmon were harvested in the Kodiak Region common-property fishery in 1999. These fish comprised 29% of the total harvest and 34% of the pink salmon in the total harvest. Of the harvest of hatchery salmon, pink salmon comprised 79%, sockeye 16%, coho 3%, and chum salmon 2%. Common-property fisheries harvested all hatchery salmon produced in the Kodiak Region; none were taken for recovery of hatchery operating costs (data from McNair, 2000).

2.3. Closing Ineffective Hatcheries

Contrary to the experience elsewhere in North America that salmon hatcheries, once built, continue to operate indefinitely regardless of whether or not they contribute salmon to fisheries or reach other performance goals (Hilborn, 1992, 1999; Lichatowich, 2000), the Alaska hatchery program has built and closed a total of 14 hatcheries since its beginning in the 1970s. Closures have occurred in all regions for a variety of reasons including potential disease or genetic effects on wild stocks, intractable disease problems in the hatchery, intractable harvest management problems, and cost inefficiencies. Because of the close involvement of regional fishing industries with funding of the hatcheries, either through a direct assessment on the value of landings or through an allocation of harvest to the operation of hatcheries, Alaska's salmon enhancement program has emphasized accurate monitoring and evaluation of the effectiveness of hatcheries in producing harvestable salmon and has demanded economic efficiency.

3. EFFECTS ON WILD SALMON

Three major kinds of interactions between hatchery salmon and wild salmon in Alaska have been recognized as potentially deleterious to the fitness of wild populations:

1. deleterious genetic (interbreeding) interactions, which are those that threaten the locally adaptive structure of genetic variation within and between stocks of wild salmon;
2. disease-causing organisms that could be introduced to wild salmon by hatchery salmon, a particularly dangerous interaction if exotic pathogens were to be introduced;
3. harvests of unrecognizable wild salmon in mixtures with abundant hatchery salmon, which may be too intense and not sustainable by the wild populations.

Rigorously enforced policy has been promulgated in Alaska to prevent or ameliorate all of these interactions (policies entitled Genetic Policy, Salmon Escapement Goal Policy, Stock Transport Policy, Pathology Policy and Escapement Goal Policy are described in ADFG, 2004). The Alaska Administrative Code (5 ACC, Chapter 41) governs the transport of live salmon, as would occur for the establishment of a salmon hatchery broodstock or in additions to a broodstock (the regulations are available on the Internet, website: http://www.cf.adfg.sta-ww.cf.adfg.state.ak.us/geninfo/regs/cf_regs.php).

3.1. Genetic Interactions

Conservation of genetic diversity has been long recognized as the central issue facing stewards of wild salmon in Alaska (reviewed, e.g., by Gharrett and Smoker, 1993). All interactions between cultured and wild salmon can be understood through their effects on genetic diversity. The spread or intensification of disease is avoided not merely because either would create obstacles to hatchery operations but also because both would reduce the fitness of wild-spawning populations. Any harvest mortality above the sustainable amount reduces fitness and threatens diversity. However, there is also a class of interactions that are directly genetic; several Alaska regulations address them directly.

An important feature of Alaska policy (GPRT, 1985) has been the prohibition of transports of non-local salmon into hatcheries, which would place them into close proximity with wild populations where interbreeding might occur. This policy followed from the growing understanding that geographic and genetic distances between salmon populations are correlated, i.e., that the evolved genetic differences between wild stocks are roughly measured by their geographic separation, and that the loss of diversity and adaptability from the interbreeding of hatchery-produced salmon with wild populations could be minimized if the hatchery broodstocks were derived only from nearby wild populations (reviewed by Campton, 1995).

Virtually no transports from outside of Alaska have been permitted in the past 30 years. Transports between river basins or between zoogeographic regions have been regulated and restricted. Transports have been allowed only within the geographic regions of the hatcheries and not between regions, and not even then if interactions with significant wild populations were foreseen. For instance, there have been no transports from the southern part of Southeast Alaska—around Ketchikan—to the northern part—around Juneau. These regions roughly agree with major stock groupings of salmon.

Alaska policy also seeks to minimize the loss of genetic diversity through inbreeding within hatchery broodstocks. Because salmon can produce a large number of eggs, the size of a broodstock absolutely necessary for the economic success of a hatchery in the short term may be small, for instance smaller than 100 fish. Because wild spawners can be difficult to obtain in some species, particularly chinook, the size of a hatchery's founding population also can be small. Rates of inbreeding and random loss of genetic diversity and fitness can be high in such small populations. Alaska policy sets a recommended lower limit on the effective population size of broodstocks at 400. This guideline effective population size has been generously exceeded in chum, pink, and sockeye projects; it has been more difficult to meet in chinook and coho projects.

The policy seeks also to minimize losses of genetic diversity due to selection and specifies that broodstock should be taken proportionately from all temporal segments of the population of returning fish and that matings otherwise should be at random with respect to phenotype. Most hatcheries attempt to follow this part of policy by setting aside brood animals from among fish arriving the hatchery terminal area at weekly intervals during each year's run.

Losses of genetic diversity in hatchery populations and divergence of hatchery populations through artificial or domestication selection are potentially dangerous to wild-spawning salmon because a portion of hatchery fish are likely to stray and spawn with wild salmon. There is little empirical data to let science assess this danger. But the policies that limit fish transport, limit inbreeding, and limit selection are meant to minimize the dangers.

3.2. Disease Control

Alaska's goal has been to prevent the introduction of exotic pathogens into Alaska or regions of the state and to prevent any substantial increase in the "load" of naturally occurring pathogens carried by populations (SPRC, 1988). Applications for permits to transport live salmon (or any species of fish or shellfish) at any life stage are not only reviewed by ADFG's pathologist, who may require a survey for the presence of pathogens not only in the donor population but also in populations near the destination of a proposed transport. Thus, the establishment of a salmon hatchery broodstock, or of any addition to a hatchery's broodstock, is carefully regulated. No transports are permitted that involve populations in which "new" pathogens are found, i.e., pathogens not known in the receiving watershed.

Permits, when granted, stipulate that transported salmon eggs must be disinfected before they can be cultured at the receiving site. Hatchery facilities and operations are inspected annually and operators are required to use thorough prophylaxis. Operators are also required to report occurrences of certain critical diseases, and stocks experiencing outbreaks of critical diseases are destroyed (critical diseases are specified in the state regulations cited above and include dangerous diseases caused by pathogens that are not known to occur in Alaska). Preventing introductions of disease pathogens is also an important justification for Alaska's prohibition of transports from outside of the state.

3.3. Overharvest in Mixed-Stock Fisheries

For wild-spawned populations, a major detriment associated with hatcheries can be the excessive and unsustainable harvest of the population in mixtures with salmon produced by hatcheries. A drastic example is the loss of wild coho salmon populations in the lower Columbia River in the states of Washington and Oregon, USA. A major contributing factor to their loss was that, after about 1960, a commercial fishery was sustained by production from hatcheries but the rate of harvest was too great to be sustained by the wild populations (Weitkamp et al., 2000).

In Alaska, one strategy for reducing this risk has been to locate hatcheries in places where returning hatchery salmon can be harvested in relative isolation from wild stocks, sometimes to the benefit of weak wild populations, which otherwise would be exposed to harvest. Examples of this strategy include the chum salmon hatchery programs in Southeast Alaska. They include Neets Bay Hatchery (the harvest area is at the head of a long fiord devoid of other salmon populations), Hidden Falls Hatchery (the hatchery and harvest area are on the steep shore of a long strait where relatively few wild salmon occur), Boat Harbor-Lower Lynn Canal harvest area (in a location where few wild salmon are mixed in the fishery), and Deep Inlet harvest area (an isolated inlet on Sitka Sound) (Smoker et al., 2000). These "isolated-from-wild-stocks" programs account for more than half of the hatchery chum salmon production in Alaska.

Other hatchery programs, however, were developed to enhance characteristically mixed-stock fisheries. Many salmon fisheries in Alaska occur at places and times where returning mature salmon are spatially concentrated before sexual maturation has reduced their value to the fishery; these locations are typically capes and entrances to sounds, straits, and bays. Managers control these fisheries week by week. They construct catch-per-effort indexes of wild stocks and restrict the fisheries if weekly indexes indicate a scarcity of wild salmon. Separate indices of abundances of wild-spawned and hatchery-produced salmon can be estimated from catch and effort by the managers only if a portion of the hatchery-produced fish are marked at the hatchery and are detected during the fishing season. In practice, the fishery manager opens the weekly fishing seasons at the beginning of the fishing year, judges the strength of the annual run based on the size of the initial catch and a comparison of it to historical records, and then either leaves the fishery open or closes it. The process is repeated week by week during the annual run. The judgment of run strength can be confused by the presence of an unknown portion of hatchery-produced fish unless an estimate of the portion can be made from the presence of marks or tags on hatchery salmon; without marks or tags, the presence of hatchery-produced fish will bias the manager's judgment of run strength upward, thereby increasing the likelihood that the fishery will be allowed to continue even when the run of wild salmon is weak.

In some fisheries, these weekly estimates have been made by detection of the marks and microwire tags applied to a portion of fry released from the hatchery (reviewed by Smoker et al., 2000). In other mixed-stock fisheries, however, the proportion of hatchery salmon that can feasibly be marked by excision of adipose fins and tagged by coded microwires is too small. The development of a mass-marking technique has improved the situation markedly in the past ten years. Cyclic manipulations of incubation temperature after the early embryonic stages (e.g., a cooling of 2°C for 24 hours during a 72-hour period) results in a recognizable dark layer in the microstructure of otoliths (Volk et al., 1990). These "otolith thermal marks" can be economically applied to the entire production of hatcheries (Munk et al., 1993). Repeated manipulations are used to encode specific marks at each of several hatcheries. Samples are taken in each fishing period and immediately decoded; the proportion of marks detected in the samples provides a powerful estimate of the proportions of hatchery and wild-spawned salmon in the catch (Hagen et al., 1995; Geiger and Munk, 1998; Joyce and Evans, 1998; Jensen, 2000). More than 600 million fry are marked each year in Alaska; more than 30 different codes can be applied in a given year (data from Alaska Department of Fish and Game, Juneau, Alaska, USA).

3.4. Real-Time in-Season Use of Marks and Tags

There are three notable regional fisheries in Alaska that are now managed based on real-time information from otolith thermal marks. Pink salmon enter PWS through the narrow entrances in the southwest, enroute to spawning streams in all parts of the sound. Mixtures of wild and hatchery fish are harvested at the entrances during the early part of the season. Because all of the 600 million hatchery fry produced in PWS are marked, the relative strengths of the wild stocks in the entrances are known from samples of otoliths taken each week during the season. The fishery can then be regulated by opening or closing restricted districts along the migration path of the salmon on specific days. Later in the season, aggregations of hatchery salmon can be identified and targeted for harvest (Joyce and Evans, 1998; T. Joyce, Area Management Biologist, Alaska Department of Fish and Game, Cordova, Alaska, USA, personal communication June 2000).

Fisheries for chum salmon from Gastineau Hatchery and Hidden Falls Hatchery in the northern region of Southeast are situated in relative isolation from other chum salmon fisheries and from migrating wild salmon. They present a low risk to wild-spawned salmon populations. Even so, fishery managers depend on assessments made using otolith thermal marks as a reliable indicator of the weekly abundance of wild chum salmon (A. MacGregor, Area Management Biologist, Alaska Department of Fish and Game, Douglas, Alaska, USA, personal communication June 2000).

Sockeye salmon fisheries on the transboundary Stikine River are enhanced by the harvest of fish returning to two headwater lakes. One of the lakes, Tuya, is inaccessible to returning salmon but is remarkably productive; it is stocked each year with fry derived from gametes taken from sockeye returning to the second lake, Tahini. The embryos are incubated and the otoliths thermally marked at Snettisham Hatchery, north of the mouth of the Stikine. The marks are crucial for managing the gauntlet of fisheries in the USA near the river mouth and in Canada at intervals on the river (Jensen, 2000).

Biologists are also learning from otolith thermal marks that substantial straying of pink salmon does occur from hatcheries in PWS when large returns are present, and that the number of strays into wild-spawning beds is related to the distance from the hatchery (Joyce and Evans, 1998). It is not known, however, how much detrimental gene flow is associated with this straying and how different this straying may be from the apparently very frequent straying between wild populations of pink salmon in the region (Sharp et al., 1993; but see Habicht et al., 1998). Harvest managers are learning how to micromanage fisheries to minimize such straying (T. Joyce, Area Salmon Management Biologist, Alaska Department of Fish and Game, Cordova, Alaska, USA, personal communication).

4. DISCUSSION

Depressed wild stocks were the impetus for the current hatchery program in Alaska. A novel system of public and private non-profit hatcheries evolved to augment, not replace, wild salmon in common-property fisheries. One goal of the program is to smooth out some of the sharp downside fluctuations in abundance (Koernig and Noerenberg, 1976). Over the past two decades, wild stocks in Alaska have made dramatic recoveries from their historical minima 25–30 years ago. Because of this and the contribution of fish from the implementation of the hatchery program, the common-property commercial harvest of Alaska salmon has reached record high levels. In some recent years, the harvest has not been restricted by abundance of salmon but has been constrained by lack of economic demand; processing companies have limited their purchases of salmon from fishermen. Since 1980, the commercial salmon catch has exceeded 100 million fish in all but one year and catches over the past 19 years have averaged 145 million fish (range: 97–218 million). Even during this era of very high harvest, however, many local fisheries in Alaska have depended in some years on salmon produced by hatcheries because local wild populations have not been abundant enough to provide harvestable salmon, i.e., salmon that are surplus to the population's requirements for its reproduction.

The Alaska ocean ranching program contribution to harvest has been considerably larger than other hatchery programs in the North Pacific Ocean, but not as large as the Japanese program (Table 1; NPAFC, 1999). Hatchery contributions to harvest are particularly important in sustaining the Japanese salmon harvest (Kaeriyama, 1999) because Japan's harvest is derived almost solely from hatchery production; this has been Japan's primary basis for salmon production for over a century. There has not been an emphasis on protection of wild-stock productivity or habitat. Northern Japan is near the southern extent of the range of Pacific salmon; its subtropical summer climate provides only seasonally accessible habitat to salmon. It is unlikely that annual harvests like those provided by the Japan ocean ranching program (in excess of 30 million chum salmon annually in the past two decades; Kaeriyama, 1999) could be sustained by wild-spawning populations in Japan even if pre-settlement habitats were restored.

There are strong correlations between survival of salmon in the ocean and climate-driven fluctuations of environmental factors (Beamish and Bouillion, 1993; Francis and Hare, 1994; Hare and Francis, 1995; Mantua et al., 1997; Beamish et al., 1998). The variations in harvest between regions of the North Pacific Ocean are probably principally determined by differences in productivity between oceanic regimes; i.e., differences between the California Current and the Alaska Gyre. Stocks dependent on the California Current ecosystem have been depressed in recent decades whereas stocks dependent on

Table 1. Harvest of Pacific salmon, releases from hatcheries, and the proportion of hatchery-produced salmon in harvests in regions of the Pacific rim, in 1995. Data source: North Pacific Anadromous Fish Commission, Vancouver, British Columbia, Canada

Location	Harvest (thousands of metric tons)	Hatchery fry released (billions)	Hatchery-produced salmon in harvest
Canada, British Columbia	50	0.5	>50%
Japan	253	2.1	>90%
Russia, far eastern	218	0.4	<20%
USA, Alaska	451	1.5	~30%
USA, southern	16	0.5	>50%

the Alaska Gyre have been abundant (Hare et al., 1999). Many scientists now believe that the recent two decades of high marine survivals of salmon from Alaska (and also from Asia) may be shifting into a declining mode due to major shifts in climatic patterns in the North Pacific Ocean (Klyashtorin, 1998; Klyashtorin and Rukhlov, 1998; Noakes et al., 1998; Welch et al., 1998). However we note that, in 1999, the industry produced yet another record harvest of salmon in Alaska—216 million fish, a harvest that was restricted by economic demand and not by salmon abundance. Although Alaska hatcheries currently have a good record of enhancing wild-salmon catches, it remains to be seen if they can mitigate sharp downturns in abundance when marine survival rates decline.

Changes in climate that affect ocean survival can also directly affect freshwater life stages of salmon; e.g., colder winters are associated with reduced survival of eggs and fry in nature. In theory at least, hatchery salmon would have survival advantages over wild salmon if the two types were subjected to the same marine conditions in a colder climate because the environment of the hatchery salmon is controlled during freshwater life stages. Indeed, because Alaska's salmon enhancement program began during the period of high marine survivals in the late 1970s, it will be important to maintain continued careful evaluation of the program before, during, and after any future environmental changes that could affect the effectiveness of the program.

Alaska's hatchery program has enjoyed considerable success during its first quarter century; however, as pointed out by Hilborn and Winton (1993), a longer time horizon may be needed to properly evaluate such enhancement programs. The annual reporting requirement under which Alaska hatchery operators must monitor important performance criteria will be important. This is particularly true for the annual catch of hatchery-produced salmon, both in the mixed-stock, common-property fisheries and in the terminal fisheries where catches are allocated to the recovery of hatchery operating costs (e.g., McKean, 1991; McNair and Holland, 1993, 1994; McNair, 1999, 2000). Alaska hatchery operators should continue to emphasize monitoring and evaluation to fulfill this requirement and because PNPs and the regional salmon fishing industries and communities have a close economic association.

Two issues of major concern often raised with salmon hatcheries include the potential ecological displacement of wild salmon by hatchery fish in freshwater habitats and overharvest of less abundant wild stocks in fisheries that target more abundant hatchery fish. The planning for Alaska's hatchery program addressed these issues in several ways. Hatchery locations were carefully evaluated in the RPT process and, as a result, interactions between wild and hatchery juveniles in freshwater environments have been minimized. Most facilities are located at or near tidewater at a distance from major wild populations; for example, near streams where there are no natural salmon runs. Fry and smolts from tidewater hatcheries are released directly into the marine environment. As a result, hatchery juveniles tend not to co-mingle with their wild counterparts; in particular, hatchery salmon do not interact with wild salmon as they migrate through hundreds of miles of riverine waters, a problematic characteristic of salmon hatchery programs in other parts of North America.

Provisions for terminal harvest areas are also carefully considered so that fisheries can target hatchery-fish returns and avoid mixed hatchery/wild-stock populations to the greatest extent possible. Where major mixed hatchery/wild-stock fisheries do occur, extensive marking programs are now in place to allow identification of the hatchery fish in those fisheries. Coded-wire tagging or thermally induced otolith marking of hatchery juveniles together with real-time monitoring of the proportion of marked fish in the harvest allow managers to know, with a high degree of certainty, ratios of hatchery and wild fish in the mixture and to make the best management decisions to protect the wild stocks (see reviews by Heard, 1998; Smoker et al., 2000 and see also Munk et al., 1993; Joyce and Evans, 1998; Geiger and Munk, 1998; Volk et al., 1990).

Two particular regions of Alaska's hatchery program have been criticized: the large pink salmon hatchery program in PWS and the predominant hatchery production of chum salmon in Southeast. In both instances, over 75% of the harvest is attributable to hatchery production. Eggers et al. (1991), in a review of trends in wild and hatchery pink salmon abundances in PWS, raised concerns over apparent declines in wild-stock escapements and in the ability concomitantly to conduct fisheries on large hatchery runs and reach target escapement goals for wild stocks. Hilborn (1992) also criticized pink salmon hatchery production in PWS, saying that the program is without merit and "...should be terminated." Recently Hilborn and Eggers (2000) argued that the release of hatchery-produced salmon in PWS has not significantly increased production beyond the level that would have been available from wild stocks. They elaborated by speculating that hatchery salmon have driven out wild stocks or deprived them of ecological opportunity. They reach three conclusions:

1. The recent era of increased hatchery production compared to that of the preceding era is proportionately no greater in PWS than in other regions not affected by hatchery production.
2. The abundance of any cohort of wild salmon is largely determined by escapement in the preceding generation (i.e., the abundance of adult salmon not harvested by the fishery) and escapement in PWS has declined steadily during the era of hatchery production.
3. The productivity of wild populations (the number of returning offspring per spawning adult) correlates negatively over the years with the number of fry released from hatcheries in PWS. Thus, if hatchery salmon had not been present, productivity of wild stocks would have been commensurately higher.

Wertheimer et al. (2001) find fault with their analysis and interpretation in each of their findings and note the following:

1. Compared to that of other areas, the productivity of wild stocks in PWS was particularly high in the years before hatchery production began, and it remained high in the hatchery-influenced era.
2. Escapement or wild-stock spawning abundance during the recent era of hatchery production may have been smaller than during the earlier era, but escapement came closer to harvest managers' goals, i.e., escapements declined because harvest managers were better able to control the fishery and to reduce the number of years when escapement was above the goal.
3. Productivity of wild stocks is more likely influenced by environmental conditions other than the presence of hatchery-produced salmon in PWS; thus, Hilborn's and Eggers' model (2000) of wild-stock productivity in the absence of hatchery salmon is unrealistic.

Furthermore, Wertheimer et al. (2004) find that year-to-year variations in marine ocean conditions explain more of the changes of wild-stock productivity than can be explained by the presence of hatchery salmon.

Another regional criticism of the Alaska hatchery program—this one of the production of chum salmon in southeast Alaska where hatcheries produced almost half of the total Alaska harvest of 20 million fish in 1999—comes from fishermen in regions where both price and production of chum salmon have declined. The criticism is that prices would be higher for chum salmon caught

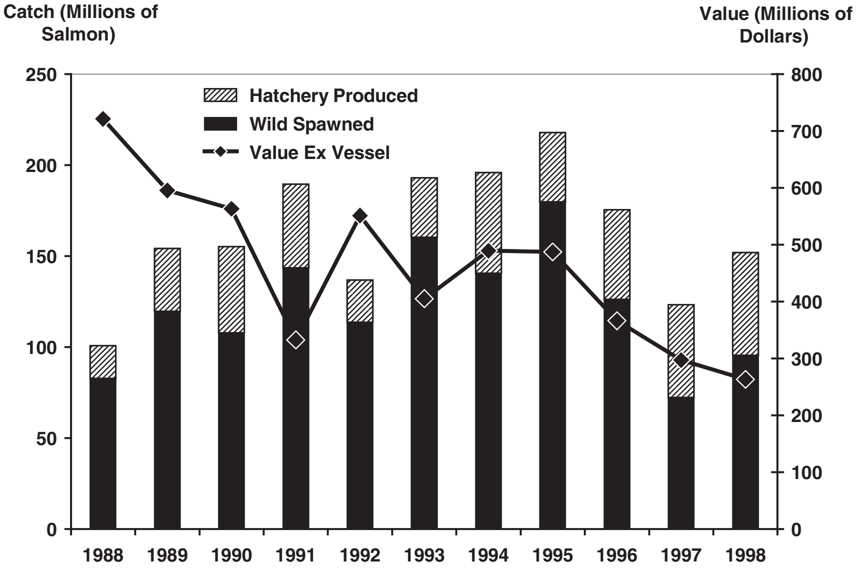

Figure 2. Commercial catch and exvessel value of wild-spawned and hatchery-produced Alaska salmon, 1988–1998. Hatchery salmon include fish taken in both common-property and cost-recovery harvests. Data source; Alaska Department of Fish and Game, Juneau, Alaska, USA

in other regions if there were not so many chum salmon from Southeast hatcheries.

In fact, there has been an overall decadal decline in the commercial value of salmon fisheries (Figure 2). Many factors interact and fluctuate in determining prices paid to salmon fishermen. However, no factor is more relevant than the increasing world supply, which is principally due to the burgeoning increase in production of farmed salmon by many countries (Heard, 1997; Knapp, 1998; Sylvia et al., 2000). While capture fisheries for salmon by all nations combined have remained relatively stable at around 600 to 800 thousand metric tons annually over the past 14 years, farmed salmon production has grown from less than 250 thousand metric tons in 1984 to over a million metric tons in 1998 and, in 1996, it first exceeded capture fisheries (Figure 3). There are more salmon available today in commercial markets worldwide than ever before, despite the unsettling fact that wild stocks in many areas are badly depressed and threatened with extinction, especially where major habitat losses have occurred (reviewed by Williams, 2000). It is therefore difficult to attribute declines of chum salmon prices in other regions solely to the increase of hatchery production in Southeast Alaska.

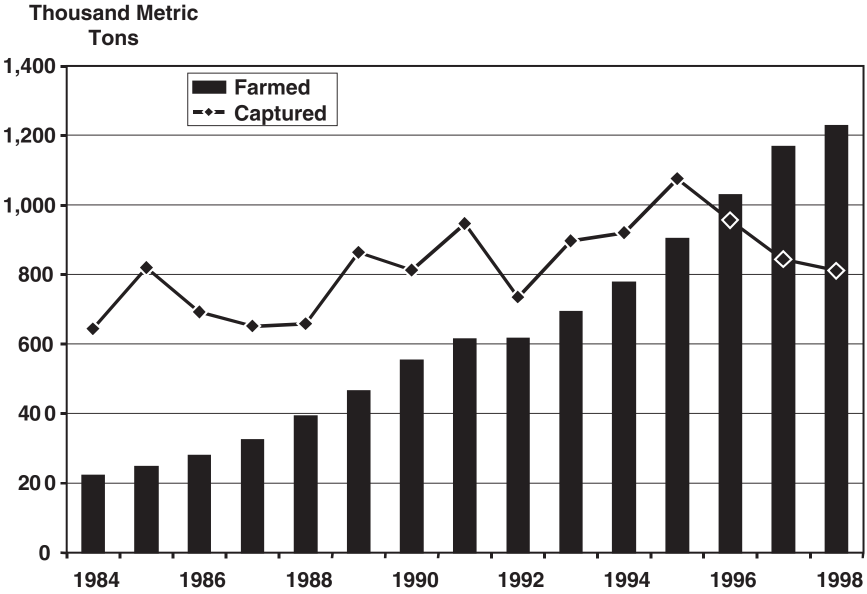

Figure 3. Worldwide production of farmed and wild-caught (captured) salmon and trout, 1984–1998. Capture fisheries include both hatchery and wild-spawned salmon. Both freshwater and marine environments are included. Data source: Yearbook Volume 86/1 and Volume 86/2, Food and Agriculture Organization of the United Nations, Rome, Italy

5. CONCLUSIONS

Alaska salmon runs and the fisheries that depend on them are unique in that a successful hatchery program coexists with abundant and healthy wild populations that are, in general, at or near record high abundance (Baker et al., 1996; Wertheimer, 1997), despite sharp declines in some stocks in some regions in some years (e.g., Kruse, 1998). After two decades of operations in several regions, hatcheries are successfully making meaningful contributions to fisheries with little, if any, evidence of significant detrimental impacts either on the environment or on wild populations of salmon in Alaska.

Salmon management in Alaska is strongly directed by law, policy, and regulation toward maintaining sustainable, productive wild-stock spawning populations. Even where hatchery fish are not involved, Alaska's fisheries management policies are directed toward reaching established escapement goals for wild populations rather than any predetermined harvest goal for the benefit of fisheries. Strong habitat laws have prevented catastrophic losses of salmon habitats. These, and a carefully implemented hatchery program, are the hallmarks of Alaska's commitment to maintaining healthy runs of Pacific salmon and the fisheries that depend on them (Holmes and Burkett, 1996). We conclude that the current salmon hatchery program in Alaska, from its beginning in the 1970s to the present, and despite some difficulties, conflicts, and adjustments, is a notable success.

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CHAPTER 21

EMPIRICAL RESULTS OF SALMON SUPPLEMENTATION IN THE NORTHEAST PACIFIC: A PRELIMINARY ASSESSMENT

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Abstract: For over a century, aquaculture of Pacific salmon has been used to provide increased harvest opportunities and to mitigate reductions in natural populations due to factors such as habitat destruction, overharvest, and blockage of migratory routes. More recently, attention has focused on the potential of hatchery propagation to reduce risks to and speed recovery of depleted natural populations. A large number of these "supplementation" programs have already been initiated and many more are planned, in spite of the fact that there is almost no empirical information on their long-term effects. Here we present preliminary results of a survey of 22 salmon supplementation programs in northwestern North America. Rather than using a single measure of "success," we evaluated programs according to how well they have accomplished a series of specific objectives. Some major conclusions emerge from the review: (1) many supplementation programs have achieved a measure of success in the aspects of fish culture traditionally associated with salmon hatcheries (e.g., high egg-to-smolt survival; adult-to-adult replacement rates in excess of 1.0); (2) to date, however, little information is available about the performance of hatchery fish and their progeny in the natural environment. Therefore, the premise that hatchery supplementation can provide a net long-term benefit to a natural population is a hypothesis that has not yet been tested. This fact should be kept in mind in evaluating the appropriate use of supplementation programs.

Key words: aquaculture, assessment, empirical, hatcheries, environment, Pacific salmon, review, supplementation

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1. INTRODUCTION

For over a century, artificial propagation of Pacific salmon (*Oncorhynchus* spp.), including steelhead (anadromous steelhead trout [*O. mykiss*]) in the Pacific Northwest has been used primarily to mitigate declines and losses of wild populations. Because the root causes of the declines (e.g., habitat loss and degradation, overharvest, blockage of migratory routes) were too economically, socially, or politically difficult to resolve, hatcheries were used as a substitute for conservation of wild populations (Lichatowich, 1999). More recently, there has been growing recognition that the genetic, ecological, and life-history diversities manifest in wild populations are integral to the long-term sustainability of the resource (National Research Council, 1996). Within the last decade, the listing of many populations of Pacific salmon as threatened or endangered species under the U.S. Endangered Species Act (e.g., Waples, 1995) has required managers to focus on conservation and recovery of natural populations, and this has spurred an increased interest in the use of artificial propagation for conservation purposes—for example, to prevent extinction or speed recovery of a population. Hatchery programs used for these purposes often are referred to as *supplementation* programs.

The potential conservation benefits of artificial propagation are readily apparent: the *raison d'etre* of a salmon hatchery is to bypass the high mortality that occurs in early life stages in the wild, and if a hatchery is successful in this regard, it has the potential to produce many times more fish than a wild population can. Although this demographic boost is a necessary component of a successful supplementation program, it is not sufficient by itself to provide a net long-term benefit to wild populations. For the latter to occur it is necessary for the hatchery fish to survive and spawn in the wild and to produce viable progeny that contribute to the natural population. Successful supplementation thus involves the integration of hatchery and natural production, a process that entails significant genetic and ecological risks to the wild population as well as potential benefits (Busack and Currens, 1995).

Evaluating the "success" of supplementation, therefore, requires a comprehensive evaluation of potential benefits and risks, with both being evaluated from the perspective of net long-term effects on wild populations. The last major review of salmon supplementation (Miller et al., 1990) is more than a decade old, and even at the time of completion had some significant limitations. This was illustrated in a recent U.S. Federal Court case involving appropriate use of supplementation of steelhead in Oregon, in which results of the Miller et al. study were cited by both sides. One side quoted the study in support of the contention that most supplementation programs have been successful, while the other side cited the same study to the effect that no supplementation program has been shown to provide a net long-term benefit to a wild population. In fact, both sides were right, as illustrated by the following quote from Miller et al. (1990, p. 4):

"Twenty-five of the 26 supplementation projects we reviewed were considered successful *by the principal investigator* [emphasis added]. Eighteen of the

26 projects were quantitatively evaluated. Of the 18, 14 are ongoing and four are supplementation evaluation studies. We found no evaluated projects that had rebuilt wild/natural runs to self-sustaining levels.''

The explanation for this apparent inconsistency is straightforward. Although the review evaluated the ''success'' of supplementation, no general definition of success was offered; instead, managers of supplementation programs were asked to evaluate their own programs by whatever criteria they chose to use. Not surprisingly, virtually all programs were judged ''successful'' in the self-evaluations. In contrast, Miller et al. (1990) found no supplementation programs that could be considered successful if the criterion of success was a self-sustaining natural population.

In this paper we present preliminary analyses from an updated review of supplementation programs for Pacific salmon. Our review attempts to address some of the shortcomings of previous efforts. First, we offer the following definition of supplementation: the intentional demographic integration of hatchery and natural production, with the goal of improving the status of an existing natural population (either in an absolute sense or relative to what its status would be without supplementation). This definition excludes introductions into new habitat or reintroductions into currently barren habitat that formerly supported a native population. Although these are legitimate conservation applications for artificial propagation under appropriate circumstances, such programs present a different set of challenges than does supplementation of an existing population and therefore should be evaluated separately.

Second, instead of using a single, subjective measure of ''success,'' we identify a series of objectives of supplementation programs and suggest quantitative ways of measuring the degree to which the objectives have been achieved. This approach accomplishes several things:

1. It results in a database that allows one to determine which aspects of salmon supplementation are working and which are not.
2. It allows programs to be evaluated directly against their goals, which are not identical across programs (for example, failure to meet a particular criterion might be due to biological or logistic difficulties in executing the program, but it might also occur because meeting that criterion is not one of the program's goals).
3. It highlights uncertainties that should be considered in determining the appropriate use of supplementation.
4. It points to areas critically in need of more research and/or better monitoring and evaluation.

2. METHODS

2.1. Choice of Programs to Include

For Pacific salmon within their natural ranges, we attempted to obtain information on all programs that met our definition of supplementation. Lists of potential supplementation programs were obtained by soliciting information from representatives of state, tribal, and federal agencies that operate hatchery facilities, and by searching through the scientific literature and agency reports. Through this process, we obtained a list of over 250 projects in California, the Pacific Northwest, and Alaska that at least someone thought could be considered "supplementation." Many of these were small, episodic programs for which little or no information was available. After eliminating these programs, we were left with a much smaller list that appeared to meet our definition of supplementation and for which we were able to obtain written reports or other documentation. Finally, to ensure that comparisons and summaries across programs were as meaningful as possible, we included in our analyses only those programs meeting the following criteria:

1. had been in operation long enough and consistently enough to have experienced at least some returns of adults produced in the hatchery;
2. collected broodstock adults from the wild and released juveniles into the wild (that is, we excluded programs that raise captive or wild-caught juveniles to maturity);
3. used broodstock derived principally from a local, native population.

Programs that did not meet one or more of these criteria may meet some definitions of supplementation and may provide benefits to natural populations, but it was not feasible to evaluate them in this study.

In the end, we found 22 projects that met these criteria, and these formed the information base for this review (Table 1).

2.2. Data Collection and Analysis

To collect information on the programs, we developed a worksheet consisting of 73 questions. The questions were divided into categories related to information about project administration; the natural population targeted for supplementation; broodstock collection; spawning, rearing, and release methods and results; non-targeted or control populations; and project goals. The questions were designed to elicit the raw data necessary to quantitatively and objectively evaluate the programs, rather than to rely on self-evaluation.

In filling out these worksheets, we first attempted to find the information in papers published in the scientific literature or in agency reports. We sent partially completed worksheets based on this information to the lead agencies operating the supplementation programs for their review. In many cases, the agencies were able to provide additional data. These data were also incorporated into the revised worksheets, which are available from the authors upon request.

Geometric means were used to compute averages across years for survival rates in captivity, adult-to-adult replacement rates, and relative survivals of hatchery and wild fish. Peterman (1981) showed that the geometric mean is more appropriate than the arithmetic mean in studies of stock–recruitment relationships and survival rates because the underlying distributions are typically log-normal rather than normal.

Table 1. List of supplementation programs considered in evaluating the results of Pacific salmon supplementation programs. Agencies and their contact locations for these programs are provided in Appendix 1. Ag. = agency; Init. = initial; Cur. = current

Program/ species	Run	Water body	Area	Ag.[1]	Date of first release	Principal goal[2] Init.	Principal goal[2] Cur.
1/chinook	Spring	North Fork, Nooksack River	Puget Sound	W	1977	C	A
2/chinook	Spring	White River	Puget Sound	W	1975	A	A
3/chinook	Spring	White River	Puget Sound	W	1989	A	A
4/chinook	Summer	Stillaguamish River	Puget Sound	ST	1981	A/C	A/C
5/chinook	Summer	Methow River	Columbia River	W	1991	B	B
6/chinook	Spring	Chiwawa River	Columbia River	W	1991	B	A
7/chinook	Spring	Methow River	Columbia River	W	1992	B	A
8/chinook	Fall	Hanford Reach	Columbia River	W	1973	B	B
9/chinook	Fall	Snake River	Snake River	W	1985	B	A
10/chinook	Spring	East Fork, Salmon River	Snake River	I	1991	B	A
11/chinook	Spring	Tucannon River	Snake River	W	1986	B	A
12/chinook	Spring	Imnaha River	Snake River	O	1983	B	A
13/chinook	Spring	Upper Salmon River	Snake River	I	1986	B	A
14/chinook	Summer	Pahsimeroi	Snake River	I	1970	B	A
15/chinook	Summer	South Fork, Salmon River	Snake River	I	1981	B	A
16/chinook	Fall	Cowichan River	British Columbia	DFO	1982	A	A
17/chum	Summer	Big Quilcene River	Puget Sound	FWS	1993	A	A
18/chum	Summer	Salmon Creek	Puget Sound	WOS	1993	A	A
19/chum	Fall	Stave River	British Columbia	DFO	1983	A	A
20/pink	Fall	Quinsam River	British Columbia	DFO	1980	A	A
21/sockeye	—	Wenatchee River	Columbia River	W	1989	B	B
22/steelhead	Summer	Imnaha River	Snake River	O	1983	B	B

[1] Abbreviations for the lead agencies responsible for these programs are as follows: DFO = Department of Fisheries and Oceans, Canada; FWS = United States Fish and Wildlife Service; I = Idaho Department of Fish and Game; O = Oregon Department of Fish and Wildlife; ST = Stillaguamish Tribe; W = Washington Department of Fish and Wildlife; WOS = Wild Olympic Salmon. In most cases additional groups, such as tribal co-managers, are also involved in project planning and operation.

[2] Goals: A = conservation; B = mitigation or harvest augmentation; C = research or monitoring.

2.3. Program Evaluation

Using the data collected in the worksheets, we evaluated each program according to 12 specific criteria (Appendix 1) that are relevant to 5 basic objectives that can be used to characterize the success of a supplementation program (Table 2). Summarizing the data in this way allows a hierarchical evaluation of the performance of individual programs, as well as an overall assessment of

Table 2. Basic supplementation objectives and how they were evaluated to estimate the success of Pacific salmon supplementation

Objective	How objective was measured
(1) Collect broodstock	
Collect a representative sample of the target population	Directly, by comparing distributions; or indirectly, by evaluating collection methods
Avoid collection of non-target populations	By using genetic and physical marks and evaluating collection methods
(2) Maintain higher survival (prespawning, egg-to-release, adult-to-adult) in the hatchery than in the wild	By calculating the geometric means over all years of data (We used literature values if survival data for the wild population were not available. If adult-to-adult return rates were not reported but release-to-adult return rates were, we used the release-to-adult rate, fecundity estimates [either reported or literature values], and reported egg-to-release survival rates to obtain an estimate of the adult-to-adult return rate.)
(3) Hatchery-produced fish and their progeny spawn and reproduce in the wild	Method varied among programs
(4) Increase abundance of natural spawners	By comparing geometric mean abundance for 4 years prior to supplementation with mean abundance during most recent 4 years
(5) Population remains at higher abundance level after supplementation ceases	By comparing abundance before and after supplementation and evaluating trend after supplementation

the performance of supplementation in general. This approach also allows a particular program to be evaluated in the context of specific goals for that program.

3. RESULTS

The majority of the 22 programs included in this study are for chinook salmon (*Oncorhynchus tshawytscha*) from the Columbia River, but 6 programs from Puget Sound and 3 from British Columbia are also included, as are programs for chum (*Oncorhynchus keta*), sockeye (*Oncorhynchus nerka*), and pink (*Oncorhynchus gorbuscha*) salmon and steelhead (anadromous rainbow trout, *Oncorhynchus mykiss*) (Table 1). Although we will continue to expand the geographic and species coverage of the supplementation database, we believe that the results presented here represent the majority of the supplementation programs in the Pacific Northwest that have been conducted for long enough to allow some evaluation of adult returns. All of the programs considered here have run for at least two salmon generations, and some have been in existence for over 20 years. Program performance with respect to the nested sets of objectives is summarized below.

3.1. Broodstock Collection

The first step in a supplementation program is collection of broodstock. Although a few programs in the Pacific Northwest now focus on collection of juveniles for rearing to maturity in captivity, only programs that collected adults were considered here. To minimize founder effect in developing the hatchery broodstock, supplementation programs typically try to ensure that broodstock collection is as representative as possible of the target population. As discussed by Waples (1999), any process of sampling (unless the whole population is taken into captivity) will result in a hatchery broodstock that differs in some respects from the target population. We considered two criteria in evaluating the ability of programs to obtain representative samples of broodstock: run timing and age structure. For only about a third of the programs were we able to obtain adequate data to determine whether broodstock collection was representative. About as many others documented the collection methods well enough that a qualitative assessment could be made (Table 3A). Of the programs with direct or inferential information, the majority suggested that the run-time and/or age distributions were similar in the hatchery broodstock and the wild population. Failure to obtain a representative sample of broodstock (as occurred in some programs) often was the result of inability to collect fish over the entire spectrum

Table 3. Characterization of supplementation programs listed in Appendix 1 for six important measures of success. Data shown are numbers of programs falling into each category ($N = 22$ programs total). A. Broodstock collection information. B. Survival in the hatchery environment. C. Adult-to-adult survival of hatchery-produced fish. D. Performance of hatchery-reared fish that spawn naturally. E. Population status before and after supplementation. F. Treatment/control response to supplementation. Dash = zero

A.

Broodstock collection	Yes	(Yes)[1]	No	(No)[1]	No data
Representative with respect to run timing?	4	7	2	1	8
Representative with respect to age structure?	4	6	1	1	10
Collected only from the target population?	17	–	5	–	–

[1] Direct data not available, but evaluation of broodstock collection methods suggests whether or not broodstock was representative.

B.

Survival in hatchery	Prespawning[1]	Offspring, egg-to-release
>90%	12	1
80–90%	6	12
70–80%	–	6
<70%	–	2
No data	4	1

[1] Survival of adults in captivity after collection from the wild.

(*Continued*)

Table 3. Characterization of supplementation programs listed in Appendix 1 for six important measures of success. Data shown are numbers of programs falling into each category ($N = 22$ programs total). A. Broodstock collection information. B. Survival in the hatchery environment. C. Adult-to-adult survival of hatchery-produced fish. D. Performance of hatchery-reared fish that spawn naturally. E. Population status before and after supplementation. F. Treatment/control response to supplementation. Dash = zero—cont'd.

C.

Ratio	In hatchery[1]	Hatchery:wild[2]
>5x	5	6
2–5x	5	6
1–2x	2	–
Equal	1	3
<1x	2	–
No data	7	7

[1] Adult-to-adult replacement rate for broodstock spawned in the hatchery.

[2] Relative adult-to-adult replacement rate for hatchery fish compared to wild fish. Numbers include programs for which data are available only for the hatchery population and an estimate has been made of adult-to-adult survival in the wild.

D.

Hatchery:wild ratio	Reproductive success	Offspring survival
>1x	–	–
About equal	1	1
<1x	2	–
No data	19	21

E.

Population status	Before[1]	After[2]
Healthy	1	–
Depressed	8	–
At risk	10	–
Critical	3	2

[1] "Before" status assessments represent judgments of those involved in the supplementation programs.

[2] Nineteen of 21 programs are still being supplemented and therefore do not allow an evaluation of "after supplementation" status.

F.

	Treatment	
Number of natural spawners[1]	Supplemented	Control[2]
Increased >20%	8	1
Unchanged	1	2
Declined >20%	10	5
No data	3	–

[1] Geometric means of most recent 4 years and 4 years immediately preceding collection of broodstock.

[2] Unsupplemented control populations were not available for most programs.

of run timing—for example, because it was impossible to operate a collection weir (or because the weir became ineffective) at high stream-flow levels.

Another critical measure is the degree to which the program was able to avoid collection of fish from non-target populations. For 17 of the 22 programs, available data either provided evidence that the managers were effective in collecting only the target population or provided no evidence to indicate this was not the case. In the remaining five programs, however, the integrity of the broodstock was compromised by unintentional collection of individuals from other populations. Factors that led to this situation included placing collection facilities at locations downstream of areas that support multiple geographic or temporal populations, inability to screen out stray hatchery fish, and collecting mixtures of populations with different run timings.

3.2. Survival in Captivity

Most programs showed high survivals of cultured fish while they were held in captivity (Table 3B). Two-thirds of the programs for which data were available (12 of 18) had prespawning survival of the broodstock in excess of 90% (the rest had survivals over 80%), and 19 of 21 programs with data available had egg-to-smolt survivals of offspring in excess of 70%. Some programs had high in-culture survivals in most years but occasionally experienced much lower survivals. Other programs showed consistently high in-culture survivals in later years after experiencing difficulties in some early years. Factors contributing to the occasionally high in-culture mortality included disease outbreaks and unfavorable water temperatures (especially during holding of prespawning adults).

3.3. Adult-to-Adult Survival

Adult survival of program fish (i.e., broodstock and hatchery offspring) was evaluated from two perspectives (Table 3C). First, we computed the geometric mean adult-to-adult replacement rate for fish collected as broodstock—that is, the number of adults produced in the next generation for each broodstock adult taken from the wild. Surprisingly, we were unable to obtain data for this key performance measure for almost one-third of the programs. Of those with data, all but three showed a net replacement rate of greater than 1:1. In ten programs, the geometric mean replacement rate was in excess of 2.0, which suggests the potential for rapidly increasing overall population size through artificial propagation.

Second, we compared adult-to-adult replacement rates for the hatchery broodstock to those experienced by the wild population. This allowed us to answer a key question for supplementation programs: whether taking fish into captivity produces more adults the next generation than would have been achieved by letting those same adults spawn naturally. In addition, this relative measure provides a potential means of demonstrating a supplementation benefit that might otherwise be overlooked: even if a program has an adult-to-adult replacement rate less than 1.0, it may still be providing at least a short-term conservation benefit (by slowing the population's rate of decline) if the replacement rate is even lower in the wild population. Again, for many programs we were not able to obtain sufficient data to make such an evaluation. In most programs for which data were available, the hatchery provided at least a twofold increase in the adult-to-adult return rate compared to the wild population.

3.4. Performance of Hatchery Fish in the Wild

Data are almost non-existent for the performance of hatchery-spawned fish after they return as adults (Table 3D). We did not find comprehensive data for any program on the reproductive success of hatchery-produced fish that spawn in natural habitat. For three programs we had partial data relevant to this determination; of these, two suggested a reduction compared to the wild population (hatchery fish that returned to the rivers to spawn were younger, smaller, or had lower fecundity) and one showed no difference (naturally spawning hatchery and wild fish had similar fecundity; see Appendix 1). We found only one program (Tucannon River spring chinook salmon) with even partial data on the survival or performance of the progeny of naturally spawning hatchery fish. For this program, the relationship between the number of redds and the number of progeny did not substantially change as the fraction of hatchery spawners increased, suggesting similar productivity of hatchery and wild fish (J. Bumgarner, Washington Department of Fish and Wildlife, personal communication). In this same program, data for the early 1990s showed that, compared to natural adults, returning hatchery fish were younger, were smaller for the same age, and had lower fecundity for the same size (Bugert et al., 1992). These conflicting results emphasize the need for more rigorous evaluation of the performance of hatchery fish in the wild.

Even if naturally spawning hatchery fish have reduced success in the wild, a supplementation program may still provide a net short-term demographic benefit if the reduction in productivity is more than offset by the substantial survival benefit during the juvenile phase that typically occurs in a hatchery. We found no programs with sufficient data to make a direct, short-term evaluation of this type. A rigorous evaluation of long-term demographic benefits of supplementation also would have to include an assessment of the long-term fitness consequences of reduced reproductive success by hatchery fish and an evaluation of the rate at which fitness could be naturally restored after supplementation ended. Again, research that would address these questions has not been conducted for any of the programs we evaluated.

3.5. Population Response

An ideal long-term study of the effects of supplementation would include a number of supplemented populations and a number of comparable, control populations that were not supplemented. The ideal study would also include information from before, during, and after supplementation in the treatment and control streams. If supplemented populations were more robust than controls, and if this difference persisted even after supplementation was terminated, it would be a convincing demonstration of the long-term effectiveness of supplementation. Because we found no studies that satisfied these ideal conditions, we considered various types of analyses that might provide at least partial insight into the effectiveness of supplementation. (Note: The experimental design for some current supplementation programs [e.g., Bowles and Leitzinger, 1991] includes paired control and treatment streams, but the studies are ongoing and a complete analysis of their effectiveness is not possible at this time. Preliminary data for these ongoing programs have been incorporated into this report.)

A comparison of the status of populations before and after treatment is largely uninformative with respect to salmon supplementation. Only two programs we evaluated can be considered completed (Table 3E), but neither was terminated because the population recovered. One program (White River spring chinook) was terminated but a different type of supplementation program was started soon thereafter in the same basin, and another (East Fork Salmon River) was suspended because too few fish returned to support broodstock collection. Therefore, it is impossible at this point to collect any "after treatment" data for most supplementation programs. (After this review was completed we received a report [Ames and Adicks, 2003] on supplementation programs for summer chum salmon in two areas of South Puget Sound; the programs were conducted from 1976 to 1991. Using the same criteria applied elsewhere in this report, recent run sizes in Case Inlet and Hammersley Inlet streams were approximately 1.5–2.5 times as large as presupplementation values. This report, therefore, describes an example in which population size was higher after supplementation ended than it was before. However, the report does not contain comparable information for unsupplemented control streams. Recent abundance of chum salmon in other areas of Puget Sound has also been quite high, which complicates the interpretation of these results.)

Another approach is to compare the population abundance before supplementation with the current abundance. If a goal of supplementation is to help promote a viable population after the program ceases, it should at a minimum be able to increase population abundance during supplementation. About half (10 of 22) of the supplemented populations declined in size after supplementation began, while nine populations increased in size or were stable (Table 3F; data are not available for three populations). This result by itself is difficult to interpret because external factors unrelated to supplementation undoubtedly affected the abundance of many of these populations. For example, most populations in this study were considered depressed or at some risk of extinction before supplementation began (Table 3E), and long-term recovery is not likely even with supplementation unless the factors that contributed to the initial decline are addressed.

In a few of the cases we examined, significant improvements in survival were achieved (e.g., by harvest rate reductions) concurrently with initiation of the supplementation program. In these cases, it can be difficult to determine the actual cause of a population's increase in abundance.

Some insight into the effects of these external factors might be gained from evaluating the behavior of unsupplemented control populations, but comparable control populations were available for only about a third (8 of 22) of the programs. Overall, the response of the supplemented populations was slightly better than the control populations. Paired supplemented and control populations had similar abundance trends in five of the eight cases; the supplemented population outperformed the control population in two cases, while the control population performed better in another program. Considering all programs with available data, a much higher percentage of the supplemented populations increased (8 of 19 supplemented populations increased versus 1 of 8 control populations). However, a majority of the supplemented populations that increased did not have paired control populations, thus limiting the conclusions that can be drawn from these data.

4. DISCUSSION AND CONCLUSIONS

This review is brief and preliminary in nature, and in it we do not attempt a comprehensive evaluation of salmon supplementation. A number of important considerations are outside the scope of this study. For example, we did not do the following:

1. provide detailed discussion of individual programs or detailed analysis of the factors believed to be responsible for the degree of success in attaining each objective;
2. analyze information on a number of important population attributes that might be affected by supplementation, such as genetic and life-history traits and spawning distribution;
3. evaluate program performance as a function of differences in culture techniques (e.g., mating, rearing, and release strategies);
4. evaluate program performance with respect to specific goals of the program.

Each of these factors is important and could form the basis of one or more subsequent reports.

Instead, in this paper we have focused on meta-analysis of empirical data for several performance criteria that should be associated with successful supplementation programs. Results summarized above and in Tables 3 and 4 make it clear that there is a major dichotomy in the degree to which supplementation programs have achieved their objectives. In terms of the ability to boost overall numbers of fish, many of the programs have been relatively successful. Examples of this type of success include high survivals of both broodstock and offspring in captivity and increases in the number of returning hatchery adults compared to the wild population. Many supplementation programs, therefore,

Table 4. Summary of program performance with respect to hierarchical objectives. Data shown are numbers of programs listed in Appendix 1 and falling into each category. Unc. = uncertain; H = hatchery; W = wild; N_t = number at completion of study; N_o = number at initiation of study

Objective	Criterion	Was objective met?[1] Yes	No	Uncertain
Broodstock collection				
Representativeness				
Run timing	Similar to wild	11	3	8
Age	Similar to wild	10	2	10
Integrity	<5% non-native	17	5	–
Survival in culture				
Prespawning survival	>90%	12	6	4
Egg-to-smolt survival	>70%	19	2	1
Adult-to-adult survival	>2.0 in hatchery or > 2.0 H:W ratio	12	4	6
Reproductive success in the wild	Comparable to wild fish	1	2	19
Population increase	$N_t > 120\% N_0$	8	11	3
Viability of natural population	Population stable at higher level after supplementation	–	2	20

[1] Data shown are numbers of programs falling into each category.

have achieved a measure of success in the aspects of fish culture traditionally associated with salmon hatcheries.

Producing fish, however, is only the first step in a successful supplementation program; it is also necessary that fish produced by the program and their progeny contribute to productivity of the natural population in future generations. From this perspective, the success of salmon supplementation cannot be evaluated because there are essentially no data (Table 4 and Appendix 1). To date, only a few studies have evaluated the performance of hatchery fish and their progeny in the natural environment. Theoretical considerations lead to the conclusion that cultured fish should have reduced fitness in the wild, and the experimental data that are available (e.g., Reisenbichler and McIntyre, 1977; Fleming and Gross, 1993; Reisenbichler and Rubin, 1999; Hindar and Fleming, 2007) support this premise. However, some of these experimental studies confound the effects of domestication with the effects of stock transfers, making it difficult to make predictions about supplementation programs using locally derived broodstock (as considered in this report). The key question to resolve in evaluating long-term benefits of salmon supplementation is whether the demographic boost provided by the hatchery more than offsets reduced fitness in the wild of hatchery-produced fish and their progeny. This can best be evaluated by empirical studies in the natural environment, which have not yet been conducted rigorously for any supplementation program for which we have information.

Two major conclusions emerge from this preliminary evaluation of salmon supplementation. First, the premise that supplementation can be used to provide a net long-term benefit to natural populations remains an untested hypothesis. We, like Miller et al. (1990), have not found any examples in which salmon supplementation has been used to help a natural population become self-sustaining. This does not mean that supplementation cannot provide this type of benefit; most supplementation programs have not been terminated yet, which makes it difficult to evaluate sustainability of the natural population. Furthermore, supplementation alone cannot be expected to result in a viable population if the factors responsible for the original decline have not been remedied. However, the fact that one of the ultimate goals of salmon supplementation has never been empirically demonstrated should serve as a cautionary note to those considering initiating new programs or continuing existing ones.

Second, results presented here make it clear that the biggest gap in our knowledge about supplementation relates to the performance of hatchery-produced fish and their progeny in the natural environment. More research is critically needed in this area. Ideally, such evaluations should be conducted over a number of generations to permit distinguishing between ecological and genetic effects of fish culture and to evaluate the effectiveness of natural selection to restore fitness in a natural population of mixed hatchery-wild ancestry. Gathering this type of information is challenging but feasible using highly polymorphic molecular genetic markers that allow fine-scale resolution of reproductive success in the wild. Parallel studies designed to identify the ecological, behavioral, and physiological factors responsible for fitness of hatchery fish in nature could suggest ways to make supplementation more successful in the long term.

These considerations also suggest some basic recommendations regarding supplementation:

1. Because of the largely unproven track record with respect to key objectives, salmon supplementation should be considered experimental. The appropriate use should be determined only after a comprehensive risk–benefit analysis that considers details specific to the target population and the proposed program as well as more general issues associated with supplementation.
2. When supplementation is used, comparable unsupplemented populations should be included as controls, and performance of both treatment and control populations should be measured with a rigorous monitoring and evaluation program. Doing this would ensure that valuable research and adaptive management information is compiled during the course of these "experiments."

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Appendix 1. Summary data for 22 supplementation programs. Primary sources for the program data are listed below the data table

	Program[1]																						
Questions/reply choices	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total
Was broodstock collected from target population?																							
a) Yes		X	X	X				X		X	X	X	X	X	X	X	X	X	X	X	X	X	17
b) Yes, but other populations unintentionally collected also	X				X	X	X		X														5
c) No																							0
d) No data																							0
Was broodstock collection representative of target population?																							
Across run time																							
a) Yes (demonstrated)							X				X		X					X					4
b) Yes (assumed/estimated)	X			X				X		X		X			X							X	7
c) No (demonstrated)																			X		X		2
d) No (assumed/estimated)			X																				1
e) No data		X			X	X			X					X		X	X			X			8
Across age structure																							
a) Yes (demonstrated)							X			X	X									X			4
b) Yes (assumed/estimated)				X				X				X	X					X			X		6
c) No (demonstrated)															X								1
d) No (assumed/estimated)			X																				1
e) No data	X	X			X	X			X					X		X	X		X			X	10
Prespawning survival of collected adults																							
a) Greater than 90%				X	X	X	X	X		X			X	X			X	X			X	X	12
b) 80–90%	X								X		X	X			X	X							6
c) 70–80%																							0
d) Less than 70%																							0
e) No data		X	X																X	X			4

Egg-to-release survival of juveniles inhatchery																						
a) Greater than 90%							X															1
b) 80–90%	X		X	X		X		X	X			X		X		X	X		X	X		12
c) 70–80%					X					X	X		X		X						X	6
d) Less than 70%																		X^{2}				X	2
e) No data		X																					1
Adult-to-adult survival of hatchery fish																						
a) Greater than 5X	X															X		X^{3}		X	X^{3}		5
b) 2–5X			X	X							X	X			X								5
c) 1–2X								X														X	2
d) About equal							X																1
e) Less than 1X						X				X													2
f) No data		X			X				X				X	X			X		X				7
Adult-to-adult survival compared to wild																						
a) Greater than 5X, data available				X		X						X				X				X			5
b) Assumed greater than 5X, but no data available for wild																					X		1
c) Greater than 2X, data available	X										X				X								3
d) Assumed greater than 2X, but no data available for wild			X															X				X	3
e) About equal to wild, data available								X					X										2
f) Assumed to be about equal to wild, but no data for wild										X													1
g) Worse than wild, data available																							0
h) Assumed worse than wild, but no data for wild																							
i) No data for hatchery population		X			X		X		X					X			X		X				7

(*Continued*)

Appendix 1. Summary data for 22 supplementation programs. Primary sources for the program data are listed below the data table—cont'd.

	Program[1]																						
Questions/reply choices	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total
Relative success of naturally spawning program fish compared to natural fish																							
a) Greater than wild fish, data available																							0
b) Assumed greater, but no data available for wild																							0
c) About equal to wild fish, data available																						X[6]	1
d) Assumed about equal to wild, but no data for wild																							0
e) Worse than wild fish, data available											X[5]	X[5]											2
f) Assumed worse than wild fish, but no data for wild																							0
g) No data	X	X	X	X	X[4]	X	X	X	X	X			X	X	X	X	X	X	X	X	X		19
Survival of the progeny of naturally spawning program fish compared to the progeny of natural fish																							
a) Greater than wild fish, data available																							0
b) Assumed greater, but no data available for wild																							0
c) About equal to wild fish, data available											X[7]												1
d) Assumed about equal to wild, but no data for wild																							0
e) Worse than wild fish, data available																							0
f) Assumed worse than wild fish, but no data for wild																							0
g) No data	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	21
Did the natural population increase over course of program?																							
a) Population increased >20%			X					X	X						X		X	X	X	X			8
b) Population size remained same + /−20%					X																		1
c) Population declined >20%	X	X		X		X	X			X	X	X	X								X		10
d) No data														X		X						X	3
If an unsupplemented control was monitored, did it increase?																							
a) Population increased >20%																	X						1
b) Population size remained same + /−20%	X														X								2
c) Population declined >20%							X			X	X		X					X					5
d) No data		X	X	X	X	X		X	X			X		X		X			X	X	X	X	14

Status of the natural population before supplementation started																						
a) Healthy								X														1
b) Depressed but not at serious risk					X						X	X						X	X	X	X	X	8
c) Unhealthy; some extinction concern		X	X	X					X	X			X	X	X	X	X						10
d) High risk of extinction	X					X	X																3
Status of the natural population after supplementation ceased																						
a) Increasing																							0
b) Stable, at higher abundance than before supplementation																							0
c) Stable, no significant change compared to before supplementation																							0
d) Stable, at lower abundance than before supplementation										X[8]													1
e) Decreasing		X																					1
f) Population is still being supplemented	X		X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	20

[1] Program numbers are as in Table 1.
[2] Last 4 years all >90%.
[3] Estimate is based on a single brood-year.
[4] Size and egg voidance similar.
[5] Hatchery fish returned younger and/or smaller.
[6] Based on fecundity only.
[7] Similar spawner-recruit relationship at various levels of naturally spawning hatchery fish.
[8] Abundance critically low.

Primary sources of information for these programs were as follows (program numbers are as above and in Table 1):

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SECTION FOUR

POSITIVE APPROACHES TO ENVIRONMENTALLY SUSTAINABLE AQUACULTURE

CHAPTER 22

MACROBENTHOS AS BIOLOGICAL INDICATORS TO ASSESS THE INFLUENCE OF AQUACULTURE ON JAPANESE COASTAL ENVIRONMENTS

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Abstract: To delineate patterns in the gradients of macrobenthic communities around fish farms and to generate site-selection guidelines for sustainable fish farms, a quantitative survey was conducted in August–September 1998 and in February 1999 in fish-farming areas along the coast of Kumano-nada, central Japan. The biomass peaked in sediments containing 1.2 mg/g of total nitrogen or 9.2 mg/g of total organic carbon, suggesting that these values are indicative of possible aerobic mineralization of the loaded organic wastes. Macrobenthos was scarcely found in sediments with acid-volatile sulfides (AVS) >1.9 mg S/g, which suggests critical AVS conditions for maintaining sustainable and environmentally "friendly" aquaculture. An index, "ED," which serves as an index for bathymetry of the sampling site, was devised. ED was highly correlated with four community parameters (biomass, density, species diversity, and species richness) and with five environmental factors (sediment total nitrogen, total organic carbon, total phosphorus and acid-volatile sulfides, and bottom-water dissolved oxygen). Compared with small-scale farms, environmental deterioration and decline in macrofauna were obvious in large-scale farms (≥600 t/yr of fish production) that were located in inner parts of embayments and that had comparatively high ED values. However, in areas near open waters and that had comparatively low ED values, the impacts of aquacultural activities were not clear. These findings suggest that the variation in macrobenthos and environmental factors found in the study area was attributable principally to the area's bathymetry and, secondly, to aquacultural activities. Seven assemblages, recognized on the basis of cluster analysis, were placed in a gradient of ED versus fish production. These assemblages were classified into three groups: a group characteristic of a healthy zone, a group characteristic of a cautionary zone, and a group characteristic of

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a critical zone. As fish production increased, the location of the assemblage characteristic of the cautionary zone shifted to more open, deeper areas (lower ED values). An azoic-site group was composed of large-scale farms in a stagnant basin. The community type of the macrobenthos in the vicinity of open-water, net-pen fish farms is an indicator of the condition and assimilative capacity of the benthic environment in that area and can be used to evaluate the suitability of the site for continued fish farming. The index of embayment degree, ED, can be used as a simple and effective substitute indicator for this evaluation.

Key words: aquaculture, assimilative capacity, bathymetry, bio-indicator, criteria, fish farm, macrobenthos, sulfide

1. INTRODUCTION

Over the last four decades, marine cultivation of fish has become a well-established industry in Japan. The present output from marine fish farming accounts for 30% of the total value of coastal fishery production. Intensive fish farming, however, often results in adverse effects on both the fish farm itself and the ecosystem beneath and around the fish farm through changes such as deoxygenation (Hirata et al., 1994), outgassing of hydrogen sulfide (Tsutsumi, 1995), and blooms of harmful plankton (Nishimura, 1982). Clear evaluation and minimization of the impacts of fish farming are necessary from standpoints of fish-farm management and conservation of natural resources.

The macrobenthos community has often been used as a sensitive indicator for environmental monitoring of organically polluted areas (reviewed by Pearson and Rosenberg, 1978). Assessments using macrobenthos as a bio-indicator have also been conducted at fish farms in Finland (Laurén-Määttä et al., 1991), Scotland (Brown et al., 1987), North America (Weston, 1990; Findlay et al., 1995), Australia (Ritz et al., 1989), China (Wu et al., 1994), and Japan (Tsutsumi, 1995; Sasaki and Oshino, 1997; Yokoyama, 2002). These studies showed that a reduction in species richness and/or species diversity; a decrease in the number of large-sized species; the disappearance of echinoderms; and the appearance of dense populations of the opportunistic polychaete *Capitella* species complex (especially species I), which often results in an increase in total macrofaunal abundance, are typical effects of mariculture farming on the macrobenthos. However, each of these surveys was confined to one or a few fish farms. We conducted a quantitative survey of the macrobenthos in 22 fish farms distributed in ten bays along the coast of Kumano-nada, central Japan. The preliminary results have been reported elsewhere (Yokoyama et al., 2002a, b; Yokoyama, 2003). In this paper, we describe abiotic and biotic components of the fish-farm environment in a gradient of bathymetry, assess the possible effects of aquacultural activities on these components, and suggest site-selection guidelines for sustainable fish farming.

2. MATERIALS AND METHODS

2.1. Study Area

The Japanese coast from the Shima Peninsula to the Kumano district (Kumano-nada) in Mie Prefecture, central Japan, consists of many small bays of varying underwater bathymetries; many of these bays contain densely distributed fish farms (Figure 1). In this area, fish farming has developed steadily since the introduction of yellowtail (*Seriola quinqueradiata*) culture in the early 1960s. Since the middle of the 1970s, a total of 15,000–20,000 metric tons (t) of fish, composed mainly of red sea bream (*Pagrus major*) and yellowtail, have been annually produced. In this area are 34 fish farms of all sizes; their fish production ranged from 41 to 1507 t in 1998 (Tokai Regional Agricultural Administration Office, 1999). Each is managed by a cooperative association.

In Kumano-nada, the inflow of fresh water is small. Thus, the coastal embayments have high salinities (>32) over the seabed throughout the year—even in Owase Bay, where freshwater inflow is substantial (average flow rate: $40–80\,\mathrm{m}^3/\mathrm{s}$) (Mie Prefectural Science and Technology Promotion Center, unpublished data). In the Kumano district, the river basins are thinly populated ($65{,}000$ people/$690\,\mathrm{km}^2$), and industries other than fisheries and aquaculture have not yet developed. Thus, the input of organic matter originating from sewage and industrial wastes into the coastal waters is small. For instance, total organic input from sewage, industry, and cattle-breeding into Gokasho Bay (Figure 1A) accounts for only 10% of the total organic input into the bay and organic input from woodlands accounts for only 20%, whereas input from fish farming accounts for 70% (Mie Prefectural Government, unpublished data). Most particulate organic wastes from aquaculture are deposited on the seabed at distances of <150 m from the fish cages (Hevia et al., 1996; Pawar et al., 2001). In fish-farming areas, therefore, organic input from aquaculture comprises most of the total organic matter deposited on the seabed.

2.2. Sampling and Data Analysis

We conducted a survey of the benthic epifauna and infauna at 22 fish farms distributed throughout ten bays in the coastal waters of Kumano-nada (Figure 1) from August 24 through September 4, 1998 and from February 17 through 25, 1999. Samples of the macrobenthos were collected from 51 stations located near fish cages (<10 m from the edge of each fish cage) using a 0.04-m^2 Ekman grab and a 1-mm-mesh sieve. The collected animals were identified; the number of individuals of each species and the number of species per grab were counted; and the biomass of each species (wet weight, excluding shell weight) was recorded to the nearest 1 mg after blotting the individual with filter paper. To evaluate species diversity, H' (the Shannon–Weaver function), $H'_{\max}$ (the species richness index, expressed as $\log_2 S$, where S is the number of species),

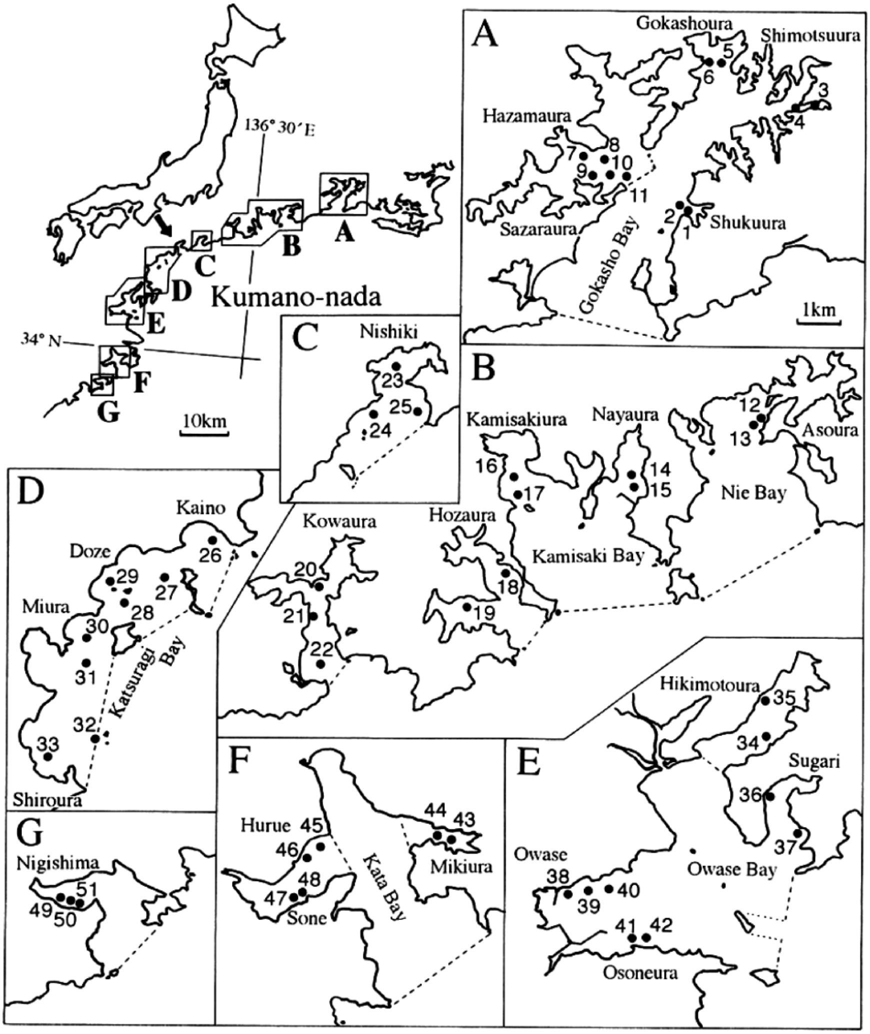

Figure 1. Map of the coast of Kumano-nada, Japan showing the study areas (A–G) and the sampling stations (1–51) for an investigation of the gradient in macrobenthic community structure and chemical factors beneath fish farms. Broken lines indicate the width of the bay mouth or the inlet mouth, which was used for the calculation of the index of embayment degree ED (see text)

and J' (the species evenness index) were calculated on the basis of the number of species and the abundance of each species. Species diversity has components of species richness and evenness; this relationship is expressed as $H' = H'_{\max} \times J'$ (Pielou, 1969). Kimoto's similarity index, $C\pi$ (Kimoto, 1967), and cluster analysis (Mountford, 1962) based on the abundance data were used to identify distinct macrofaunal assemblages in the study area.

For analysis of total nitrogen (TN), total organic carbon (TOC), total phosphorus (TP), and acid-volatile sulfides (AVS), sediment samples of the upper 1-cm layer were obtained by a corer attached to the inside wall of the Ekman grab (Yokoyama and Ueda, 1997). The water just above the sediment surface was also obtained by this corer for analysis of dissolved oxygen (DO). Relationships between the macrofauna and environmental factors were analyzed mainly on the basis of the data obtained from the summer survey because negative effects of environmental deterioration on the macrofauna have often been found in this season. Four stations were azoic in summer. To enable us to include them in analyses involving logarithmic transformations, we assumed that biomass, density, and number of species were, respectively, $0.001\,\mathrm{g/m^2}$, 10 individuals $/\mathrm{m}^2$, and 0.1 species/$0.04\,\mathrm{m}^2$. These values are considerably smaller than those from other stations (minimum values by actual measurement: biomass $= 0.005\,\mathrm{g/m^2}$, density $= 75$ individuals/m^2, number of species $= 1$ species/$0.04\,\mathrm{m}^2$).

As an additional abiotic environmental component, an index of the embayment degree, ED, was devised. The index, which is based on bathymetric conditions, including water depth, is expressed by the following equation:

$$\mathrm{ED} = (L/W)(20/Ds)(45/Dm),$$

where L is the shortest distance (km) from the bay mouth to the sampling station or to the mouth of the inlet in which the sampling site is located, W is the width (km) of the bay mouth, Ds is the water depth (m) at the sampling station or, if present, the depth of any sill which exists between the sampling station and the bay mouth, Dm is the maximum depth at the bay mouth, 20 is the mean depth (m) of all the sampling stations, and 45 is the mean depth (m) of the bay mouths in the study area. When the fish farm is located in an inlet in which the inlet axis crosses the axis of the main bay at an angle of $< 90^\circ$, ED is expressed by the following equation:

$$\mathrm{ED} = (L_1/W_1 + L_2/W_2)(20/Ds)(45/Dm),$$

where L_1 is the shortest distance from the bay mouth to the inlet mouth, W_1 is the width of the bay mouth, L_2 is the shortest distance from the inlet mouth to the sampling site, and W_2 is the width of the inlet mouth (all in km).

As an indicator of the level of aquacultural activity, we used annual fish production of each fish farm, obtained from statistical data collected by the Tokai Regional Agricultural Administration Office (1999).

3. RESULTS AND DISCUSSION

3.1. Relationship between Biotic and Abiotic Factors

Table 1 shows relationships between community parameters of the macrobenthos and environmental factors on the basis of the summer data. There were significant negative relationships between all community parameters other

Table 1. Correlational relationships between environmental factors and community parameters of the macrobenthos in coastal embayments of Kumano-nada, Japan, August–September 1998. TN = total nitrogen; TOC = total organic carbon; TP = total phosphorus; AVS = sediment acid-volatile sulfide; DO = dissolved oxygen; H' = Shannon–Weaver index of species diversity; H'_{max} = index of species richness; J' = index of species evenness.* = $P < 0.05$; ** = $P < 0.001$

	Environmental factors				
Community parameters	TN	TOC	TP	AVS	DO
Biomass[1]	−0.718**	−0.703*	−0.797*	−0.815**	0.821**
Density[1]	−0.778**	−0.773**	−0.766*	−0.807**	0.803**
H'	−0.499**	−0.488**	−0.499**	−0.722**	0.415*
H'_{max}	−0.565**	−0.589**	−0.454**	−0.811**	0.593**
J'	−0.148	−0.098	−0.299*	−0.275	−0.029

[1] Values transformed into logarithms.

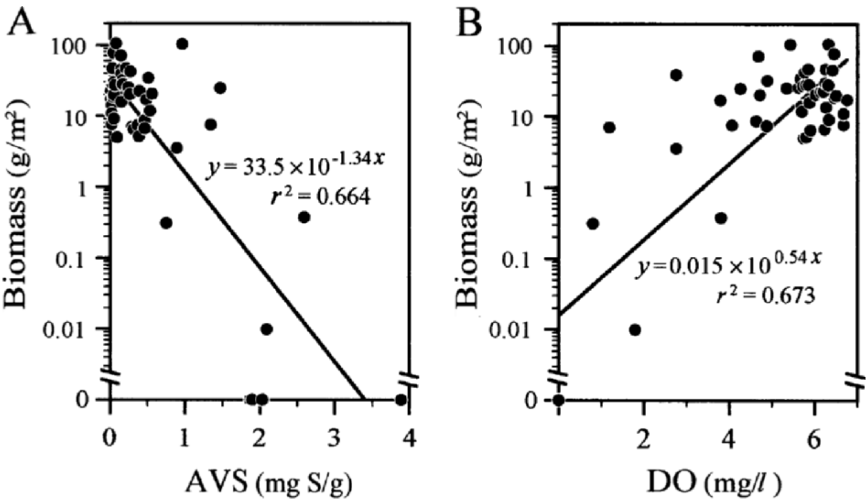

Figure 2. Relationships between macrobenthos biomass and abiotic components of the benthic environment. A. Acid-volatile sulfides (AVS) in the sediment. B. Dissolved oxygen (DO) of the bottom water

than J' (i.e., biomass, density, H', and H'_{max}) and all sediment parameters (total nitrogen, total organic carbon, total phosphorus and acid-volatile sediment). In contrast, significant positive relationships were found between all community parameters except J' and DO of the bottom water. Critical content limits of AVS and DO, as defined by macrobenthos biomass of $< 0.1\ g/m^2$ and as estimated by regression lines imposed on the data, were, respectively, 1.9 mg S/g of sediment and 1.5 mg O/l of water (Figure 2).

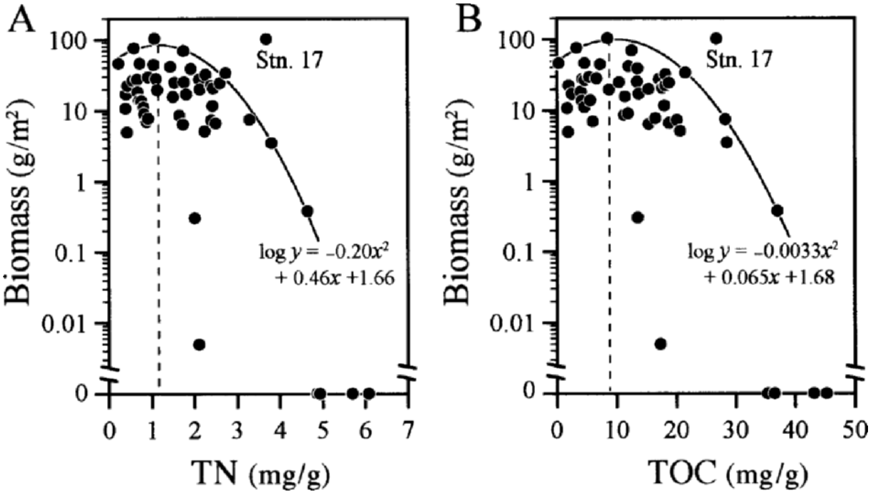

Figure 3. Relationships between macrobenthos biomass and total nitrogen (TN; A) or total organic carbon (TOC; B) in the vicinity of open-water, net-pen fish farms

Figure 3A shows the relationship between biomass and TN. The curve obtained by plotting the maximum values of biomass except the value at Stn. 17, where the carnivorous gastropod *Ergalatax contractus* aggregated in exceptionally high densities, has a peak at 1.2 mg TN/g. In areas with <1.2 mg TN/g, the loaded organic matter did not seem to affect biomass. In areas with ≥1.2 mg TN/g, however, the negative correlation between TN and biomass was highly significant ($r = -0.756$, $n = 30$, $P < 0.001$), suggesting negative effects on the macrobenthos. Thus, the presence of 1.2 mg TN/g or more in the sediment suggests that the allowable input of organic matter has been exceeded. A similar pattern was also found between biomass and TOC in the sediment (Figure 3B). Sediments with ≥9.2 mg TOC/g were negatively correlated with biomass ($r = -0.742$, $n = 32$, $P < 0.001$) whereas sediments with <9.2 mg TOC/g seemed to have no negative effects on macrobenthos biomass, suggesting that 9.2 mg TOC/g is indicative of possible aerobic mineralization of the loaded organic wastes. Near azoic conditions were found in extremely enriched sediments, that had >4 mg TN/g of sediment or >30 mg TOC/g, suggesting that these values are indicative of critical conditions for sustainable aquaculture.

3.2. "ED" as an Index for Site Selection Guidelines

The values in summer for the macrobenthos community parameters and the environmental factors were tested for correlation with aquacultural activities, expressed as fish production, and bathymetric conditions, expressed as ED

Table 2. Correlational relationships between fish production or the index of embayment degree (ED) and benthic or epibenthic components of the fish-farm environment. H' =Shannon–Weaver index of species diversity; $H'_{\max}$ = index of species richness; J' = index of evenness; TN = total nitrogen; TOC = total organic carbon; TP = total phosphorus; AVS = sediment acid-volatile sulfide; DO = dissolved oxygen; * = $P < 0.05$;** = $P < 0.001$

Benthic components	Fish production	ED
Biotic community parameters		
Biomass[1]	−0.353*	−0.727**
Density[1]	−0.326*	−0.797**
H'	0.141	−0.566**
$H'_{\max}$	0.172	−0.827**
J'	0.025	0.129
Environmental factors		
TN	0.287*	0.691**
TOC	0.225	0.695**
TP	0.409*	0.568**
AVS	0.258	0.752**
DO	−0.379*	−0.743**

[1] Values transformed into logarithms.

(Table 2). Fish production was positively correlated with TN and TP and negatively correlated with biomass, density, and DO; ED was highly and negatively correlated with all community parameters except J' and was positively correlated with all environmental factors.

It may be that the influence of fish production is site-specific. At fish farms located in more open, deeper areas (those with ED values <2), environments were not noticeably deteriorated, even in summer, and regardless of fish-production levels. For instance, at most of the stations in these areas, sediment enrichment levels were low. At most stations, TN was <3 mg/g of sediment, TOC was <20 mg/g, TP was <4 mg/g, AVS was <0.6 mg S/g, and DO was >5 mg/l of water (Figure 4A–E). The good quality of the benthic environment and an enhanced food supply from fish cages probably resulted in large biomasses ($> 10\,\mathrm{g/m^2}$, Figure 4F), high densities of individuals ($> 2000/\mathrm{m^2}$, Figure 4G), and large numbers of species (> 30 species/$0.04\,\mathrm{m^2}$, Figure 4H) in the macrobenthos in these areas. In contrast, levels of organic pollution, as characterized by enriched and reduced sediments (high levels of TN, TOC, TP, and AVS; Figure 4A–D), deoxygenation of the bottom water (Figure 4E), and impoverished macrofauna (Figure 4), increased progressively with movement toward fish farms located in inner, shallower, more sheltered areas that had high ED values. This tendency was more evident in large-scale farms (>600 t/yr) than in small-scale farms (<600 t/yr). In each comparison of an environmental factor or community parameter versus ED, the two regression slopes were significantly different (see Figure 4A–E for regression lines and Table 3 for regression equations, regression coefficients, and significance levels).

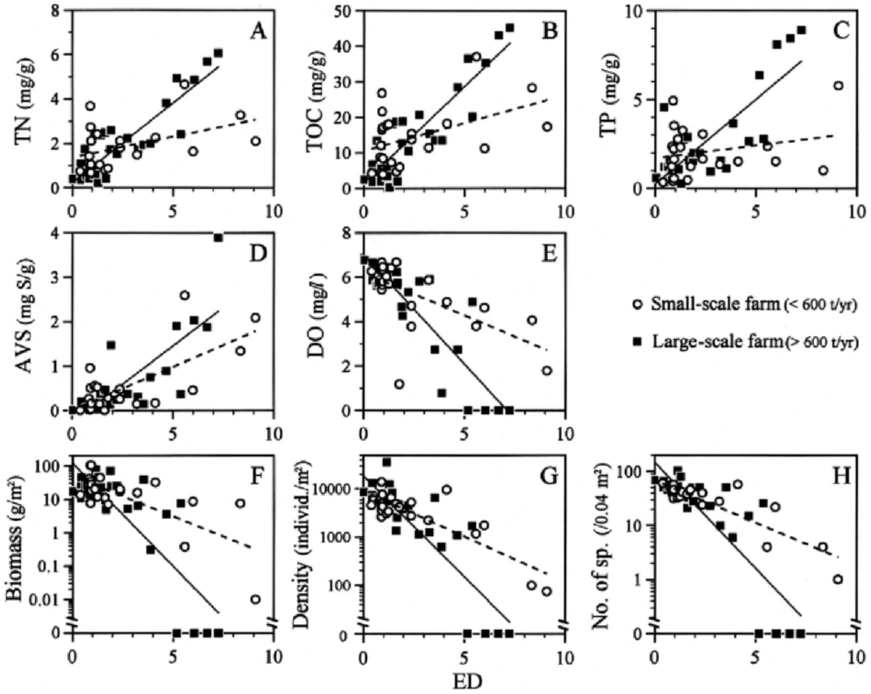

Figure 4. Relationships between abiotic or biotic components of the benthic environment and the embayment degree (ED) in summer. Broken lines: regression lines based on data obtained from small-scale farms, where fish production was <600 t/yr (open circles). Solid lines: regression lines based on data obtained from large-scale farms, where fish production was ≥600 t/yr (solid squares). Regression equations and coefficients are provided in Table 3. A. Total nitrogen (TN) in the sediment. B. Total organic carbon (TOC) in the sediment. C. Total phosphorus (TP) in the sediment. D. Acid-volatile sulfides (AVS) in the sediments. E. Dissolved oxygen (DO) of the bottom water. F. Macrobenthos biomass. G. Macrobenthos density. H. Number of species (spp.) in the macrobenthos

Organic input from fish farming exceeds that from other sources in the study area. Therefore, it seems that aquacultural activities are also influencing the benthic environments, habitats, and communities in this area.

3.3. Suitable Siting Based on Macrofauna

Figure 5 shows the dendrogram of the sampling stations as defined by species composition of the macrobenthos in summer. Six station assemblages (I–VI), identified by their species similarities and distinguished from each other by a similarity index (Cπ) of ≥0.4, are defined. They are characterized principally by their predominant polychaete species (Table 4). In addition to these station groups, the four stations that were azoic in summer were also regarded as one cluster (VII).

Table 3. Effects of ED (x) on benthic components (y) in small-scale aquaculture farms ($n = 23$) and large-scale aquaculture farms ($n = 28$). Regression equations and regression coefficients (r^2) for each graph appear in Figure 4, and significance (P) levels for differences between the slopes of the two regression lines are presented

	Small-scale farm		Large-scale farm		
Benthic components	Regression equation	r^2	Regression equation	r^2	P level
Total nitrogen	$y = 0.186x + 1.37$	0.20	$y = 0.719x + 0.228$	0.81	<0.001
Total organic carbon	$y = 1.58x + 10.5$	0.21	$y = 5.44x + 1.60$	0.80	<0.001
Total phosphorus	$y = 0.139x + 1.71$	0.06	$y = 0.952x + 0.255$	0.65	<0.001
Dissolved oxygen	$y = -0.382x + 6.19$	0.41	$y = -0.980x + 6.99$	0.77	<0.001
Acid-volatile sulfide	$y = 0.196x + 0.01$	0.52	$y = 0.346x - 0.271$	0.65	<0.05
Biomass	$y = 51.6 \times 10^{-0.256x}$	0.52	$y = 122 \times 10^{-0.619x}$	0.69	<0.001
Density	$y = 8950 \times 10^{-0.188x}$	0.74	$y = 18600 \times 10^{-0.418x}$	0.75	<0.001
Number of species	$y = 68.5 \times 10^{-0.157x}$	0.77	$y = 147 \times 10^{-0.392x}$	0.73	<0.001

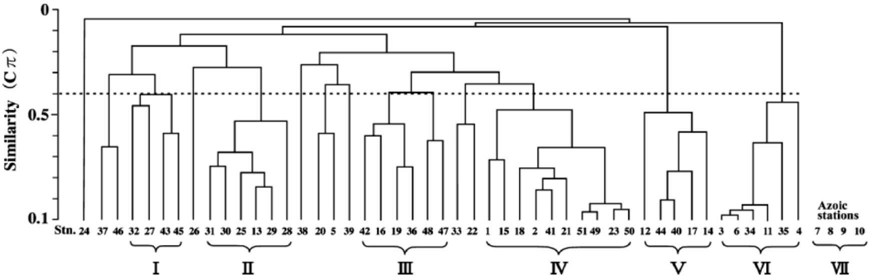

Figure 5. Cluster analysis of the macrobenthos collected in summer from 51 stations in Kumano-nada, Japan. Six clusters (I–VI) are defined based on a similarity-index value of <0.4 (dotted line). Four azoic stations (cluster VII) were also grouped together

Figure 6 shows biotic and abiotic characteristics for each of these seven station groups. In summer, assemblages I to V had mean biomass values of 14–37 g/m^2, mean densities of 4200–7100 individuals/m^2, and relatively high mean species diversity (H') values of 3.1 to 4.7. In contrast, assemblage VI is characterized by an impoverished fauna in summer (mean biomass = 3.7 g/m^2, mean density = 75 individuals/m^2, mean $H' = 1.7$); at that time, values of biomass, density, and species diversity differed significantly from those of assemblages I–IV ($P < 0.05$, Mann–Whitney U-test). Also, assemblage VI is characterized by the predominance of *Prionospio pulchra* (Table 4), which is known as the last surviving species in hypoxic Japanese coastal waters (Kuwahara and Shimizu, 1989; Yokoyama, 2002).

Biomasses and densities in the seven station groups increased in winter. In particular, the highest densities were found at the stations that were azoic in summer (assemblage VII), mainly due to the dense colonization of *Capitella*

Table 4. Densities (N, as numbers of individuals/m^2) and biomasses (W, as g wet weight, excluding shell weight, per m^2) of the two most common species in seven macrobenthos assemblages (I–VII) defined through cluster analyses (see Figure 5). Percentages of the total density and total biomass of the macrobenthos are shown in parentheses. Asm = assemblage

	August–September 1998					February 1999				
Asm.	Species[1]	N		W		Species	N		W	
I	*Prionospio paradisea*	875	(14.7)	3.8	(19.2)	*Polydora flava orientalis*	1,690	(17.5)	2.0	(7.4)
	Cerapus tubularis	681	(11.5)	0.3	(1.3)	Unidentified Maldanidae	994	(10.3)	1.4	(5.1)
II	*Chaetozone* sp. A	1,420	(33.4)	2.8	(20.5)	*Caprella californica*	3,380	(17.5)	5.7	(9.1)
	Chaetozone sp. B	246	(5.8)	0.3	(2.4)	*Polydora flava orientalis*	2,510	(13.0)	3.5	(5.6)
III	*Paradoneis* sp.	733	(15.9)	2.9	(7.8)	*Capitella* spp.	3,730	(36.6)	5.8	(19.1)
	Petrasma pusilla	421	(9.1)	2.6	(7.0)	*Schistomeringos* sp.	2,380	(23.4)	6.3	(20.9)
IV	*Schistomeringos* sp.	3,980	(56.4)	6.0	(17.0)	*Schistomeringos* sp.	3,750	(41.4)	7.5	(18.8)
	Nebalia bipes	400	(5.7)	0.6	(1.7)	*Capitella* spp.	665	(7.3)	0.4	(0.9)
V	*Scoletoma longifolia*	1,930	(34.7)	17.2	(50.8)	*Scoletoma longifolia*	1,300	(17.2)	6.4	(17.2)
	Prionospio depauperata	385	(6.9)	0.6	(1.7)	*Schistomeringos* sp.	505	(6.7)	0.9	(2.0)
VI	*Prionospio pulchra*	492	(59.3)	0.1	(3.4)	*Capitella* spp.	2,600	(41.3)	3.8	(22.1)
	Prionospio krusadensis	33	(4.0)	<0.1	(0.3)	*Schistomeringos* sp.	900	(14.3)	1.1	(6.5)
VII	Azoic					*Capitella* spp.	16,100	(65.9)	21.7	(57.3)
						Caprella californica	3,440	(14.1)	7.8	(20.6)

[1] The first species listed for each assemblage is the predominant polychaete in that assemblage.

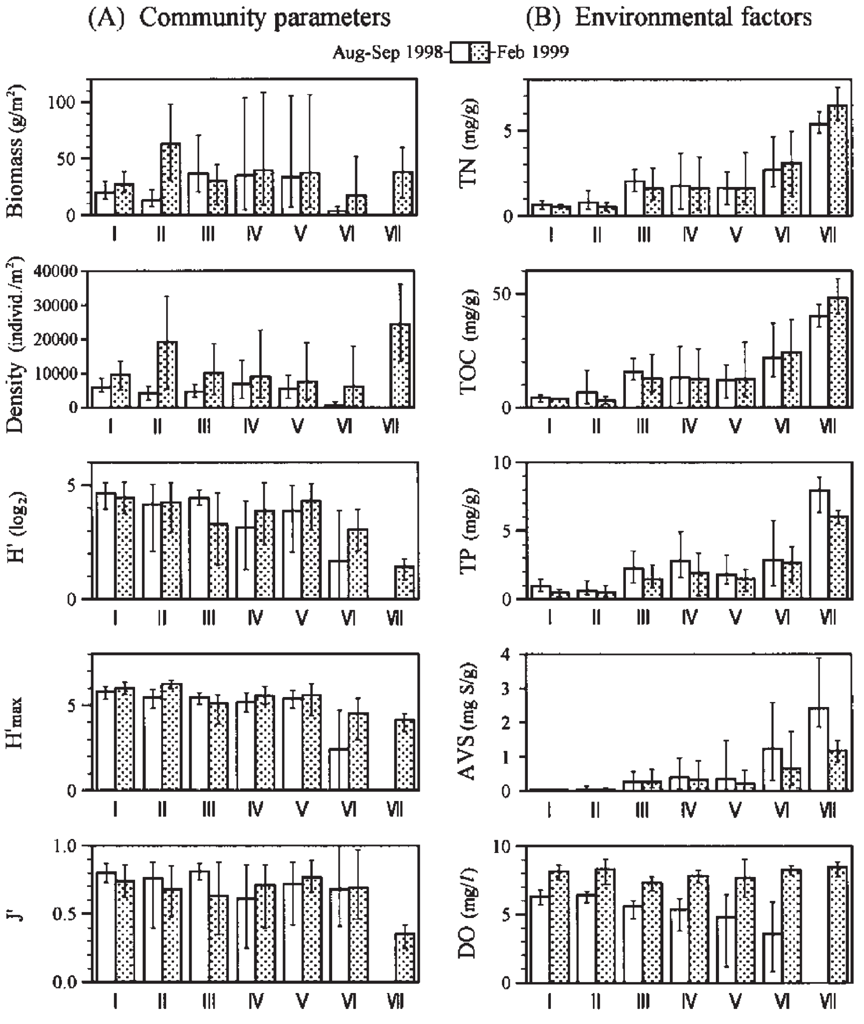

Figure 6. Biotic and abiotic factors in seven macrobenthos assemblages (I–VII). A. Community parameters of the macrobenthos. H' = Shannon–Weaver index of species diversity; $H'_{\max}$ = index of species richness; J' = index of species evenness. B. Environmental factors. TN = total nitrogen; TOC = total organic carbon; TP = total phosphorus; DO = bottom-water dissolved oxygen; AVS = sediment acid-volatile sulfide. White bars = samples collected August–September 1998; shaded bars = samples collected February 1999. Vertical lines represent the ranges of values

sp. I, which is known as a short-lived, typically opportunistic polychaete species adapted to unpredictable environments by virtue of its ability to reproduce rapidly (Grassle, 1980). The stations in assemblage VII were characterized by an overwhelming predominance of *Capitella* spp. in winter (mean values: 16,100 individuals/m^2 and 21.7 g/m^2); in that assemblage, *Capitella* spp. constituted a high percentage of the total macrofauna (65.9% of the abundance and 57.3% of the biomass, respectively). In winter, this species was also among the most common species in assemblages III, IV, and VI (Table 4). However, in these assemblages, mean density and mean biomass of this species were only 665–3730 individuals/m^2 and 0.4–5.8 g/m^2, which respectively comprised 7.3–41.3% of their total densities and 0.9–22.1% of their total macrobenthos biomasses. Thus, in assemblage VII, both J' (mean = 0.35, range = 0.25–0.41), and H' (mean = 1.5, range = 0.9–1.8) were low and significantly different from those values for assemblages I, II, and IV–VI ($P < 0.05$, Mann–Whitney *U*-test).

The values of our measured environmental factors in the habitats of assemblage VII indicate that those environments were conspicuous deteriorated (Figure 6B). Levels of sediment enrichment were very high; TN, TOC, and TP values respectively averaged 5.9, 44, and 7.0 mg/g (respective ranges: 4.9–7.5, 35–57, and 5.5–8.9). In summer, the bottom water became anoxic and large amounts of sulfides were produced in the sediment (summer AVS; mean = 2.4 mg S/g, range = 1.9–3.9). Although in winter, the amounts of sulfides were reduced by approximately one-half at the stations in assemblage VII (mean = 1.2 mg S/g, range = 0.9–1.5), AVS values were still higher at these stations than at those in other assemblages (means ranged 0.02–0.7 mg S/g).

Environmental deterioration in the habitats of assemblage VI was not as conspicuous as that in the habitats of assemblage VII. In assemblage VI, mean TN (2.9 mg/g of dry sediment, range = 1.2–4.9), TOC (23 mg/g, range = 8–39), TP (2.8 mg/g, range = 1.0–5.8), summer AVS (1.2 mg S/g, range = 0.3–2.6), and summer DO (3.5 mg/l, range = 0.8–5.9) were intermediate between values for other assemblages and assemblage VII. In the habitats of assemblages I–V, levels of sediment enrichment were relatively low (range in mean values: 0.5–2.0 mg TN/g, 3–16 mg TOC/g, 0.5–2.8 mg TP/g), summer DO was high (range in mean values: 4.8–6.4 mg/l), and summer AVS was low (range in mean values: 0.03–0.4 mg S/g).

We placed the stations that are members of the seven assemblages and other stations that are omitted from any assemblage in a grid of ED versus fish production (Figure 7). Assemblages I–V were roughly numerically arranged on the gradient of ED. Assemblage I, composed of stations located near a mouth of Katsuragi Bay (Stations [Stns.] 27, 32; Figure 1) and in a deep basin of Kata Bay (Stns. 43, 45), had ED values of <1.1, and low to medium fish-production levels (210–1112 t/yr). Assemblage II, composed of stations in open bays (Stns. 25, 30, 31) and, when fish production was low (90 t/yr), also in nearshore areas (Stns. 28, 29) had ED values ranging from <0.9 (open bay stations) to those ranging from 1.6 to 3.2 (nearshore stations). Assemblage III, composed of stations in relatively deep or open embayments, had ED values of 0.6 to 1.9 at all levels of fish production. Assemblage IV, composed of stations in areas similar to those of assemblage III, had ED values of 0.7–2.4 and low to

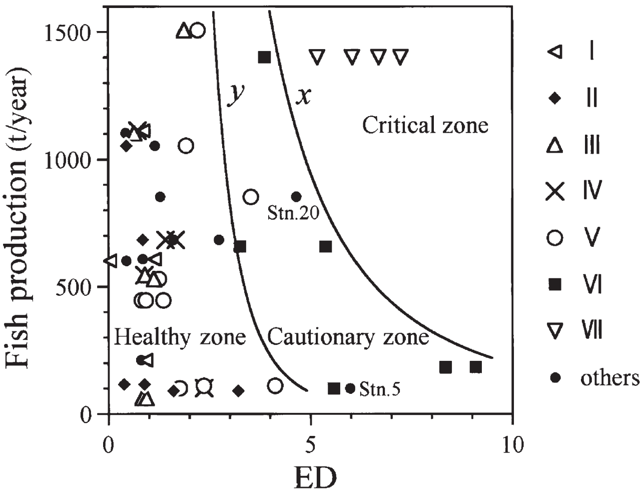

Figure 7. Distribution of seven station clusters (I–VII, defined in the text and Figure 5) and stations that were omitted from any clusters in a gradient of the index of embayment degree (ED, defined in text) versus fish production. The critical, cautionary, and healthy zones, divided by boundary lines *x* and *y*, are explained in the text

medium levels of fish production (101–1112 t/yr). Assemblage V, composed of stations in the central or inner parts of embayments, had ED values ranging 0.8–4.1 and all levels of fish production (110–1507 t/yr). Assemblage VI, composed of stations in the inner, shallower, sheltered part of embayments, had ED values of 3.3–9.1 and all levels of fish production. As fish-production levels increased, the habitat of assemblage VI stations shifted to more open, deeper areas (smaller ED values), suggesting that environmental deterioration in fish farms within that assemblage was related to organic input from aquaculture. Assemblage VII, composed of stations at a single location (Gokasho Bay), had high values of ED (5.2–7.2) and a high level of fish production (1400 t/yr).

Based on analyses of the biotic and abiotic factors and on species composition of the macrobenthos, we divided the stations into three zones (Figure 7): a healthy zone, where assemblages I–V occurred and characterized by little environmental deterioration and high species diversity of the macrobenthos; a cautionary zone, where assemblage VI occurred and characterized by moderate environmental deterioration and impoverished macrofauna; and a critical zone, where assemblage VII occurred and characterized by conspicuous environmental deterioration and defaunation in summer. It was difficult to specify the range of the critical zone because assemblage VII occurred only at one location in the study area. Therefore, the boundary line, *x*, can be defined only by the periphery of the cautionary zone. Most of the stations that are omitted from any clusters are located in the healthy zone. Thus, the healthy zone contains various benthic community assemblages with a diversity of species compositions that reflect conditions relatively free from the negative effects of fish farming and it is varied in habitat structure and composition. Stations 5 and 20, which were not included in any cluster, were located in the cautionary zone. They had relatively low macrobenthos community parameter values (3.5 and 8.6 g/m^2 of biomass, 1100 and 1750 individuals/m^2, and $H' = 3.4$ and 3.9) and relatively high AVS values (0.5 and 0.9 mg S/g) in summer, suggesting that these stations can be included in the cautionary category.

These results suggest that all levels of fish production could be sustained in areas where ED is <3.0 and small-scale fish production could possibly be conducted in areas where ED is <10.0, but medium- and large-scale production should be limited to areas where ED is <5.0. A fish farm with large-scale production (e.g., 1400 t/yr) and located in the critical zone (e.g., ED = 6) should be shifted to an area with ED values <4.0 or annual production should be reduced to <600 t, to alleviate the critical conditions (see Figure 6).

4. CONCLUSIONS

Macrobenthos responds rapidly to environmental deterioration caused by high organic input from fish farming (reviewed by Gowen et al., 1991). A reduction in species richness, a decrease in echinoderm densities, and an increase in total faunal abundance with a high proportion of small-sized organisms such as *Capitella* spp. are common features of the macrobenthos in fish farms; highly reduced conditions occasionally result in the elimination of all macrofauna during summer (Brown et al., 1987; Ritz et al., 1989; Weston, 1990; Laurén-Määttä et al., 1991; Wu et al., 1994; Findlay et al., 1995; Tsutsumi, 1995; Sasaki and Oshino, 1997; Yokoyama, 2002). In our study area, these phenomena were observed in large-scale farms located in the inner, sheltered parts of embayments. Yokoyama (2002) estimated that the organic carbon load produced by fish farming in Gokasho Bay, the location in our critical zone, is 71 times greater than that produced by the neighboring pearl-oyster farms. Such a large amount of organic matter generated from fish farming seems to affect both the abiotic and biotic components of the benthic ecosystem in the study area.

Macrobenthic communities progressively assume the appearance of undisturbed communities as the locations of fish farms shift to more open and deeper areas. The observed relationship between the gradient in abiotic and biotic components suggests that proximity to open water and currents are the most important factors in locating environmentally efficient fish farms. Locating culture facilities near wide, deep mouths of bays without depressed basins is better for sustaining high aquacultural production, but the facilities must be tolerant to strong wind and waves. In these types of areas, environmental deterioration will be minimized; organic wastes will disperse because seawater exchange will be effective, and the loaded organic matter may be aerobically mineralized.

Macrobenthos can play an important role in mineralizing the organic matter that originates in fish feed (Chareonpanich et al., 1993). Therefore, evaluating the assimilative capacity of farm environments and establishing environmental criteria based on the macrobenthos community is rational from an ecological point of view. Faunal composition and community parameters of the macrobenthos, as well as TN, AVS, and other chemical parameters proposed in this study, seem to be of practical use for assessing fish-farm environments in Kumano-nada. Similar surveys in other localities would be necessary to establish appropriate environmental criteria for sustainable aquaculture in those areas. However, our findings suggest that the index of embayment degree, ED, devised in this study may be used as a simple and effective substitute indicator for such extensive surveys when evaluating sites for the establishment of fish farms.

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CHAPTER 23

A SIMPLE EXPERIMENT IN POLYCULTURE: RED SEA BREAM (*PAGRUS MAJOR*) AND ULVALES (*ULVA PERTUSA*)

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Abstract: Mixing fauna and flora in culture cages is a fundamental approach for attaining homeostasis of ecosystems in aquaculture farms. We conducted an experiment to explore the benefits of culturing fish as fauna and seaweed as flora within single, open water, aquaculture cages. The aim of this study was to examine the effect of polyculture on the oxygen and carbon dioxide concentration of the water in the polyculture cage and on the growth, survival, feeding efficiency, and condition factor of the fish in the polyculture cage (Cage A, which contained red sea bream [*Pagrus major*] and a green alga [*Ulva pertusa*]) versus these measures in a monoculture cage (Cage B, which contained red sea bream only). The experiment was conducted from August 1992 through February 1993. The two cages each were 7 m × 7 m × 7 m. The red sea bream used in this experiment were three years old, had an average body weight of 654 g at the beginning of the experiment, and were the product of selective improvement for more than 25 years. Each cage contained 1750 fish. The alga was a variety of *U. pertusa* that had been improved by selection every two weeks for two years. The *U. pertusa* was cultured in floating net bags at the surface of Cage A and harvested every two weeks. The best-growing plants in the harvested group were used to re-inoculate Cage A. The remaining algal fronds were dried, crushed, formulated into pellets with standard red sea bream fish food, and fed back to the fish in Cage A. The fish in the control cage were fed the standard red sea bream fish food. The partial pressure of dissolved oxygen (pO_2) and of carbon dioxide (pCO_2) of the water within the cages and the growth of the fish (wet weight, standard length) were measured. Average pO_2 was significantly higher (9.0%) and average pCO_2 was significantly lower (5.2%) in the polyculture cage than in the control cage. Nearly all fish in both cages survived throughout the experiment. The average growth, average feeding efficiency,

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and average condition factor of the fish in the polyculture cage were, respectively, 3.2% higher, 6.0% higher, and 2.2% higher than those factors were in the fish in the control cage. In addition, the polycultured fish were redder in color (and, therefore, were more marketable) than were fish in the control cage. This simple project suggests the potential benefits of this particular type of polyculture in Japanese marine waters and, from a broader perspective, of algal/fish polyculture in general.

Key words: aquaculture, ecosystem, environment, Japan, pCO_2, pO_2, polyculture, red sea bream, Ulvales

1. INTRODUCTION

Self-induced pollution in mariculture farms (defined as a decline in environmental quality within and around open-water aquaculture cages due to the aquaculture operation itself) is increasing year by year. Studies directed toward the mitigation of such pollution are necessary for sustainable development of aquaculture (Folke and Kautsky, 1989, 1992; Hirata, 1994, 2000). In most current aquaculture systems in Japan, fish or seaweeds alone are cultured; in general, aquaculturists have not adopted the concept of the mutual benefit to fauna and flora when they are cultured together. Lack of attention to such a fundamental ecological concept might have greatly contributed to the self-induced pollution of mariculture operations in Japan.

The ecosystem homeostasis that occurs in an aquaculture environment when fauna and flora are cultivated together has been studied in our laboratory since 1976 (Yamasaki and Hirata, 1989; Yamasaki et al., 1990a, b, c; Danakusumah and Hirata, 1991a, b). Initial small-scale experiments were carried out by Yamasaki and Hirata (1989) and Yamasaki et al. (1990a, b, c) in 130-l tanks that contained the rotifer *Brachionus plicatilis*, and the microalga *Nannochloropsis* sp. Later, the prawn *Penaeus japonicus* and the green alga *Ulva pertusa* (Ulvales) were cultivated together by Danakusumah and Hirata (1991a, b) and Ali et al. (1994). Polyculture of various fish species and *U. pertusa* was also conducted by Xu and Hirata (1990a, b, 1992) and Xu et al. (1993). Their experiments demonstrated that maintaining a balance of fauna and flora in culture is one of the most fundamental approaches for achieving homeostasis in the aquaculture ecosystem. Our experiment was conducted to examine the effect of polyculture on the concentration of oxygen and carbon dioxide in the culture cage and to compare fish growth, survival, feeding efficiency, and condition factor in a polyculture cage (fish + algae) versus a monoculture (fish only) cage.

2. MATERIALS AND METHODS

The experiment was conducted from about August 1992 to February 1993 in the cage farms of Azumacho Fish Raising Center, Kagoshima, Japan. The red sea bream, *Pagrus major*, used in this experiment was the product of selective improvement of this species for more than seven generations (25 years, from the 1960s to the 1980s) by Kinki University personnel (Murata et al., 1996). The fish used were three years old; average body weight of the fish placed into each cage was 654 g the beginning of the experiment. Two cages, 7 m × 7 m × 7 m each, were employed: Cage A was for polyculture, and Cage B served as a control (monoculture of red sea bream only). Each cage contained 1750 fish.

The seaweed used in this experiment was a variety of *U. pertusa* (Maesako et al., 1985; Migita, 1985) that had been selectively improved by researchers at Kagoshima University through selection every two weeks for two years (1990 to 1992; Hirata and Kohirata, 1993). The alga was cultured at the surface of the cage on lines in floating net bags made of 0.8-cm mesh; each line was encased in a separate net bag, which extended the length of the cage. Each bag was 0.5-m wide and 7.0-m long and was structured to fit into Cage A. A total of 14 lines were set parallel to each other and to the length of the cage. The *P. major* inhabited the middle and lower parts of the cage.

The alga was harvested one line per day. The weight was measured after spin-drying for 3 min in a washing machine to attempt to uniformly dehydrate the algal mass. Re-inoculation of the alga into Cage A was conducted every two weeks. The algal fronds used to re-inoculate the cage were selected from the largest (which were assumed to be the best-growing) of the harvested plants. The remaining fronds harvested were processed for feeding to the polycultured fish in Cage A.

The polycultured fish were fed a dry-pellet mixture containing 2% dried *U. pertusa* mash, this food was made by a local feed company (Tiochu) by mixing the dried *U. pertusa* mash with a standard fish-feed mix for red sea bream and processing the mixture into pellets. The fish in the control cage were fed the standard dry pellets for red sea bream, which were commercially made by the same company as the standard food-*U. pertusa* pellets.

The partial pressure of dissolved oxygen (pO_2) and carbon dioxide (pCO_2) were measured every 2 hours at ebb tide, in the daytime, September 27–29 using a Radiometer ABL-330. Water was sampled from the upper and lower areas of both the control and experimental cages at 1.5-m and 3.0-m depth, respectively. Fish body weight and length were measured by randomly sampling 20–30 fish at the beginning (August 1), middle (December 19), and end (February 17) of the experiment.

Percentage survival in each cage was determined simply as follows:

$$\frac{100 \times \text{Number of individuals in each cage at the end of the study}}{\text{Number of individuals in each cage at the start of the experiment}}$$

As a crude estimate of feeding efficiency, we used the following calculation:

$$\frac{\text{Total body weight gained}}{\text{Total weight of food supplied}}$$

Condition factor was calculated as follows:

$$\frac{\text{Fish weight(gm)} \times 100{,}000}{\text{Fish standard length (mm)}^3}$$

Proportional changes between treatments in pO_2, pCO_2, growth rate (g), feeding efficiency (f.e.), and condition factor (c.f.) were calculated as follows:

$$100 + 100\left(\frac{A - B}{B}\right)$$

where A is mean pO_2, pCO_2, or c.f. or total g or f.e. in the polyculture cage and B is mean pO_2, pCO_2, or c.f. or total g or f.e. in the control cage.

3. RESULTS AND DISCUSSION

Both the average pO_2 and average pCO_2 in the water of the polyculture cage differed significantly from those measures in the control cage (Single-classification ANOVA; Sokal and Rohlf, 1995); the average pO_2 was significantly higher (9.0%; $P < 0.001$) and the average pCO_2 was significantly lower (5.2%; $P < 0.01$) (Table 1). Flora absorb CO_2 and release O_2 whereas fauna consume O_2 and release CO_2. This simple phenomenon has been well known by fish culturists, but is rarely, if ever, exploited in Japanese mariculture farms, possibly for the following two reasons. First, many suitable seaweeds do not flourish in summer. Most edible seaweeds, such as *Porphyra* spp. or *Undaria* spp. grow in winter, when most cultured fishes are relatively inactive. Second, the simultaneous culture of fish and seaweeds is labor-intensive, and the market price of *U. pertusa* in Japan is lower than that of other seaweeds. Therefore, the utilization and marketing of *U. pertusa*, which contains many nutrients (Hirata, 1999), needs to be improved.

Table 1. Relative budgets of the partial pressure (pO_2, pCO_2) in polyculture and monoculture cages. The pO_2 and pCO_2 are shown as averages; standard deviations are in parentheses

Trials	Water depth (m)	pO_2 (mm Hg)	pCO_2 (mm Hg)
Polyculture	1.5	156.6 (4.0)	5.4 (0.2)
(*Pagrus major* + *Ulva pertusa*)	1.5	159.3 (5.7)	5.4 (0.1)
	3.5	155.0 (3.0)	5.6 (0.2)
	3.5	161.2 (4.2)	5.5 (0.1)
Mean		158.0 (5.0)	5.5 (0.1)
Relative concentration		109.0%	94.8%
Monoculture "control"	1.5	144.6 (1.2)	5.8 (0.1)
(*P. major* only)	1.5	146.4 (2.9)	5.7 (0.1)
	3.5	143.3 (2.6)	5.8 (0.1)
	3.5	145.1 (4.5)	5.7 (0.1)
Mean		144.9 (3.2)	5.8 (0.1)
Relative concentration		100%	100%

Red sea bream survival rates in both the polyculture and control cages were very high (99.8% and 99.6%, respectively). At the end of the study, the total growth of red sea bream in the polyculture cage was 3.2% higher than that in the control cage (Table 2). Both average feeding efficiency and average condition factor of fish in the polyculture cage were also proportionally higher (6.0% and 2.2%, respectively) than they were for fish in the control cage (Table 2). In addition, the polycultured fish were more reddish than were the control fish. In general, Japanese consumers prefer more reddish sea bream and higher condition factors. In this way, the polyculture of *P. major* with *U. pertusa* provides advantages for both the fish and consumers.

Our experiment suggests that this polyculture system, coupled with the use of fish feed enhanced with algae, could benefit aquaculturists in several ways:

1. Water quality, as estimated by pO_2 and pCO_2, could be improved in culture cages.
2. Fish growth and quality could be enhanced. (However, the exact reason for any possible enhanced growth or quality cannot be identified from our experiment—it could be due to improved water quality, the mixed fish/algal algal food, the presence of the physical structure of the seaweed lines and nets, higher feeding rates of the fish in the polyculture cage, or any number of other factors.)
3. Multiple crops could be simultaneously cultured; the harvested algae could be sold or recycled as a fish-food component.
4. Clearly, our study suggests that further experiments in this direction are needed.

Table 2. Feeding efficiency and condition factor in a polyculture cage containing red sea bream (*Pagrus major*) and the seaweed *Ulva pertusa* versus those measures in a monoculture cage containing only red sea bream. Fish in both cages were fed the same commercially available food. The food provided to fish in the polyculture cage was supplemented with dried, processed *U. pertusa*, which was harvested from the cage. Feeding efficiency and condition factor are defined in Methods and Materials

Type of aquaculture	Total growth of fish (kg)	Total weight of pellets supplied (kg)	Total dry weight of *U. pertusa* supplied (kg)	Total dry weight of food supplied (kg)	Feeding efficiency	Condition factor[1]
Polyculture	1315.8[2]	2606.0	42.5[3]	2563.5	51.3%	18.4
Monoculture	1275.1[4]	2634.0	0.0	2634.0	48.4%	18.0

[1] Calculated using the samples collected at the end of the experiment.

[2] Average weight gain per individual = 753 g.

[3] 212.5 kg wet weight.

[4] Average weight gain per individual = 732 g.

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Editor's Note: Dr. Hirata, who was a true gentleman and an excellent and perceptive scientist, died while this book was in preparation. I visited him in Japan after inviting him to participate in the symposium upon which this book is based. He took the time to show me many excellent features of that country, including components of its history and culture, in addition to educating me in the extent and diversity of Japanese aquaculture. For that courtesy, I will always remember him and honor him

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CHAPTER 24

MICROALGAE, MACROALGAE, AND BIVALVES AS BIOFILTERS IN LAND-BASED MARICULTURE IN ISRAEL

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Abstract: Protein is the most expensive component in fish feed and the main source of nitrogenous pollution in fish culture. It is therefore economically desirable to maximize the conversion of feed protein into a valuable biomass, and environmentally desirable to minimize nitrogenous waste. Both ends can be achieved in algal-dependent integrated mariculture. Unlike fish-cage effluents, fishpond effluents can be treated. Use of marketable organisms as biofilters increases both diversification and income of the mariculture operation. Algal biofiltration has a stabilizing influence on water quality since, unlike bacteria, algae counteract the consumption of oxygen and the production of CO_2 by the fish. However, algal biofilters probably cost more to build and use a larger land area when compared with the alternative bacterial nitrification–denitrification aquaculture biofilter systems. Biofiltration by algae and shellfish, as has been developed as a part of integrated mariculture at the Israeli National Center for Mariculture, offsets the added cost by added sales of the biofilter organisms. This approach is based on algal sunlight-dependent assimilation of nutrients and their conversion into microalgal or macroalgal biomass. The algae are then consumed by algivore invertebrates such as bivalves, gastropods, and sea urchins. Sea urchins in particular can also be used to remove organic detritus. In the fish-phytoplankton-bivalve integrated culture system, bivalves filter microalgae that develop in fishponds and sedimentation ponds in which fishpond effluents collect. Such systems require large treatment areas relative to fish production, and are therefore suitable for extensive or semi-intensive fish culture with relatively low land costs. In fish-seaweed integrated culture, nutrients are removed from the fishpond effluents by green macroalgae such as *Ulva lactuca*. The macroalgae (seaweeds) can subsequently be fed to macroalgivores or processed for human consumption. While water from the fishponds passes through the macroalgae ponds, most of the ammonia (up to 90%) and significant fractions of other dissolved nutrients are removed from the water. The macroalgae improve the quality of the water by adding O_2 and removing excess CO_2, thus making the water suitable for recirculation into the fishponds. The seaweed produced is excellent for feeding high-value macroalgivores such as abalone and sea

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urchins. Fish-seaweed integrated systems require less extensive land area than fish-phytoplankton-bivalve integrated systems and produce cleaner effluents. However, they may require larger inputs of capital and energy. Fish culture integrated with algal and shellfish biofilters has the potential to expand sustainably, meeting economic, environmental, and social concerns.

Key words: aquaculture, biofiltration, bivalves, environment, Israel, pollution, polyculture, *Ulva*

1. INTRODUCTION

Aquaculture has increasingly been viewed as environmentally detrimental (Naylor et al., 2000). Mariculture in sea cages has been associated by the public with deterioration of water quality and eutrophication of coastal waters (e.g., Staniford, 2001). Uncontrolled nutrient release by mariculture operations harms the industry in at least three ways—it reduces coastal water quality (which can generate negative public perception and legal-regulatory consequences), it wastes valuable nutrients, and, of course, it compromises the health of the organisms that are cultured in these waters. It is in the best interest of mariculturists, therefore, to minimize nutrient release from their culture facilities into the environment. Biofiltration is the most effective way to treat aquaculture water, due to its low concentration of pollutants compared with domestic effluents (van Rijn, 1996). Biofiltration of fishpond water can be done by bacteria (van Rijn, 1996), microalgae (Neori and Krom, 1991), macroalgae (Neori et al., 1996), and suspension feeders (Shpigel and Blaylock, 1991; Shpigel et al., 1997). These approaches can often be impractical or ineffective in the treatment of effluent water from fish-cage farms (Ahn et al., 1998).

Fishpond effluents, however, can be closely managed and treated by all three biofiltration appraches. Land-based facilities have fewer problems related to weather, theft, or predation than do sea cages. However, land-based facilities are generally more costly than sea cages in their construction, land occupation, and operation. Water pumping, maintenance of acceptable water quality in ponds, and treatment of organic waste in pond effluents are also significant components of land-based mariculture expenses. Biofiltration, because it greatly reduces water exchange and pollution, can therefore cut pumping costs.

Another consideration in favor of algal biofiltration is product diversification and income increase. Protein is the most expensive component in fish feed and the main source of nitrogenous pollution in fish culture. Marine fish assimilate less than 30% of the nitrogen (N) in their diets (Porter et al., 1985; Lupatsch and Kissil, 1998). The rest is excreted into the water, mainly as dissolved reduced N (ammonia and organic N). Hence biofiltration R&D efforts have concentrated on nitrogenous waste treatment and on the recovery of the N into marketable products (Gowen and Bradbury, 1987). Bacterial biofilters, although rather effective in treatment, waste most of the N. Converting this wasted N into marketable products would improve the economics of the environmentally responsible fish farm. This reasoning has led to the emphasis on algal biofilters in integrated mariculture.

Extensive land-based aquaculture facilities have traditionally included detritus feeders and plants in the polyculture of various aquatic species, particularly in the Far East. However, single-pond polyculture is not suitable for intensification because requirements of different cultured organisms conflict. Integrated polyculture systems, on the other hand, are composed of several separate units. Excretions produced in one unit can be treated in others, often with solar energy assistance (Figure 1). The maintenance of different organisms and processes in separate units allows for intensification, optimization of the biological processes, and adjustment of parameters in the secondary units to handle water and nutrient flow from the principal units in the most efficient way. The emphasis in production may shift from one organism to another, according to practical or economical considerations. Of course, the increased complexity requires higher expenses for construction and professional operation.

In recent years, researchers at several research facilities and enterprises have initiated studies of polyculture and integrated mariculture systems. Often those studies provided qualitative or partial results with respect to design, operation, rates of production, and nutrient removal. McDonald (1987) reviewed the literature on nutrient removal by phytoplankton-fish food chain systems, and concluded that a phytoplankton-*Tilapia* integrated system was biologically feasible and economically attractive. Rakocy (1997) has reported on a commercial *Tilapia*-lettuce farm. Manzi et al. (1988) and Wang (1990) described intensive pond polyculture systems, composed of shrimp, phytoplankton, and

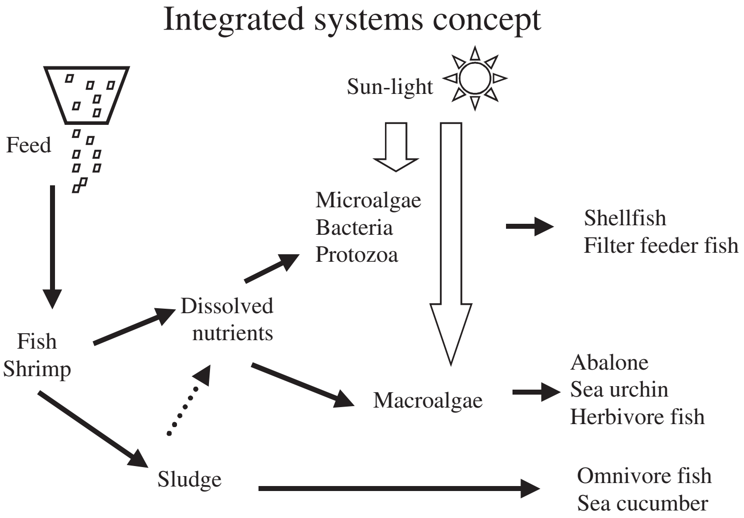


Figure 1. Basic concept of an integrated polyculture system

bivalves, that supported good survival and high yields of both types of invertebrates. Miller (1989) described commercial land-based polyculture of abalone and sea urchins. Sustainable polyculture of shrimp with oysters and mangroves in Colombia was proposed and analyzed by Larsson (1992). Jara-Jara et al. (1997) have shown the biological practicability of culturing clams in the effluents of intensive turbot farms in northern Spain. Several groups (Buschmann et al., 1994; Jimenez del Rio et al., 1996) have studied or reviewed (Troell et al., 1999) the cultivation of seaweed in the effluents of intensive fishponds. Their results were essentially similar to our results described below, with respect to yields, water quality improvement, and nitrogen removal.

Already in the early 1970s, Goldman et al. (1974) and Ryther et al. (1975) described a concept and quantitative experimental results for integrated waste-recycling marine polyculture systems. Domestic effluent, the source of nutrients, was mixed with seawater to obtain brackish water for phytoplankton culture. The microalgae, in turn, were fed to suspension feeders (oysters and clams). Additional organisms that consumed the solid wastes were cultured in a food chain. Dissolved nutrients in the final effluent were biofiltered by seaweed.

A weakness of this approach has been the concern over the potential transmission of pathogens which might be introduced with the human waste effluents. Replacement of the sewage water with effluents from fish culture, and use of the seaweed for macroalgivore (abalone) culture were subsequently proposed (Tenore, 1976).

Several approaches to sustainable integrated mariculture have been tried and developed at the Israeli National Center for Mariculture (NCM) in Eilat (Hughes-Games, 1977; Gordin et al., 1990; Shpigel and Blaylock, 1991; Neori et al., 1993, 1996; Shpigel et al., 1993a; Shpigel and Neori, 1996; Shpigel et al., 1996, 1999; Neori and Shpigel, 1999). The main features in these approaches have been the removal of dissolved nutrients by algae and removal of particulate matter by bivalves and sedimentation.

2. INTEGRATED MARICULTURE SYSTEMS TESTED IN ISRAEL

2.1. Microalgae as Biofilters

Dense microalgal populations can develop in fishponds and their effluents and can provide efficient biofiltration *in situ* if they are given proper environmental conditions, including ample sunlight and low-to-medium water exchange rates (up to about 2 exchanges/day [d], depending on season and location) (Krom et al., 1989a, b; Neori et al., 1989). The microalgae recharge the water with dissolved oxygen (DO) and recover CO_2, ammonia, and phosphate in their high-protein biomass (Krom and Neori, 1989; Neori and Krom, 1991). In the NCM's medium-flow intensive fishponds, algal blooms usually consisted of one dominant species, mainly planktonic microalgae such as *Olithodiscus* spp., *Chlorella* spp., *Tetraselmis* spp., *Chaetocerous* spp., or *Pyramimonas* spp.

These populations usually maintained good water quality in the ponds, although they were periodically grazed out by heterotrophic microflagellates and ciliates (Neori et al., 1989).

2.2. Seaweed as Biofilters

Seaweeds of various species have been studied for their suitability as nutrient biofilters (Ryther et al., 1975; Harlin et al., 1978). *Ulva* (Ulvales, Chlorophyta), a sturdy cosmopolitan green seaweed, was found to be particularly useful. Various species of this genus, cultured in both laboratory and outdoor conditions by several groups, grow well and show high capacities for nutrient removal (Lapointe and Tenore, 1981; Cohen and Neori, 1991, and references therein). The local *Ulva* species (*U. lactuca*) was therefore selected to biofilter mariculture effluents in studies at the NCM and other locations (Neori et al., 1989; Vandermeulen and Gordin, 1990; Shpigel et al., 1993b; Jimenez del Rio et al., 1996). *Gracilaria conferta* was also examined but was found to grow inconsistently, making it less promising under Israeli conditions.

The seaweed culture system that provided good growth was based on the bottom-aeration principle described by Lapointe and Tenore (1981) and Bird (1989). Optimal density for *U. lactuca* was determined to be 1 kg/m^2 (Neori et al., 1993). The nutrient uptake, yield, and protein content of *U. lactuca* grown in fishpond effluents were determined (Vandermeulen and Gordin, 1990; Cohen and Neori, 1991; Neori and Krom, 1991; Israel et al., 1995; Neori, 1996). The rate and efficiency of sustained ammonia removal by *U. lactuca* were related to the rate of ammonia supplied (Figure 2). At supply

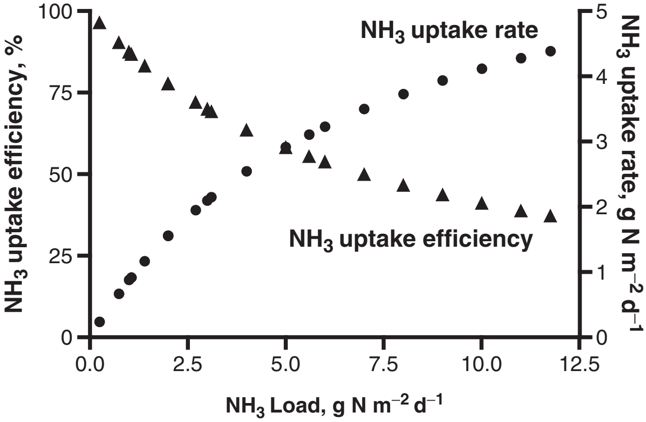


Figure 2. Relationship between ammonia-nitrogen (NH$_3$) removal (uptake) rate and removal efficiency by *Ulva lactuca* biofilters and ammonia-N areal flux in a polyculture system. Model, based on Cohen and Neori (1991)

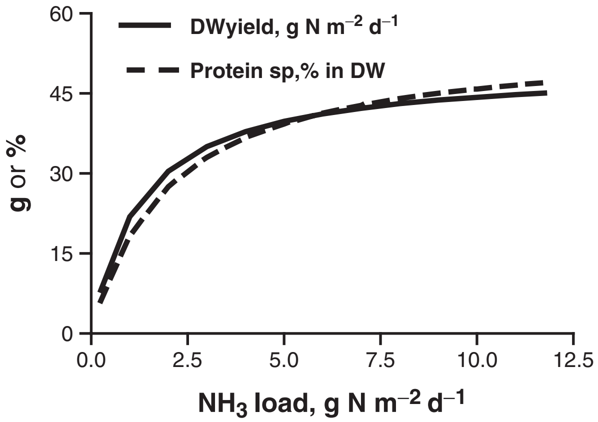


Figure 3. Relationship between yield and protein content of *Ulva lactuca* on ammonia-nitrogen (N) areal flux in a polyculture system. Model, based on Cohen and Neori (1991) and on Neori and Krom (1991). DW = dry weight

rates below 2 g of ammonia-N/m^2/d (annual average), *U. lactuca* can remove over 80% of the ammonia from the water. The ammonia uptake rate, plotted against ammonia-N load, increased with the load up to 7 g ammonia-N/m^2/d (annual average). As the ammonia supply rate increased, the removal efficiency dropped to 50% at an ammonia load of 5 g/m^2/d. The *U. lactuca* yield and protein content also depended on the load of ammonia (Figure 3). Yields (fresh weight) varied from 70 g/m^2/d in winter to over 350 g/m^2/d in summer. The *U. lactuca* biomass produced in mariculture effluents contained 2–4 times more protein (up to 40% in dry weight) than do wild *U. lactuca* stocks. The performance of the seaweed as a biofilter dropped greatly in all three parameters (N-removal, yield, and protein content) if the nitrogen supplied to the seaweed was in the form of nitrate rather than ammonia (Neori, 1996). *U. lactuca*, like most other algae, can readily take up an excess of ammonia ("luxury uptake," converted principally to protein), whereas nitrate, which must be reduced metabolically before it is assimilated, is taken up only in moderation (Neori, 1996).

The maintenance of the seaweed culture tank is simple and a crop of *U. lactuca* can be produced year-round. Although the seaweed fronds look fragmented and pale for a couple of weeks during the seasonal transition periods, it seems that the *U. lactuca* biofilter does not suffer from invasion of competitors or from culture collapses.

The high performance of the *U. lactuca* biofilter allows effluent recycling between the algae tank and the fishponds (Neori et al., 1993). When properly proportioned, the two compartments of a fish-*U. lactuca* recirculating culture system balance each other with respect to pH and concentrations of DO and ammonia, thus stabilizing the water quality and reducing the fraction of fish-feed-N released into the environment to negligible values (Neori et al., 1996;

Schuenhoff et al., 2003). Several (up to 7) kilograms of high-protein seaweed can be harvested for each kilogram of fish produced. Water exchange with clean seawater is required primarily for maintenance of salinity.

Although *U. lactuca* is an efficient and convenient biofilter, this alga is less commercially valuable than red or brown seaweeds. At an estimated overall production cost (for space, facilities, labor, and electricity in Israel, at 2002 prices) of about US $0.20/kg (fresh weight), *Ulva* biofilters add over US $1 to the production cost of each kilogram of fish. Using this species as a biofilter without selling it is thus relatively expensive. However, high-protein *Ulva* species are valuable, e.g., as human food or as a component in Japanese spice mixes (B. Tsairi, personal communication). The seaweed can also be an indispensable resource in the culture of macroalgivores such as abalone (Shpigel et al., 1999) or sea urchins (M. Shpigel, unpublished data). These organisms and their seaweed food have been depleted in the wild to the extent that world market supply falls tens of thousands of tons (t) short of the demand (Keesing and Hall, 1998). The integration of macroalgivores in the fish-seaweed culture system can therefore increase the overall profitability of land-based integrated mariculture (Shpigel and Neori, 1996; Neori et al., 2000).

2.3. Suspension Feeders as Biofilters

Microalgae are the main food for commercially valuable suspension feeders such as bivalves (Goldman et al., 1974; De-Pauw and Salomoni, 1991; Rosenthal, 1991; Shpigel et al., 1993b). Cultured bivalves, which yield nearly 10 million tons per year, already constitute the largest component of the world mariculture market (FAO, 2000). Because they filter microalgae and other particles, bivalves can clarify turbid aquaculture effluents (Tenore and Dunston, 1973; Kasprazak, 1986; Laurenstein, 1986) by digesting organic particles and converting the non-digestible particles into quickly settling feces and pseudofeces (Mariojouls and Kusuki, 1987). At high densities, bivalves have been shown to be the main factor that controls seston concentration in natural waters (Haven and Morales-Alamo, 1970; Winter, 1978; Jorgensen, 1990).

The filtration capacity of bivalves has been described in detail (reviewed by Malouf and Bricelj, 1989; Jorgensen, 1990). The clearance rate of bivalves is correlated with flow rates, food concentration, and temperature. Typical clearance rates range between 0.4 and 4.0 l/hr/g dry weight of bivalve tissue. The filtration rates by oysters and clams in fishpond effluents were above 0.3 mg particulate-N/d/g wet weight of bivalve tissue, at assimilation efficiencies of 18–26% (Tenore and Dunston, 1973; Shpigel and Blaylock, 1991).

In the fish-bivalve-seaweed integrated system developed at the NCM, effluent water from three fishponds rich with microalgae and dissolved nutrients drained into an earthen sedimentation pond. The algal population found in the sedimentation pond consisted of mixed planktonic microalgae from several fish ponds and of *in-situ*-grown benthic diatoms such as *Navicula*, *Amphora*, and

Nitzchzia—species whose mixture formed an excellent diet for the bivalves. The presence of the dissolved nutrients coupled with high solar radiation resulted in high phytoplankton production, which supported high rates of growth and production of the oyster *Crassostrea gigas* (0.7%/d; 20–40 kg/m^3/y, in tanks) and the clam *Tapes philippinarum* (0.6%/d; 8–10 kg/m^2/y, on the bottom of the sedimentation pond) (Shpigel et al., 1993a; Shpigel and Neori, 1996). These rates were significantly higher than those achieved using effluents that come directly from the fishponds (Shpigel et al., 1993b). Two factors were responsible for the better growth of the bivalves using water from the sedimentation pond—high-diversity phytoplankton populations dominated (70%) by benthic diatoms and stable overall algal density. Silicate enrichment of the sedimentation pond further increased diatom culture and hence bivalve production (Lee et al., 2004).

The integrated mariculture concept described here calls for the sedimentation-pond water to drain into polishing reactors that contain bivalves (for processing particulate matter [PM]) and seaweed (for processing dissolved nutrients) on its way back into the sea. In the total N budget of this system, less than 10% of the fishfeed N input is discharged to the sea. The fish assimilate 21%, the bivalves 15%, and the seaweed 22%. About 32% of the N budget is composed of feces, pseudofeces, and uneaten feed that sink to the bottom (Figure 4).

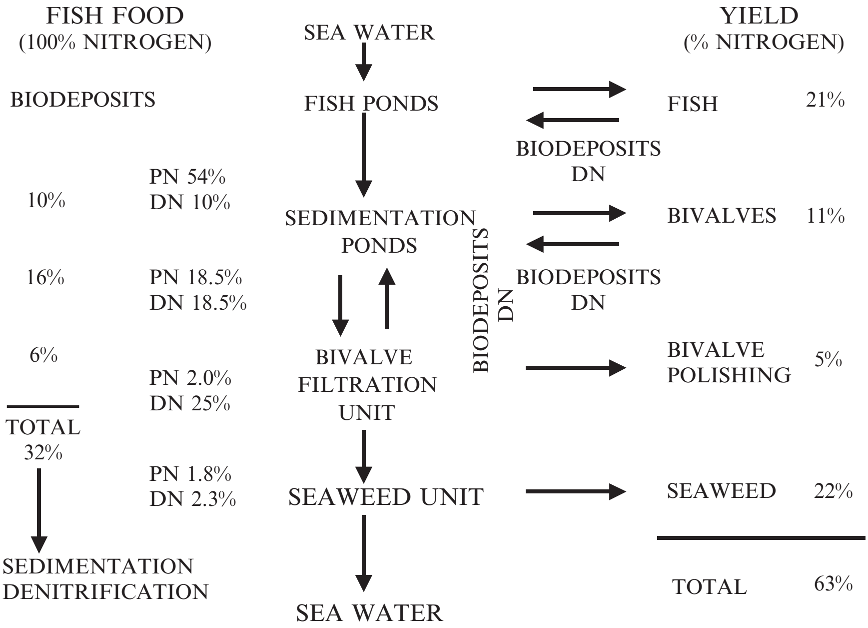
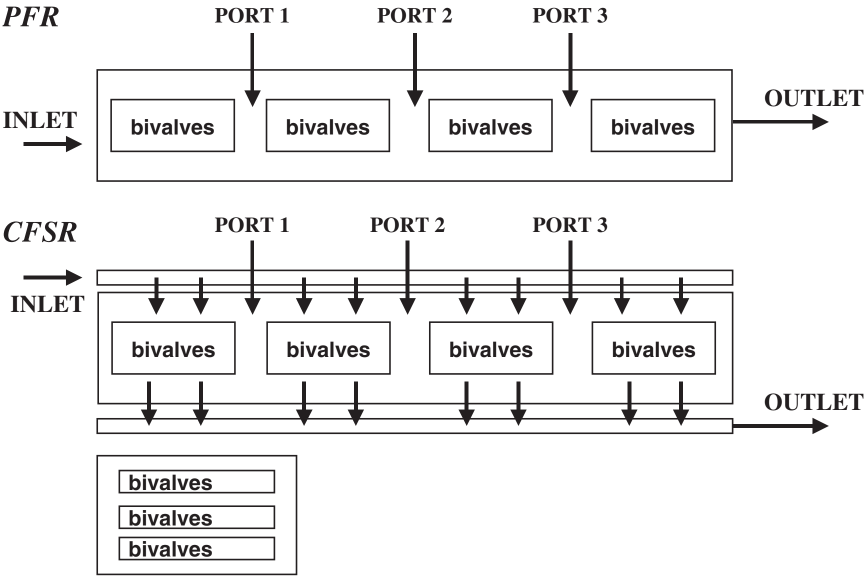


Figure 4. Nutrient budget of a fish-bivalves-seaweed integrated biofilter in a polyculture system. PN = particulate nitrogen; DN = dissolved nitrogen (after Shpigel et al., 1993b)

It is recommended that the integrated system include two bivalve units, a highly productive earthen sedimentation pond with clams, and a number of polishing reactors with oysters. Two different units are necessary because the conditions that maximize bivalve yield differ from those necessary for high filtration efficiency.

2.4. Polishing Reactors

Shpigel et al. (1997) studied the concept of mechanical biofiltration for removing PM from fishpond effluents prior to discharge. The treatment process was based on the different and complementary biofiltration performed by two species of marine bivalves (*C. gigas*, *T. philippinarum*) and by mechanical sedimentation. The filtration efficiency of the bivalves was assessed in two reactor designs with different flow patterns: a plug flow reactor (PFR) and a continuously stirred flow reactor (CSFR) (Figure 5). In the PFR, water flow is in plug form. The filtration activity of the bivalves is expected to vary as a result of the change in PM concentration along the longitudinal axis of the reactor. In the CSFR, the water is completely mixed. In an ideal CSFR, the PM is continuously re-distributed and its concentration is uniform. These reactor types have been successfully used for treating large volumes of wastewater



Plug Flow Reactor (PFR) and Continuous Stirred Flow Reactor (CFSR)

Figure 5. Schematic design of plug flow reactor (PFR) and continuous stirred flow reactor (CSFR) in an intensive polyculture filtration system (after Shpigel et al., 1997)

Table 1. Comparison of a clam's (*Tapes philippinarum*; average wet weight = 3 g) and an oyster's (*C. gigas*; average wet weight = 7 g) removal capabilities for particulate matter (PM) (expressed as removal of turbidity units [NTU]) and phytoplankton (expressed by chlorophyll *a* [Chl *a*]) in two reactor types (plug flow reactor [PFR] and continuously stirred flow reactor [CSFR]) and at high (60 l/h) and low (40 l/h) flow-rate (PM) levels (*n* = 6 replicates for each treatment). Values are given as means ± standard deviations. Efficiency was tested in two ways: by turbidity measurements in which the turbidity is an indicator of all PM in the water and by chlorophyll *a* reduction, where chlorophyll *a* is an indicator for the phytoplankton in the water. The control represents the physical sedimentation of the particles in each reactor type, in the presence of bivalve shells (after Shpigel et al., 1997)

		Inlet, initial concentration		Outlet, % removal	
Biofilter	Reactor	Turbidity (NTU)	Chl *a* (μg/l)	Turbidity (NTU)	Chl *a* (μg/l)
Control					
Bivalve shells	PFR	61 ± 2.4	27 ± 2.5	25 ± 2.5	11 ± 1.5
	CSFR	61 ± 2.4	27 ± 2.5	23 ± 1.9	15 ± 1.3
High PM level					
Tapes	PFR	48 ± 2.3	35 ± 2.5	97 ± 2.7	97 ± 3.8
philippinarum	CSFR	48 ± 2.3	35 ± 2.5	84 ± 1.4	87 ± 1.4
Crassostrea	PFR	48 ± 2.3	35 ± 2.5	91 ± 3.7	93 ± 4.5
gigas	CSFR	48 ± 2.3	35 ± 2.5	79 ± 4.6	69 ± 5.6
Low PM level					
Tapes	PFR	20.2 ± 1.8	11 ± 1.7	88 ± 3.7	83 ± 3.3
philippinarum	CSFR	20.2 ± 1.8	11 ± 1.7	69 ± 4.1	57 ± 4.1
Crassostrea	PFR	15.1 ± 1.3	11 ± 1.7	83 ± 3.7	86 ± 4.2
gigas	CSFR	15.1 ± 1.3	11 ± 1.7	75 ± 3.1	79 ± 3.5

(Metcalf and Eddy, 1983). The rationale for testing these types of reactors was based on the fact that the filtration rates and efficiencies of bivalves are species-specific and vary with flow rate and particle concentration. It was found that, in the conditions of the experiments, the PFR was more efficient in depurating aquaculture effluents (Table 1).

3. CONCLUSIONS

An environmentally friendly land-based culture facility for marine organisms is relatively expensive to build and operate. Intensive production of valuable biofilter species in integrated polyculture can offset the extra cost, increase product diversification, and improve profitability. It can also provide and sustain more jobs compared with fish sea-cage monoculture. An integrated mariculture system is modular and can optimize its production toward the most valuable product, such as luxury fish, shrimp, or abalone, or to fast growing seaweed. Its operational protocol can be shifted toward the product combination that maximizes profit, taking into account production cost and product market value. Thus, use of marketable organisms as biofilters can make land-based mariculture a profitable, sustainable industry.

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CHAPTER 25

BEYOND THE MONOSPECIFIC APPROACH TO ANIMAL AQUACULTURE — THE LIGHT OF INTEGRATED MULTI-TROPHIC AQUACULTURE

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Abstract: The focus of present-day aquaculture is typically monospecific animal culture. Even the development of "alternative" species for aquaculture usually refers to alternative species of fish or shellfish. However, although introducing another species of fish or shellfish may have short-term benefits, rarely does it balance energetically and ecologically in the long term. What is needed is appropriate proportions of different co-cultured organisms, performing different processes throughout the day and seasonally. Other than in Asia, the fundamental role and the contribution of seaweeds in coastal waters have frequently been either ignored or misunderstood. Seaweeds are rarely factored into modeling equations of coastal systems. At a time when nutrification of coastal waters is becoming a pressing issue worldwide and the contribution of the inorganic output of aquaculture to regional nutrient loading is becoming more widely recognized, integrating seaweeds, which act as biological nutrient scrubbers, into fish or shellfish aquaculture is a promising, balanced-ecosystem approach. Integrating seaweeds into aquaculture systems provides bioremediation capability, mutual benefits to the co-cultured organisms, and economic diversification of the industry by producing another value-added marine crop. We discuss these concepts and illustrate the benefits of integrated multi-trophic aquaculture (IMTA) using projects that we are conducting in New England, USA, in which the culture of the red alga *Porphyra* (nori) is integrated with salmonid culture, and in the Maritime Provinces, Canada, in which open-water aquaculture of *Chondrus crispus* (Irish moss) is conducted in proximity to mussel and oyster aquaculture operations. The aquaculture industry recognizes its

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need to practice responsible aquaculture by moving in new directions, such as IMTA. This will require wise investment in research and development.

Key words: aquaculture, Canada, environment, impacts, integrated multi-trophic aquaculture, seaweeds, *Chondrus crispus*, *Porphyra*, USA

1. INTRODUCTION

The fundamental role and the contribution of seaweeds in coastal waters have frequently been either ignored or misunderstood, especially in the Western World. Seaweeds are rarely factored into models of coastal systems. Usually, review papers on national aquaculture production either do not mention seaweed production numbers, or those numbers are not available for inclusion in such papers. In contrast, Asian countries generally have a long tradition of seaweed aquaculture. In 2000, for example, China produced 7.9 million metric tons (t) of algae—mainly the brown algae *Laminaria* and *Undaria* and the red algae *Porphyra*, *Gracilaria*, *Kappaphycus*, and *Betaphycus*. Cultivation of these genera represents 93% of the world seaweed aquaculture production (10.1 million tons, which itself represents 88% of the worldwide commercial harvest of seaweeds [FAO, 2000]). Such a tremendous biomass certainly provides significant "buffer capacity" in Chinese coastal waters, which are under considerable environmental pressure because of high human population density and related activities (e.g., reduced sewage treatment capacity [X.G. Fei, Institute of Oceanology, Qingdao, China, personal communication]).

Currently, development of the culture of "alternative" species is thought to reduce some aquaculture impacts. However, frequently those species are fish. Although introducing another species of fish into an aquaculture operation may generate short-term economic benefits, it rarely creates an energetically and ecologically balanced operation in the long term. Such aquaculture continues to be "fed" (finfish) aquaculture, in which a significant fraction of the additional food is not consumed and metabolic excretion is unidirectional (Ackefors and Enell, 1990).

Just as fish monoculture may not be environmentally sustainable, seaweed monoculture, too, has its limitations. Cultivated seaweed species are not immune to bacterial or fungal pathogenic infections, such as the "ice–ice" disease in *Kappaphycus* and *Eucheuma*, which spreads faster when plants are already stressed (Largo et al., 1999). In addition, intensive aquaculture of large macroalgae can impact current velocity, sedimentation rates, and, at night when these photosynthetic organisms also respire, oxygen consumption rates (J. Grant, Dalhousie University, Halifax, Canada, personal communication).

It is also thought that open-water aquaculture nutrification impacts will be reduced if aquaculture operations move onto land. This spatial shift should reduce the problem of concentrated nutrient loading in water bodies, which can become difficult to treat. However, concentrated effluents from on-land aquaculture operations would still need to be channeled through pipes and be appropriately treated before being re-used (close systems) or discharged (open systems).

For a balanced-ecosystem approach, "extractive" (shellfish and seaweeds) aquaculture should be integrated with fed aquaculture as an innovative aquaculture development. Aquaculture operations that utilize a diversity of co-cultured organisms to perform different processes throughout the day and among seasons are needed; the biomasses of these organisms should be of such proportion that their productivity and metabolic processes counter-balance each other.

In both open-water and on-land aquaculture systems, seaweeds not only act as renewable biological nutrient scrubbers for water quality enhancement and coastal health improvement, but also represent marine crops of commercial value. In this chapter, the concepts of bioremediation, mutual benefits for the co-cultured organisms, and economic diversification of the aquaculture industry will be developed and illustrated by projects we are conducting in New England, USA, and the Maritime Provinces of Canada.

2. DEVELOPMENT OF *PORPHYRA*/FISH INTEGRATED MULTI-TROPHIC AQUACULTURE

A consequence of finfish aquaculture activities is significant loading of inorganic nutrients, especially nitrogen (N) and phosphorus (P), into coastal waters (Beveridge, 1987). Because of improvements in feed composition, digestibility, and feed conversion efficiency in recent years, the N and P discharge per ton of salmon (*Salmo salar*) per year is now estimated at 35.0 and 7.0 kg, respectively (Chopin et al., 2001; H. Ackefors, University of Stockholm, Stockholm, Sweden, personal communication).

In New Brunswick, Canada, salmon aquaculture production is concentrated in the Quoddy Region, where 96 salmon-farming sites are located within a rectangle of approximately 50 km by 40 km. In 2001, based on aquaculture production of 35,000 t, the exogenous N and P inputs into coastal waters through aquaculture operations were 1225 and 245 t, respectively. This significant nutrient loading does not rapidly disappear because of the exceptional tidal and flushing regime of the Bay of Fundy. The circulation in this bay is more likely that of a bathtub with tides going up and down on opposite sides than that of a bay with an open-ended mouth and a unidirectional flow. Considering only Passamaquoddy Bay (an embayment within the Bay of Fundy), Ketchum and Keen (1953) estimated a flushing time of about 15 days; the water residency time for the whole Bay of Fundy is probably around 76 days (F. Page, Department of Fisheries and Oceans, St. Andrews, Canada, personal communication). This clearly indicates that nutrient bioavailability, even at diluted levels, remains significant for a long period of time, which may put the nutrient carrying capacity of the Bay of Fundy at risk, especially when a nutrient-generating activity is geographically highly localized. Of course, the aquaculture industry is not the only source of nutrification and should not be the only one to be singled out. There are other point- and non-point-sources such as agricultural runoff, industrial runoff, urban and rural effluents, and sewage treatment facilities. However, as a precautionary measure, those in charge of aquaculture operations in the bay should develop practices that ensure remediation of the consequences of their activities.

This is precisely the type of situation in which seaweeds are important to coastal ecosystems. Seaweeds can be used in integrated multi-trophic aquaculture (IMTA) systems to bioremediate the coastal-water nutrification. Physiologically, seaweeds can be viewed as bioengineered systems that take up nutrients like sponges absorb water. However, similarly to a sponge, they can become nutrient-saturated. By periodically harvesting the saturated tissues, a significant quantity of nutrients can be removed from coastal waters and the regrowth of new tissue can continue the nutrient scrubbing process. Thus, these naturally appropriately engineered systems can compete with recent, human-engineered, proposed solutions, which need the test of time.

For rapid growth and appropriate marketable pigmentation, *Porphyra* (commonly known as nori) requires constant availability of nutrients, especially in the summer, when nutrients can become depleted (Chopin et al., 1999b). Cultivation of nori in proximity to salmon cages facilitates utilization of the nutrients loaded into the water by these fish farms; those nutrients then become valued resources (wastes become fertilizer) and can be managed. The desirable algal crops compete with undesirable algal nuisances for the nutrients. This reduces the likelihood of phenomena such as green tides in the vicinity of finfish aquaculture operations (Chopin et al., 1999b). This IMTA represents a clear case of mutual benefits for the co-cultured organisms. Seaweeds utilize the surplus nutrients for growth and fish health is enhanced because the water quality is improved.

We have investigated the relationship between N, P, and pigment (phycoerythrin and phycocyanin) contents of *Porphyra purpurea*, *P. yezoensis*, and *P. umbilicalis*, and N and P concentrations in seawater at sites remote from finfish aquaculture operations and at sites of experimental nori/salmon IMTA (Chopin et al., 1999b). Figure 1 exemplifies the differences in the quality of *P. purpurea* grown in these two environments at a time of the year when seawater nutrient availability is much reduced (averaging 2.98-μM N and 0.69-μM P). The pale, slow-growing nori, collected from a location remote from aquaculture operations, contains 24.7 ± 0.1 mg N/g dry weight (DW) and 2.0 ± 0.3 mg P/g DW. The healthy, fast-growing nori, collected from a location near a salmon aquaculture cage, contains 40.6 ± 0.1 mg N/g DW and 3.3 ± 0.1 mg P/g DW. *Porphyra purpurea* grown at this site has a constant and abundant supply of nutrients in the seawater (averaging 6.70-μM N and 0.87-μM P).

Based on the N and P numbers mentioned above, 22 and 27 standard nori nets would be necessary for the complete scrubbing of N and P, respectively,

Figure 1. Samples of *Porphyra purpurea* (nori) collected from a site remote from aquaculture operations (left) and from a site in proximity to salmon aquaculture (right)

per ton of salmon per year (Chopin et al., 1999b). These numbers are manageable over a year when one considers that nets can be stacked at certain periods in the cultivation process and that several harvests can be conducted over a growing season. However, rather than complete N and P scrubbing, the objective of cultivating desirable algal crops should be to reduce nutrient concentrations in seawater and, thereby, the probability of blooms of problem algal species that can trigger costly hypertrophic events such as eutrophication, diseases, harmful algal blooms, and green tides (Bruno et al., 1989; Folke and Kautsky, 1989; Merrill, 1996). Thus, fewer nets would be necessary.

We have also been working to estimate the *Porphyra* production required to remove N and P generated by a land-based fish farm (operated in tanks by Great Bay Aquafarms, Incorporated, New Hampshire, USA). The farm has an annual production of summer flounder (*Paralichthys dentatus*) fingerlings and adults of 8000 kg/yr and produces an effluent with average inorganic nutrient concentrations of 143-μM N and 10-μM P and a flow rate of 190 l/min. Thus, the farm discharges about 547.2 g of N and 82.1 g of P per day. We are presently developing a system for obtaining the best compromise between algal stocking density, growth rate, biomass yield, N and P uptake, and harvesting frequency for optimized bioremediation capacity (optimal nutrient removal with the smallest "footprint"). An accrued benefit to operators of this type of aquaculture is that discharged (unassimilated and/or excreted) N and P, which represent a loss of money, can be captured and converted into the production of salable nori and biochemicals, hence generating revenues that more than compensate for the expenses. Additionally, as legislative guidelines, standards, and controls on the discharge of inorganic nutrients from aquaculture operations into coastal waters become more stringent, bioremediation via the production of seaweeds could help the fish aquaculture industry avoid noncompliance problems.

3. DEVELOPMENT OF OPEN-WATER AQUACULTURE OF *CHONDRUS CRISPUS*

Raking, by hand or with a horse, of the carrageenophytic red alga *Chondrus crispus*, commonly known as Irish moss, for commercial gain was practiced as early as the mid-1920s in New Brunswick, Canada (Chopin, 1998); drag-raking of nearshore beds, from boats, started in the early 1950s in Prince Edward Island. Land-based aquaculture of *C. crispus* was initiated in the 1970s (Neish et al., 1977). After 15 years of research, some believed that *C. crispus* tank aquaculture in temperate regions could not compete in the carrageenan market with the harvest of natural populations or with tropical open-water aquaculture, mostly because operational and labor costs were high and solar and thermal conditions were inadequate (Bidwell et al., 1985). Others, such as Acadian Seaplants Ltd. personnel, persevered; they developed and adapted large-scale facilities to culture *C. crispus* for the production of an edible, high-added-valued product by manipulating the color and texture of selected isolates (Craigie et al., 1999).

Open-water aquaculture of carrageenophytes such as *Kappaphycus*, *Eucheuma*, and *Betaphycus* has been extremely successful in tropical regions (Doty, 1987), but has rarely been attempted in temperate regions (Chopin et al., 1999a). We decided to re-examine the potential of *C. crispus* for open-water aquaculture. We carefully selected strains and sites, and developed a new culture method using mussel "socks" (Figure 2) and an extended grow-out period. The population of origin, from a shallow inlet in northeastern Prince Edward Island (Basin Head), is unique in the Maritime Provinces of Canada. It is made of unattached, large, thick, mostly gametophytic fronds and reproduces almost entirely vegetatively through fragmentation. However, this morphotype presently cannot be discriminated from others by the molecular techniques used thus far (Chopin et al., 1996; Donaldson et al., 1998; Donaldson et al., 2000). Chopin et al. (1999a) demonstrated that Basin Head plants can be successfully transplanted to other sites with environmental conditions that yield comparable or even higher *C. crispus* productivity.

Daily growth rates (DGRs), which ranged 3–4%/day (d) (some plants exceeded 6%/d), are lower than those recorded in tropical and subtropical farms of *Kappaphycus* and *Eucheuma*, the current main sources of carrageenans in the world (Chopin, 1998). These farms generally have DGRs that range

Figure 2. Mussel "socks" inoculated with the red alga *Chondrus crispus* (Irish moss)

3–5%/d (farms able to sustain a DGR of 7%/d are considered to be highly productive [Chopin et al., 1999a]). These relatively lower DGRs are, however, compensated for by the high carrageenan yields of this strain of *C. crispus* (58–74% DW in the summer) compared to *Kappaphycus* and *Eucheuma* (20–30% DW, or even down now to 11% DW [Chopin et al., 1999a]). The carrageenan yields of this *C. crispus* strain are also high compared to those generally reported for *C. crispus* harvested from natural beds (40–50% DW [Chopin, 1986]). This could be explained by strain selection and by nutrient levels in the algal tissues, which are correlated with ambient seawater nutrient levels at the sites (Chopin et al., 1999a). In Figure 3, we show that carrageenan contents follow the reverse trend of those of tissue P. A significant increase in carrageenan content occurred in June 1997 and corresponded to a drop in tissue total-P content; whereas, in 1998, the increase in carrageenan content and the concomitant decrease in tissue total-P content were much later. This is a clear illustration of what has been referred to as the "Chopin effect" (an inverse relationship between P and carrageenan contents [Chopin et al., 1990, 1995; Chopin and Wagey, 1999]), and is analogous to the "Neish effect" (Neish et al., 1977), which describes the impact of nitrogen nutrition on carrageenan content.

We are presently testing several sites in the proximity of mussel and oyster aquaculture operations to define the optimal physical (flushing rate, sediment, bottom vegetation), chemical (nutrient availability), and biological (biofouling) conditions for growth rates and carrageenan yields. Different sock handling

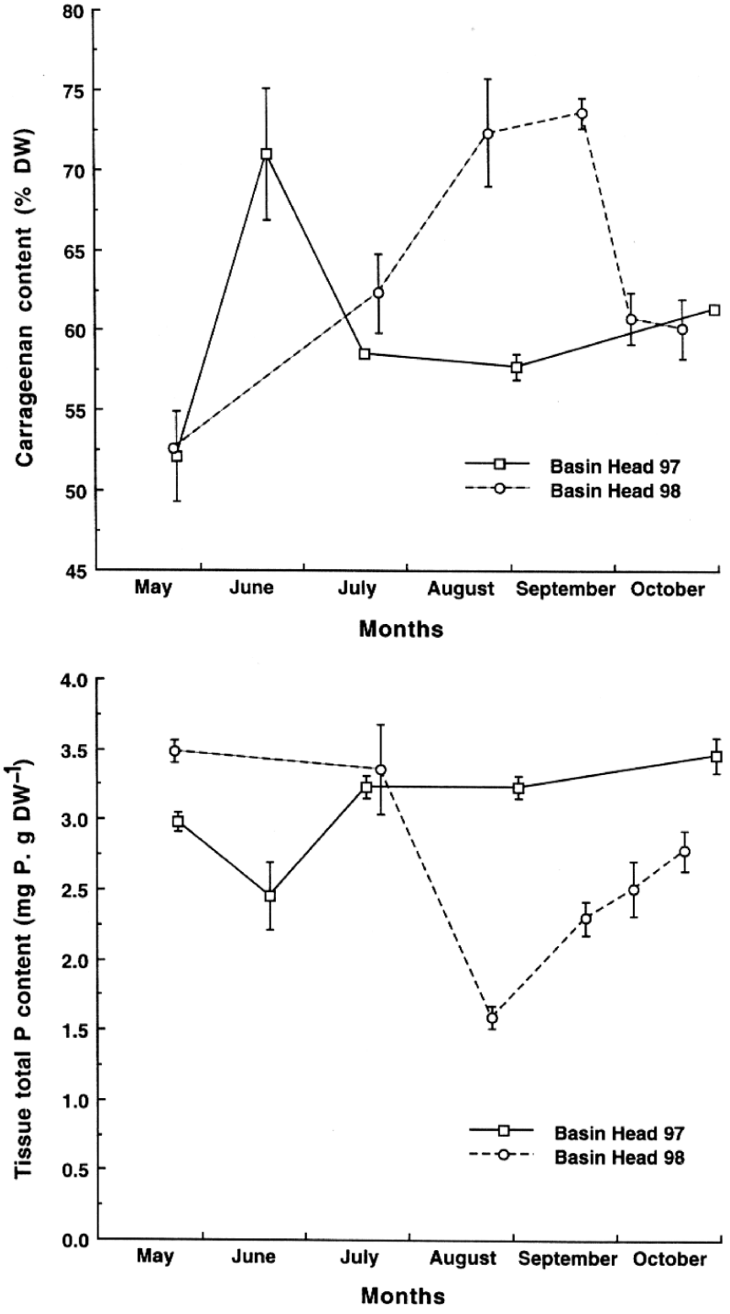

Figure 3. Variations in carrageenan content (% dry weight [DW]; top) and in tissue total phosphorus content (mg P/g DW; bottom) in *Chondrus crispus* at Basin Head, Prince Edward Island, Canada, May–October 1997 and 1998. Values represent means ($n = 3$) ± SD

methods, grow-out techniques (hanging or bottom culture, socking density, size of frond fragments) and timing strategies of inoculation and harvesting are also tested to develop the most efficient and commercially viable techniques. If DGRs could be improved and with carrageenan contents two to three times those of *Kappaphycus* and *Eucheuma*, this approach could become economically competitive with mechanization. Moreover, because the phycocolloid industry presently wants to diversify its sources of raw material, there is a renewed interest in cold-water species of carrageenophytes. *Chondrus crispus* culture could also serve as any of the following:

1. an alternative source of Irish moss that would complement the declining harvest of wild C. *crispus* (Chopin, 1998);
2. a source of high-quality carrageenans in the κ-family (instead of the κ-/λ-mixture from harvested natural beds);
3. a component of the economic diversification of the shellfish and finfish aquaculture industry, which could integrate it as a complementary activity that would provide additional income and serve as a natural scrubbing system for disposal of excess N and P.

4. CONCLUSIONS

Nutrification of coastal waters as a result of anthropogenic activities is a worldwide phenomenon increasingly recognized as a pressing issue. Finfish aquaculture can be, at a regional level, one of the contributors to this significant nutrient loading (Beveridge, 1987; Kautsky et al., 1997). This often monospecific and animal "fed" type of aquaculture is presently at a crossroad; as its economic and environmental limitations are realized, its sustainability is questioned (Naylor et al., 2000). To avoid pronounced shifts in coastal processes when the carrying capacity of the environment is exceeded, fed finfish aquaculture should be integrated with inorganic extractive seaweed aquaculture and organic extractive shellfish aquaculture to reduce nutrient loading (especially of N and P) and organic deposition. There is no doubt that the aquaculture industry is here to stay in the "coastal scape." However, it has to develop, in a timely manner, sustainable aquaculture practices. Responsible aquaculture now needs to be supported and implemented, rather than simply described in codes of good or best practices.

Considering economically important seaweeds as renewable biological nutrient scrubbers demonstrates an understanding of one of their fundamental roles in coastal ecosystems and validates their use in integrated aquaculture systems. Seaweed aquaculture is an excellent choice for eutrophication abatement (bioremediation), and also provides another value-added marine crop for diversification of the aquaculture industry (Mumford and Miura, 1988; Petrell et al., 1993; Chopin et al., 1999b).

To work, integrated aquaculture still requires fine-tuning. It is highly site-specific (e.g., what flow rates and nutrient concentrations are available?) and species-specific (which species to integrate, and in which proportions?). Thus, research and development (R&D) is still needed to arrive at the optimal system for each particular bay. Rapid overgeneralization of techniques and protocols would not take into consideration the particularities of each specific bay. If the species of seaweeds selected for cultivation are efficient biological nutrient removal systems, the productivity and carrying capacity of particular sites could be improved. Consequently, the number of fish cages or tanks could be increased and even more revenues could be generated by the aquaculture industry, which seeks sustainability, long-term profitability, and responsible management.

To successfully develop integrated aquaculture systems, much R&D remains to be undertaken, particularly in the following areas:

1. transfer and modification of cultivation technologies for use in local environments and to fit local socioeconomic situations;
2. development of cultivation techniques for marketable, fast-growing, native species that will be available for harvest at different times of the year and in diverse habitats;
3. development of site-specific modeling capabilities to define the appropriate proportions of the different co-cultured organisms.

Pivotal for its success in the future, the aquaculture industry will have to wisely invest in R&D to move in new directions, through the development of innovative bioengineering concepts and practices that will optimize its efficiency and the diversification of marine crops, while ensuring that the health of coastal waters is maintained.

ACKNOWLEDGMENTS

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CHAPTER 26

USING NATURAL ECOSYSTEM SERVICES TO DIMINISH SALMON-FARMING FOOTPRINTS IN SOUTHERN CHILE

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Abstract: Through field observations and a compilation of several manipulative and mensurative experiments carried out in freshwater and marine ecosystems in southern Chile, we here provide alternatives for using natural ecosystem services to diminish salmon-farming ecological footprints. In freshwater lakes, where early stages of salmon growth are completed, the high filter-feeding rate of the native bivalve, *Diplodon chilensis*, can significantly reduce the effect of salmon farming by maintaining oligotrophic conditions. The constant movements of *D. chilensis* on the bottom sediment substrate generate enough bioturbation to reduce the impact of nutrient accumulation (nitrogen and phosphorus) due to salmon farming. We documented a similar mitigating effect in marine mussel (*Aulacomya ater*) beds, on rocky substrates in the channels and fjords where salmon are grown in pens. There is an additional benefit in such cases because *A. ater* is a valuable commercial resource. Artificial reefs, both in lakes and the inner sea, provide refuges for crustaceans and fish. In particular, these artificial structures enhance juvenile recruitment of invertebrates and fish. In freshwater ecosystems, native endemic crustaceans (crabs [*Aegla* sp.] and crayfish [*Samastacus spinifrons*]) are capable of processing excess food deposited on the bottom from salmon pens. Marine crabs (*Cancer edwardsi*) perform a similar ecological role under salmon pens in the inner sea. In summary, artificial reefs provide a way to link salmon farming with bottom heterogeneity and thus reduce the impacts of the salmon farms by facilitating the incorporation of organic matter into benthic productivity. Excess food is utilized around salmon-farm pens by both native fish and escaped salmon. These fishes, in turn, are prime targets for sport fishing, which, if managed in an appropriate way, could become an effective way to remove assimilated nutrients and organic matter via the removal of fish, which are at the top of the food web. This practice would have the additional benefit of removing salmon that have escaped from culture pens, particularly if the fishery was conducted around the pens.

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Key words: artificial reefs, aquaculture, Chile, environment, freshwater, impacts, marine, salmon, sport fishing, trout

1. INTRODUCTION

In salmon farming, floating pens are usually utilized to grow fish during both their freshwater growth phase and (more often) marine growth phase. Such culture practices produce substantial carbon, nitrogen (N), and phosphorus (P) inputs into the lake, bay, or estuary where the pens are located. These additional nutrient loads can enhance eutrophication processes, which may cause biodiversity loses. Such an effect is considered as one of the ecological footprints of aquaculture (Folke et al., 1997). Thus far, most solutions to minimize this effect have involved diminishing the P concentration in diets and, thereby, reducing conversion factors in the farmed fish (Sandnes and Ervik, 1999). However, there are a few additional ways to handle the excess nutrients released into aquatic environments even after these actions have been taken.

In Chile, salmonids (rainbow trout [*Oncorhynchus mykiss*]; coho salmon [*Oncorhynchus kisutch*]; Atlantic salmon [*Salmo salar*]) are mainly grown in lakes, coastal seas, and fjords between 40°S and 44°S latitude. Salmon farming in Chile has increased exponentially during the past 15 years and has become a key activity contributing to Chilean economical development. Salmon farming has promoted economic growth in significant ways, both for the southern regions and for the whole country. Currently, Chile is the second largest producer of salmon in the world; the total export volume during 2005 was nearly 588,000 metric tons and had an economic value close to US $1, 8 billion (Salmon Farmers Association, www.salmonchile.cl). Salmon-farming activities involve a large number of jobs in southern Chile, including approximately 47,000 jobs directly related to salmon farming (Salmon Farmers Association, 2003). The expansion of salmon farming has created a situation in which the managers of salmon farms will have to consider the preservation of biodiversity to coexist in equilibrium with other activities and needs for which aquatic ecosystem services in Chile are used.

One key issue for sustainable farming of carnivorous finfish is the transformation of fishmeal-based feeds into fish biomass; this is inefficient and produces large amounts of organic matter as waste. If we could find alternative pathways to that of bacterial degradation for this organic matter, such as producing additional invertebrate and vertebrate biomass, the whole process would be more efficient and more environmentally friendly. Here we present possible ways to enhance incorporation of these nutrients into native-species food webs by using filter feeders, enhancing bottom habitat heterogeneity, and managing free-living fish around the net-pens containing salmon (salmon pens).

Some ecological hypotheses have proposed that the increased nutrient inputs from fish farming could provide for extended food webs (Persson, 1994) and, possibly, increase biodiversity, at least within a certain range of the salmon pens. The increased habitat heterogeneity provided by salmon pens and the increased biodiversity provided by the organisms that colonize under and around them could also promote the development of more extended and complex food webs and, thereby, perhaps faster nutrient cycling oriented to higher secondary production. Here, we integrate information from several independent experiments and mensurative studies in which we explored the potential for utilization of excess nutrients and organic matter supplied by salmon farming and examined habitat heterogeneity associated with salmon pens at both freshwater and marine sites.

2. METHODOLOGICAL APPROACH

To build our case in this paper, we developed supporting evidence from several different lines of inquiry: experiments under controlled conditions (using freshwater mussels in tanks and in a lake), field manipulations both at freshwater and marine sites (using artificial reefs), and direct observations and data-gathering on free-living populations (using marine mussels, fish abundance, and diets) at sites with and without salmon farms in freshwater and marine channels.

In our initial experiment, conducted in both freshwater juvenile-salmon-farming tanks and in the field (lakes), we followed the environmental conditions under salmon net-pens with and without the freshwater mussel *Diplodon chilensis* on the bottom. We measured the effect of freshwater mussels as bioregulators of eutrophication caused by salmon farming. Soto and Mena (1999) more precisely described the methodology and results for the experiment conducted in the tanks. In the field, the evaluations were performed in several freshwater and marine areas in southern Chile (Figure 1). One of these was Lake Llanquihue (41°08′S and 72°47′W), the largest lake in Chile (870 km^2) and the one in which 35% of the total salmon smolt production in the country is conducted. There, we monitored mussel populations within one particular bay, under salmon pens and at control sites (net-pens without salmon) nearby where no salmon farming is conducted. Additionally, we monitored three bays with salmon-farming activities and another three bays without farms (control sites). To analyze the effect of the mussels on the sediments under two salmon pens and at one control site, we deployed open, 80-cm × 80-cm boxes containing 20 mussels each and another set of equal number but without mussels on the bottom. The boxes were covered by coarse mesh to avoid predation on the mussels. After two months, we took three sediment samples from each box to analyze nutrient content (total P and total N).

As another approach, we collected information on biomass and biodiversity development at marine artificial reefs deployed on flat bottoms in the inner seas

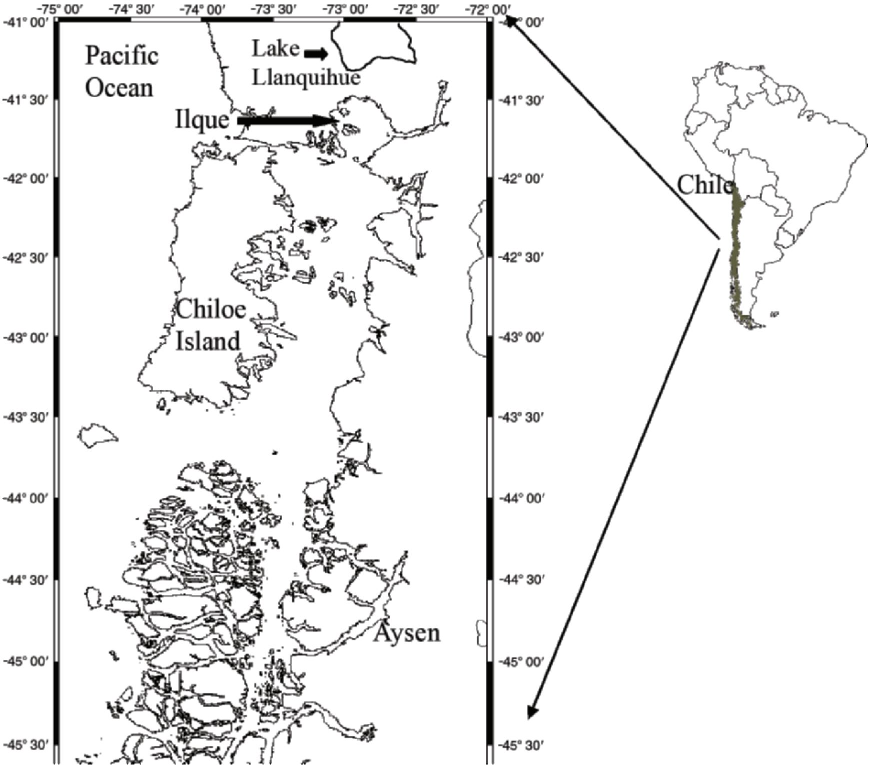

Figure 1. General map of study location, showing Lake Llanquihue, and Ilque bay within the inner seas of southern Chile. Inset: location of Chile in South America

of Chiloé (Jara and Cespedes, 1994) (Figure 1). Later, with this information in mind, we deployed artificial reefs under salmon pens both in lakes and at marine sites to evaluate native-species abilities to utilize the organic matter produced by salmon farming and non-eaten feeds. In Lake Llanquihue, we tied 12-, 18-, 23-, and 46-mm PVC tubing pieces 0.8 m in length together to form a cubic structure of 0.8 m × 0.8 m × 0.6 m (Figure 2). Each tube piece was open on one end (the exposed one) and sealed on the other. Three structures of this sort were installed under each of two salmon pens and another three were located at each of two control sites; that is, 12 structures in total (Soto et al., 1995). These structures were intended to host freshwater crayfish and crabs, which are common in Chilean lakes (Soto and Campos, 1995) and could benefit directly or indirectly from the organic matter that filtered through the salmon pens to the bottom (Soto et al., 1995). At Ilque, a small marine bay in the inner sea (Figure 1), we deployed cement cubic structures of 0.015 m^3 to form artificial reefs under and around salmon pens and we followed species colonization and community development at those sites. For comparison to similar areas

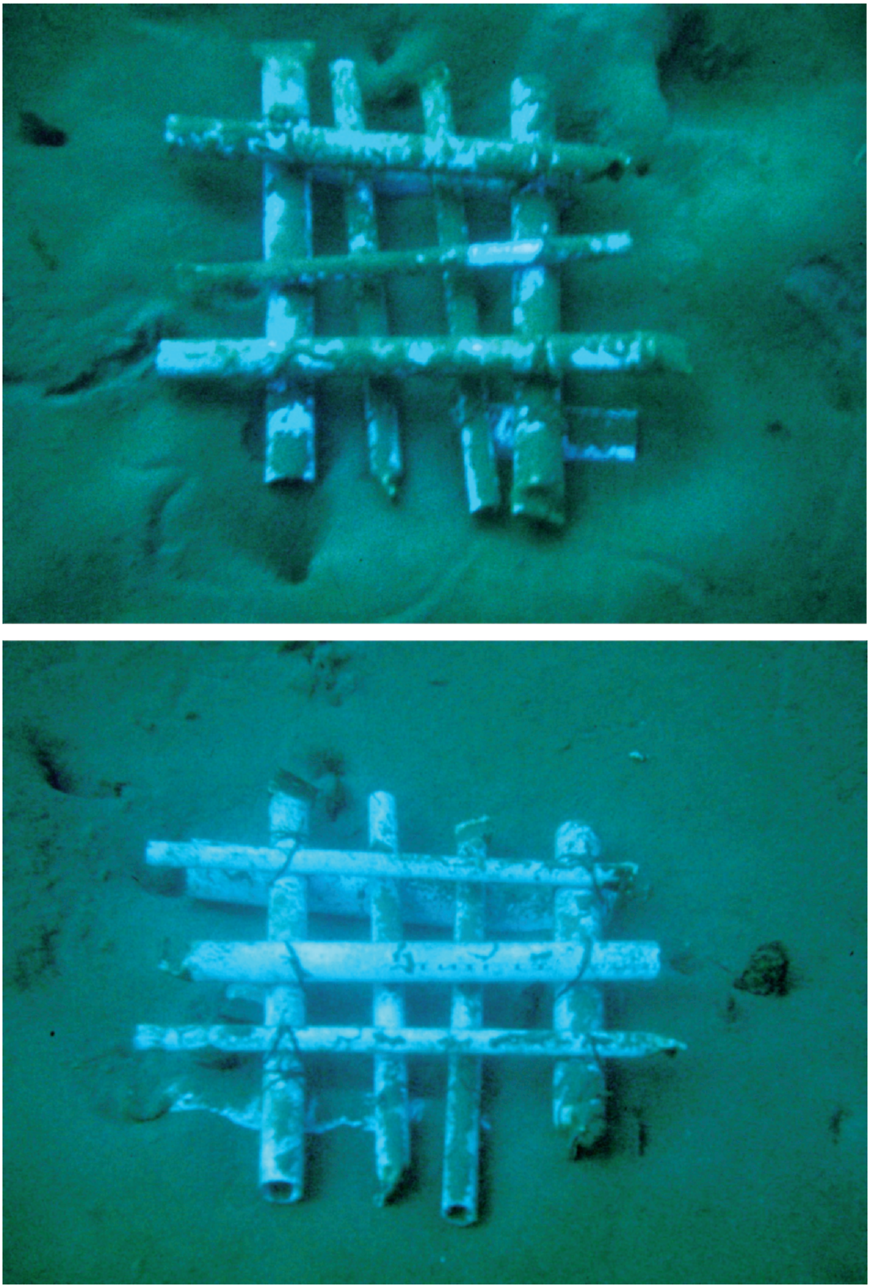

Figure 2. Examples of artificial (PVC tubes) reef structures placed on lake bottoms for freshwater crustaceans

distant from salmon pens, we referred to a previous artificial reef experiment in which we demonstrated the ability of artificial reefs to improve total biomass and biodiversity (Jara and Cespedes, 1994).

As a final approach, we also report our observations regarding the tendency of free-living fish (mostly native species, but some introduced salmon as well) to aggregate and feed around salmon farms and to utilize salmon feeds and other resources associated with the pens. As an extension to the different alternatives proposed, we also explore the use and management of sport fishing as a way to enhance nutrient cycling and control exotic salmon species.

3. RESULTS AND DISCUSSION

One reason for the success of salmon farming in Chile has been the water quality in the farming areas, particularly the lakes, which are deep, oligotrophic, and very transparent. However, this quality may change since salmon farming in floating pens adds nutrients to the benthic environment and the water column. Approximately 70% of the P and 30–50% of the N in salmon feed are not assimilated by the cultured fish; thus, these nutrients are released to the environment (Ackefors and Enell, 1990). One way to diminish this environmental impact is to prevent the nutrients from being lost to bacterial degradation. This can be achieved by finding pathways that are alternative to direct bacterial degradation and that utilize native species and ecosystem processes. Coupling these processes to aquaculture activity is still a challenge, but we propose here some first steps that could be successful in Chile.

3.1. Native Filterfeeder Bivalves Provide Ecosystem Services and Natural Spatial Structuring

One of our approaches to reducing the environmental "footprint" of open-water net-pen salmon farming is to improve the ability of native species to use the excess nutrients produced by this activity. Excess nutrients can be assimilated by other species to produce additional biomass that may not have been produced in the absence of salmon farming. One alternative we considered has been the management and use of mussel beds as filtering devices under fish farms, both in freshwater and marine environments.

Native freshwater mussels have a great filtering capacity and at the same time generate bottom heterogeneity, which provides opportunities for other species to use the space and energy (Soto and Mena, 1999). In our tank experiments, the chlorophyll *a* concentration was reduced by two orders of magnitude (from ~300 to 3 μg/l) in tanks with *D. chilensis* compared to tanks with only salmon (Figure 3). When mussels were included in polyculture with salmon, the chlorophyll *a* concentration was reduced by up to one order of magnitude. Concentrations of total phosphorous, PO_4, and NH_4 were also reduced by about one order of magnitude (data not shown). The mussels were able to change the water

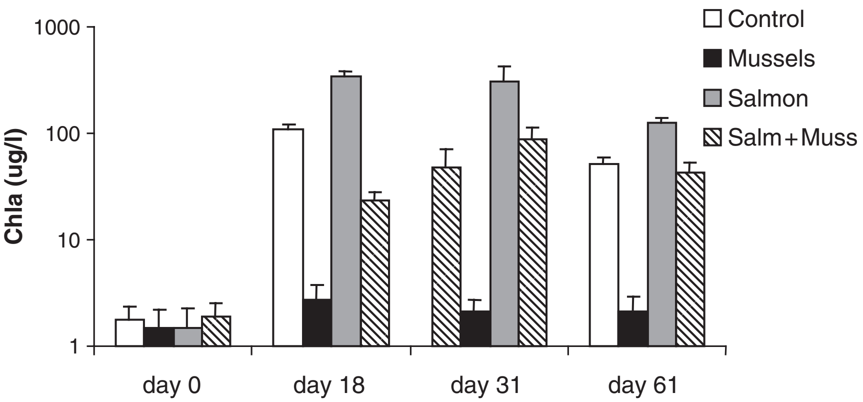

Figure 3. Chlorophyll *a* (chla) concentration in experimental, juvenile-salmon-farming tanks in southern Chile. Control tanks had no freshwater mussels or salmon; experimental tanks had salmon only, mussels (*Diplodon chilensis*) only, or both salmon and mussels (Salm + Muss). The experiment started on day 0, bars are averages of three replicates plus standard errors (vertical lines) (redrawn from Soto and Mena, 1999)

Table 1. Change in sediment chemical proportions (percentages, ± standard errors) with (*Dip*) and without (No *Dip*) mussels (*Diplodon chilensis*) under salmon pens ($N = 2$) and at a control site ($N = 1$). *P* values represent statistical difference (Kruskal–Wallis test) between salmon pens with and without mussels. NS = not significant

	Control		Salmon pens		
Chemical	*Dip*	No *Dip*	*Dip*	No *Dip*	P
P	70	9	158 ± 16	122 ± 8	NS
N	2	93	9 ± 8	69 ± 6	0.026

column conditions in the tanks from hypereutrophic (a consequence of salmon farming) to oligotrophic or mesotrophic (Soto and Mena, 1999).

Diplodon chilensis can change the N/P ratio of the sediments (and probably the water column) by trapping more P than N in the sediments, mostly by the production of pseudofeces. Thus they could increase P input to the sediments (although we could not demonstrate it statistically) and significantly contribute to N exports into the water column, probably by excreting and facilitating bacterial action (Table 1). Although the mussels may enhance the accumulation of organic matter in the bottom, they actually contribute to dispersion of material by promoting perturbation and oxygenation of sediments through their continuous active displacements and movements in the sediments. In general, *D. chilensis* density is greater in areas with greater organic-matter input—for example, in bays with salmon farming or in areas with sewage outflows. However, the mussels do not concentrate at the sources of the nutrients but spread and move around in proximity to them (Soto and Mena, 1999).

These bivalves also serve as a food source and, because they are large, long lived, stand upright on the bottom, and protrude 2–3 cm above the sediments, they contribute to increased bottom heterogeneity by acting as substrate for other invertebrates such as freshwater sponges. Both a native freshwater crab (*Aegla* sp.), and a common freshwater crayfish (*Samastacus spinifrons*) feed actively on the mussels as soon as these crustaceans are large enough to break and open the shells. Native fish and free-living salmonids are also attracted to these areas and, in turn, feed on the *Aegla* sp., *S. spinifrons*, and aquatic insect larvae. Thus, these mussels serve as an energy source to the benthic and pelagic food webs, act as a sink for nutrients, and contribute to a more rapid recycling of organic matter and nutrients. We have also found that total species richness is improved in areas under salmon pens with mussels (Soto and Mena, 1999). Persson et al. (1992) has shown that habitat structure, more than other factors, can enhance food-web length and species richness. In addition, these mussels clearly benefit from salmon farming; in our study, their biomasses were significantly higher at sites with farms compared with sites without farms (*t*-test to compare average values for three sites with and three sites without salmon, $P = 0.042$; Figure 4).

Based on our *D. chilensis* research and other information, we could expect that freshwater mussels, clams, and other large bivalves would be key species in association with salmon pens in the following ways:

1. a large proportion of the particulate material supplied by salmon farms could be collected and processed;
2. rates and pathways for nutrient cycling would be controlled;
3. a food supply, refuge, and spatial complexity would be provided for other species (Jones et al., 1994), thus enhancing biodiversity.

Salmon farmers can benefit from the natural "services" performed by *D. chilensis* and other bivalves by locating the farms in areas with large populations of these species or by introducing more mussels and other bivalves

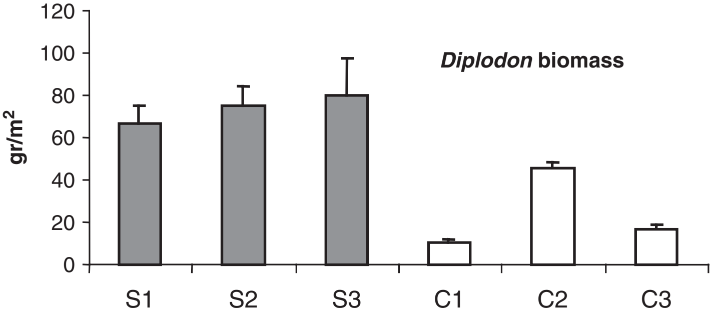

Figure 4. Average *Diplodon chilensis* biomass/m^2 in southern Chilean bays with salmon farming (S), and in bays without salmon farming (C). Means are calculated on ten replicates per site; lines above bars are positive standard errors

into areas of low mussel density. A requisite, however, is that salmon farmers avoid the use of chemicals, which may be accumulated by these mussels.

In the marine stage of salmon farming, marine mussels and other filter-feeding invertebrates (e.g., other bivalves, barnacles, sea squirts) could provide similar services by concentrating and processing organic matter (Prins and Smaal, 1994; Stirling and Okumus, 1995). This is often the case around salmon farms within the inner seas of Chiloé and Aysen, in southern Chile (Soto et al., 1999). Due to over-exploitation, marine bivalve beds are often restricted to certain areas where fisheries for these invertebrates cannot operate; for example, in the vicinity of salmon farms and in areas frequently affected by red tides. Indeed, some bivalve populations are only expanding or remaining viable around salmon-farming sites (Soto et al., 1999). In areas of salmon farming, and particularly under salmon pens, density of the large bivalve *Aulacomya ater* is high (Figure 5A); whereas in open areas where marine resources are harvested, it is virtually absent (Figure 5B). In this case, the salmon farms may even be assisting in the preservation of this species at a local level. (However, testing for potential contamination [pigments, antibiotics, etc.] of mussels that feed near salmon cages is a remaining issue.)

In general, the nutrient and organic-matter inputs from salmon farming in Chile could be utilized and processed by ecosystems in more efficient ways. Appropriate management of these systems should enhance their efficiency and reduce the environmental impact of nutrient loading from salmon farms into the water. As an ancillary benefit, the bivalves themselves could be harvested. The growth of benthic bivalves should be enhanced under salmon pens, where nutrients and particulate matter are abundant and can be utilized by these bivalves.

3.2. Artificial Reefs: Linking Salmon Farming to Bottom Heterogeneity

Our second approach was to provide artificial habitats (reefs; Figure 2), to enhance native-species use of nutrients and, thus, provide extra biomass for harvesting. Artificial reefs are commonly used to provide refuge and promote concentration of fauna for harvesting by humans. However, they have also been blamed for concentrating fauna for easier over-exploitation and resource depletion. This may be true when resources and nutrients are limiting and when fishers deplete the system of biomass. Here, however, the idea is to enhance the use of extra nutrient inputs from salmon farming to increase faunal biodiversity and biomass. Artificial reefs or some other type of improvement regarding habitat availability and structure can certainly improve species richness and biodiversity (Jara and Cespedes, 1994).

We have explored the ability of two types of artificial structures (reefs) we constructed to improve biodiversity and productivity both in freshwater and marine environments, with and without salmon farming. Three aspects were significantly enhanced by the artificial reefs:

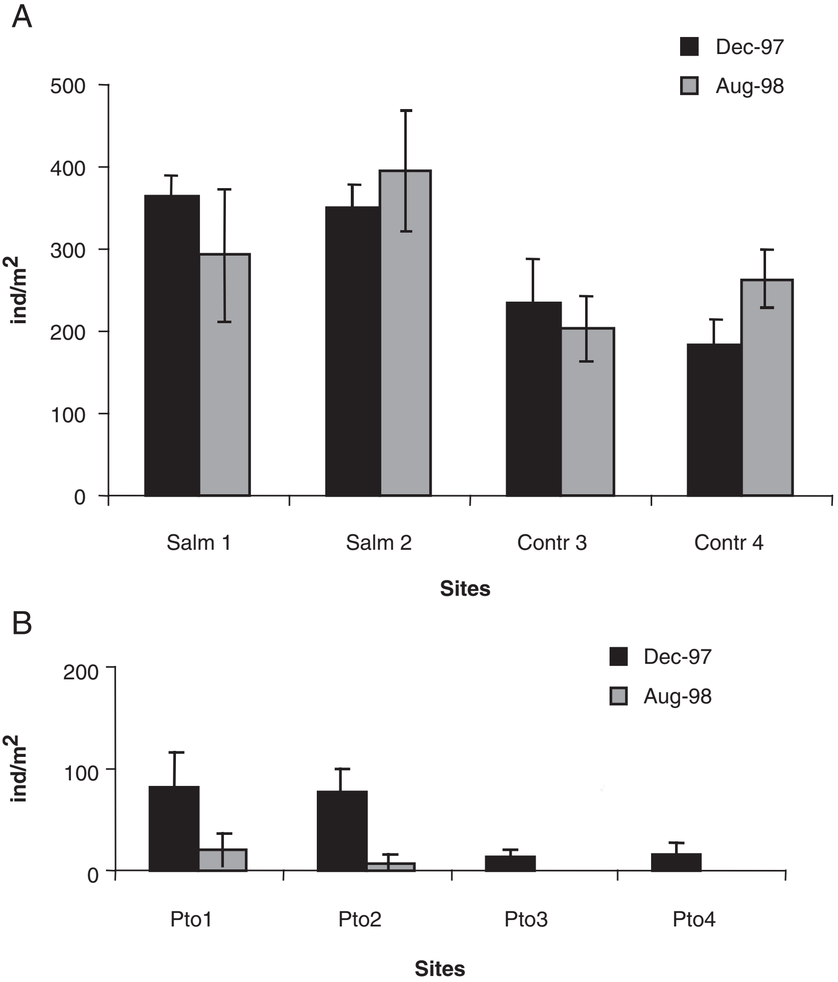

Figure 5. Bivalve density (individuals [ind]/m^2) of *Aulacomya ater* in southern Chilean sea channels with and without salmon farming. Average values represent mean of at least five independent samples obtained by diving. A. In proximity to salmon farming. Salm 1 and Salm 2 represent collections made under salmon pen locations; control sites (Contr 3 and Contr 4) were further away from pens. B. In a sea channel without salmon farming. Pto = sampling location. This channel was affected by human harvesting, particularly at Pto3 and Pto4

1. juvenile crustacean recruitment;
2. overall species richness and biomass;
3. nutrient cycling, as evidenced by a 30% to 50% decrease in total phosphorous in sediments (Soto et al., 1996).

As expected, the reef structures were readily colonized by crayfish and crabs in freshwater (Soto et al., 1996). The crayfish are valuable as quality food. Indeed, *S. spinifrons* could be an attractive crayfish for the food market; however, massive production of this species has not yet been attempted. Crayfish recruitment inside the reefs under salmon pens containing salmon (salmon pens) was, overall, not significantly different from recruitment inside reefs under empty pens (control sites) (Figure 6A). However, burrows (indicating greater crayfish concentration and activity) were significantly more common under reefs beneath salmon pens regardless of the presence or absence of salmon in the pens, than in reefs located in open water ($P < 0.01$; Figure 6B). In contrast,

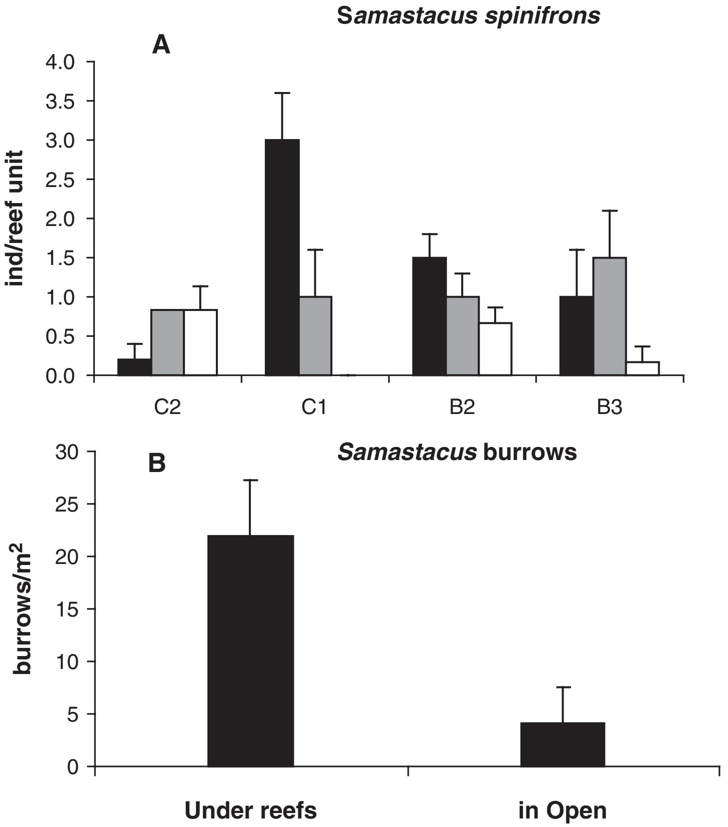

Figure 6. Artificial reef habitat usage by freshwater crustaceans. All reef units were the same size, the same number of reef units was placed under each salmon pen ($N = 3$), and all salmon pens were the same size. The whole reef unit was lifted and washed carefully to obtain the fauna. Lines above bars are standard errors. A. Average abundance of freshwater crayfish (*Samastacus spinifrons*) inside reef units, under salmon pens with salmon farming (B2 and B3) and under empty salmon pens (C1 and C2). Black bars = August, 1995; gray bars = October, 1995; white bars = November, 1995. B. Average number of *S. spinifrons* burrows under artificial reefs and in the open (we sampled 3 4-m^2 areas on each case). Reefs under salmon pens and at control sites (net-pens without salmon) are grouped because the average number of burrows under reefs at these locations did not differ significantly.

(*continued*)

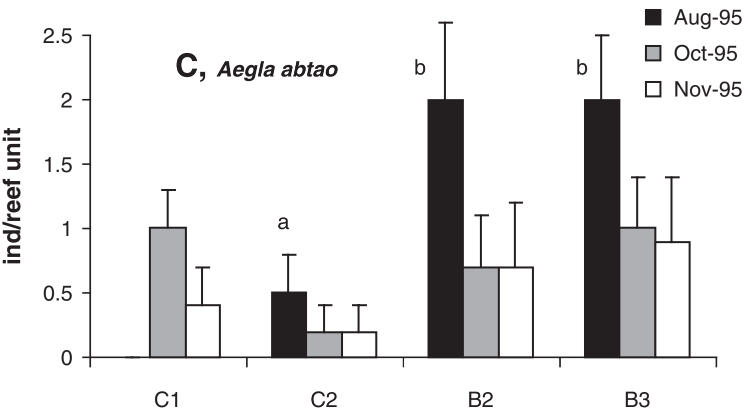

Figure 6. (cont'd) C. Average abundance (individuals/reef unit) of the freshwater crab *Aegla abtao* inside reef units under empty salmon pens (C1 and C2) and under salmon pens with salmon farming (B2 and B3). Mean values with different letters (a vs. b) were significantly different ($P < 0.05$); other means did not differ

recruitment of a freshwater crab, *Aegla abtao*, increased inside reefs under salmon pens compared with reefs at control sites; the differences between control reefs and reefs under the salmon pens were significant at the end of winter (August, $P < 0.05$; Figure 6C). Reef sites under salmon pens also had much greater abundances of free-living, carnivorous fish compared with control sites. Thus, invertebrates under the salmon pens were exposed to greater predation pressure than invertebrates at other locations; that may be why crayfish abundance in reefs under salmon pens did not differ significantly from that in reefs located elsewhere.

We also found that, although total P in the sediments was not significantly reduced under the reefs in freshwaters, total N in sediments was significantly reduced ($P = 0.04$), regardless of the reef position (under salmon pens or at control sites; Figure 7). The reduction of the N in the reef areas may be related to greater aeration of the sediments due to greater bioperturbation under the pens. Thus, the artificial reefs may facilitate an increased use of the organic matter supplied by salmon farming in freshwater; the organic matter in sediments is reduced and the energy available from that matter is transferred through the food web to free-living fish.

Habitat enhancement by artificial reefs has also successfully enriched the biota on monotonous (sandy and muddy) marine coastal bottoms (Campos and Gamboa, 1989). We have tested this at marine sites with and without salmon farming in the inner seas of Chiloé. In previous work (Jara and Cespedes, 1994), we built artificial reefs using 30-cm^3 concrete blocks to increase the biomass of fish and crustaceans in marine soft-bottomed areas. Those reefs promoted species richness; they increased the local biomass and

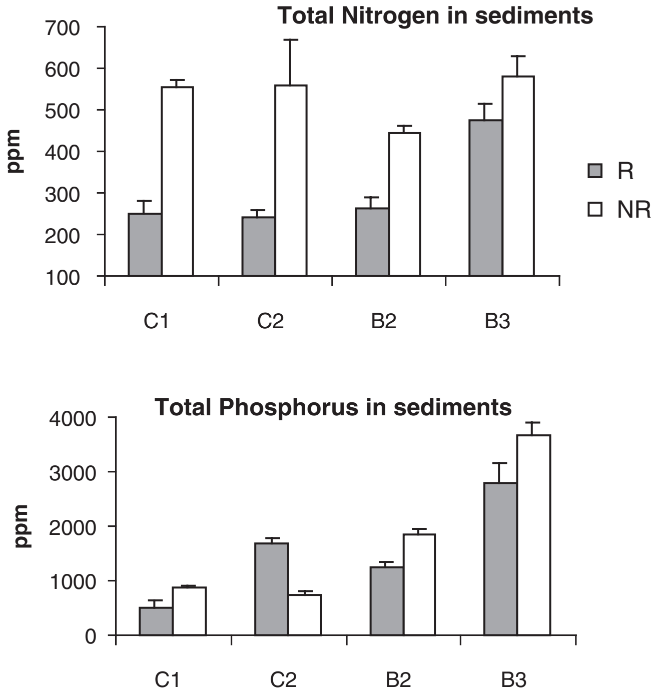

Figure 7. Sediment nutrient (nitrogen, phosphorous) content (ppm = parts per million) at artificial reef areas (R) and at control areas without artificial reefs (NR), in the open (C1, C2) and under salmon pens (B2, B3). Each sample consisted of 300 to 400 g of sediment, obtained with a corer. Nitrogen concentrations under reefs with or without salmon pens above the reefs were significantly lower than nitrogen concentrations in similarly sized areas without reefs. Vertical bars = standard errors

diversity of several groups such as fish, sea urchins, crabs, and macroalgae. Similar experiments that we conducted around salmon farms also promoted a significant increase in abundance, especially of carnivorous fish (*Genypterus chilensis*) and detritivorous crabs (*Cancer edwardsi*) (F. Jara, unpublished data), possibly because they were using the extra organic matter produced by the farms. The types of species we found around the reefs were rare or absent in areas without reefs. Both fish and invertebrate biomass was also greater in areas with both salmon pens and artificial reefs compared with areas without salmon pens. The reefs in areas with salmon pens could produce 3 to 4 times more biomass per unit area than in areas without them. The density of the crab *Cancer edwardsi* more than tripled—from an approximate equivalent of 2 to 14/m^2—in reefs located in a salmon-farming bay. *Genypterus chilensis* (kingklip), a fish of high commercial value in Chile, attained densities of up to 3/m^2 (F. Jara, unpublished data). This greater biomass may be related to increased nutrient availability and secondary production in this bay.

These preliminary experiments suggest that the use of artificial reefs in areas with salmon farming can enhance nutrient cycling and use of the extra nutrient supply. However, placement of artificial reefs under salmon pens should not interfere with water circulation around and within the pens; thus they should be placed in areas of high current flow and water exchange.

3.3. Managing Free-Living Fish Around Salmon-Farming Pens

A third approach we have taken relates to enhancing and managing the fish fauna that surrounds fish farms and actively feeds on the excess food not eaten by the caged salmon or other organisms associated with the farm's site and surroundings. Our studies, both in freshwater and marine environments, show a high degree of utilization of salmon feed and farm-derived waste products by native fishes, including free-living salmonids; 20–80% of the uneaten feed can be directly used by free-living fish (Soto et al., 2002a). This enhancement of available food is associated with an increase in fish biomass and species diversity in waters with salmon farming compared with waters without salmon farming.

The enhanced fish biomass in these bays, in turn, increases sport fishing, which not only provides alternative revenue but also could serve as an important approach and management tool for conservation. Our estimates of fish biomass in freshwater bays with salmon farming range approximately 3 to 20 times greater than fish biomass in bays without salmon farming (Table 2). For example, in several lakes, we have recorded increased native silverside (*Basilichthys australis*) biomass as well as higher total species richness around salmon-farming sites (D. Soto, personal observation). Considering that some native species may disappear due to an increase in the number of free-living trout and salmon from salmon farming (Soto et al., 1996, Soto et al., 2006), we could manage sport fishing in ways to keep these trout and salmon populations under control and thereby favor native species. Simultaneously, this approach would result in the removal of more nutrients from the salmon-farming sites through the removal of the fish, which are the top-level sinks of the excess nutrients produced by the fish

Table 2. Mean values for free-living, freshwater fish biomass and productivity in bays with salmon farms ($N = 4$) and in control sites (bays without salmon farms; $N = 3$) at Lake Llanquihue, Chile. Biomass and productivity were evaluated with gill netting and echosounding prospecting (Palma, 1996)

Free-living species	Type of bay	Biomass (kg/ha)	Productivity (kg/ha/year)
Salmon and trout[1]	With salmon farms	32.8	16.6
	Control sites	1.9	0.8
Native species[2]	With salmon farms	11.1	5.1
	Control sites	3.2	1.4

[1] *Oncorhynchus mykiss* (rainbow trout), *Oncorhynchus kisutch*, and *Salmo salar* (salmons).

[2] *Cauque mauleanum* and *Basilichthys australis* (silversides), *Percichthys trucha* (perch type), *Galaxias platei* (large whitebait).

farming activities. Similarly, in marine salmon-farm sites, the pens attract a great diversity of fish species that consume unused salmon pellets. These include species sustaining high artesian fishing pressure such as the southern hake (*Merluccius australis*), robalo (*Eleginops maclovinus*), and mackerel (*Trachurus murphi*), as well as some escaped salmonids (trout, Pacific salmon, and Atlantic salmon). Thus, extractive fishing would amplify the removal of excess nutrients in both freshwater and marine salmon-farming sites.

To pursue the idea of enhancing sport fishing in salmon-farming areas, it is necessary to clarify the situation of free-living trout and salmon in the country. Chile stands as a biogeographic island from both a terrestrial and oceanic perspectives; the high Andes range forms the eastern barrier of the country and the Pacific Ocean forms the western barrier. Thus, geological events (e.g., continental drift and the rise of the Andes Mountains) created a land in which the freshwater fauna is particularly impoverished and has a high degree of endemism. The introduction of rainbow trout and brown trout species at the beginning of the twentieth century increased biodiversity, in some cases by about 50%.

Unfortunately, the negative effects of the exotic trout on native freshwater fish biodiversity cannot be directly evaluated because, today, there are few, if any, freshwater environments from the Altiplano to Patagonia without trout. In fact, in some rivers in northern Patagonia (43°S–44°S; e.g., Rio Ñirehuao), introduced trout are the only fish present in the whole river basin. The main positive effect is that some water bodies support highly valuable sport fisheries based on these "native" free-living trout. To most Chilean people, rainbow trout and brown trout have become part of the "natural" freshwater biota, so much so that they are considered to be wild native trout suitable for sport fishing. An advantage of the perspective that introduced, naturalized fish are native species is that, because people value the introduced trout, they also value maintaining environmental conditions to keep these populations, including conservation of the accompanying natural biodiversity such as other freshwater organisms and littoral and riparian vegetation. Sport fishing is becoming one of the main reasons to save native forests in southern Chile. Pristine habitat is being provided for trout reproduction and growth; these types of habitats are declining in the northern hemisphere (Soto et al., 2002b, Soto et al., 2006).

From the perspective of the highly valued sport fishery, the introduction of new salmon species through escapes from salmon pens in some ways represents a threat to these native rainbow and brown trout. The past introduction of rainbow trout and brown trout has had strong social and economic support due to sport fishing; hence, strong protective measures are developed to care for and enhance those populations. The salmon that escape from pens constitute a peculiar challenge to the conservation of freshwater biodiversity because these free-living, introduced salmon compete with the native trout for resources.

Surprisingly, the native brown and rainbow trout are less attracted to freshwater salmon farms than are other truly native fish, such as the silverside

(*B. australis*), percids (e.g., *Percichthys trucha*), and galaxids (*Galaxias maculatus* and *G. platei*), and salmon that have escaped aquaculture pens. Indeed, in lakes with salmon farming, we often find free-living escaped salmon species such as coho, chinook, and Atlantic salmon (Table 3) aggregated around salmon pens. These "alien" species can be easily caught by sport fishermen in lakes and by artesian fishermen in the inner seas (Soto et al., 2002b). Thus, salmon-farm sites could sustain or enhance local sport fishing and fisheries without increasing the harvesting impact on the native trout species.

Alternatively, the question emerges, shall we also consider the escaped farmed salmon as components of the valued biodiversity in Chile, where long-term introductions have meant the naturalization of exotic fish? Yet, for total biodiversity to persist, including the coexistence of the introduced fishes with native species, strong sport-fishing pressure on introduced trout and salmon should be exerted. Salmon farming produces a significant local free-living salmon and trout biomass; this could be managed through sport fishing targeted toward the introduced and escaped fish to fulfill goals of biodiversity conservation, nutrient cycling, and landscape conservation.

From a broader perspective, better-integrated management that combined aquaculture activities and fisheries also could improve nutrient cycling and sustainable use of biodiversity in marine waters. For example, in southern Chile, where most marine aquaculture takes place, the more exploited fishery resources are the benthic top predator snail, "loco" (*Concholepas concholepas*), and some herbivores such as sea urchins (*Loxechinus albus*). Fishing pressure could be relieved for these species by switching to an increased harvesting of the filter-feeding bivalves that grow abundantly around salmon farms. Some bivalve populations possibly could withstand additional harvest because the nutrient loading should benefit them (Soto et al., 1999).

Table 3. Relative abundance of salmon and trout species (as percentage of all species) in major lakes and rivers of the X Region, southern Chile, as estimated by experimental fishing with gill nets (Palma, 1996; Soto et al., 1996). Sites where salmon farming is present are indicated (SF)

Species	LakePuyehue	LakeRanco	LakeRupanco	LakeLlanquihue	LakeT.L.Santos	BuenoRiver
	SF	**SF**	**SF**	**SF**		
Oncorhynchus kisutch (coho salmon)	2	8	0	22	0	0
Oncorhynchus mykiss (rainbow trout)	54	62	48	51	67	53
Oncorhynchus tshawistcha (chinook salmon)	5	0	0	0	0	0
Salmo salar (Atlantic salmon)	2	0	12	<1	0	0
Salmo trutta fario (brown trout)	37	29	40	24	33	47

Integrated coastal ecosystem management such as that described in this chapter is necessary to allow fisheries and salmon farming to coexist in Chile. This type of approach should allow for ecosystem and biodiversity conservation as well as economic and social well-being.

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CONCLUSION

CHAPTER 27

ENVIRONMENTALLY RESPONSIBLE AQUACULTURE: REALITIES AND POSSIBILITIES

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Abstract: The effects of aquaculture range from highly detrimental to highly beneficial, depending on perspective of the observer and type of the aquaculture activity. Industry leaders and those who monitor and govern the industry are aware of the adverse effects and have taken a number of actions to mitigate them. Solving these problems often requires employing common solutions that apply to many types of aquaculture but may require employing unique solutions as well. Ecologically and genetically sound solutions that have proven successful include the following: culturing native species; gathering baseline data on the distribution and abundance of native species before aquaculture is initiated so that aquaculture effects can be monitored; placing aquaculture facilities in areas able to withstand the unusual chemical and organic loads that aquaculture places on the environment and living communities; eliminating aquaculture activities in at least some selected regions; using polyculture, integrated-aquaculture, or closed-system aquaculture systems that include animals or plants capable of assisting with nutrient removal at some level; and using stocking practices and sufficient numbers of broodstock to prevent genetic problems. Considerable progress toward conducting environmentally responsible aquaculture has already been made in a number of ways and in many areas of the world. Industry participants and governmental, political, conservation, and scientific leaders have specific responsibilities associated with advancing the practice of environmentally responsible aquaculture. Because the practice of aquaculture is intimately linked to, and dependent upon, the environment, preserving the environment will ultimately preserve the ability to conduct aquaculture on a sustainable basis.

Key words: aquaculture, biodiversity, environment, impacts, ecology, genetics, solutions, stock enhancement, worldwide

Theresa M. Bert (ed.), Ecological and Genetic Implications of Aquaculture Activities, 479–514.

1. INTRODUCTION

The products and practices of aquaculture clearly benefit humans and wild stocks. Aquaculture yields food for humans and other animals; fish and invertebrates for supplementing depleted natural populations; and essential products for biotechnology, medical needs, and luxury items. Three principal objectives of the aquaculture industry are to provide food and income for people in developing countries; to reduce fishing pressure on wild stocks; and to maintain sufficient numbers of fish to sustain commercial, recreational, and subsistence fisheries.

Despite these benefits and goals, the introduction of aquaculture facilities into neighborhoods will be met with resistance if aquaculture is generally perceived as environmentally damaging in some way (Goldburg et al., 2001). But, herein lies the opportunity for the aquaculture industry to show world leadership by managing its activities for the benefit of mankind and conservation of biodiversity (Philipp et al., 1995). The industry is well poised to vigorously pursue this opportunity.

2. ACHIEVING ECOLOGICALLY VIABLE, GENETICALLY RESPONSIBLE AQUACULTURE

2.1. Common and Unique Problems, Common and Unique Solutions

The environmental effects[1] of aquaculture activities documented in this book range from perceived adverse disruptions of entire ecosystems to perceived beneficial alterations of entire ecosystems. Although the problems and solutions in the chapters are quite diverse (Table 1), some are common to many levels and types of aquaculture and thus surface as important on a broad regional or global scale. In countries where broad expanses of pristine wild environments still exist, habitat disruption and population alteration or species elimination are important concerns. In countries where aquaculture, including stock enhancement and sea ranching, is well developed as an important industry, additional concerns are pollution of the aquaculture environment by aquaculture practices themselves; land, seafloor, and water pollution by aquaculture wastes; and genetic contamination of wild stocks.

These chapters provide good examples of how, worldwide, aquaculture affects the physical environment, natural communities, individual species, and

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[1] Similarly to Chapter 1 of this book, I use the term "environmental effects" and related terms (e.g., "environmental," "environmentally responsible") in a very broad sense—inclusive of ecological, genetic, and biodiversity effects on all living natural ecosystem components and their independent and interactive processes as well as effects on nonliving ecosystem components. This special usage allows me to dispense with longer phrases, such as "ecological, biological, genetic, and biodiversity effects," when discussing the broad range of aquaculture effects that affect natural ecosystem components. When the adverse effects under discussion are pronounced and widespread, I use the term "impacts" rather than "effects."

Table 1. Summary of the ecological and genetic effects of aquaculture presented in this book

Author (country)	Problems	Solutions[1]
Bert (worldwide)[2]	• Habitat and community contamination ◦ Water enrichment ◦ Sediment and benthic community alteration ◦ Coastal ecosystem degradation • Nonnative-species escape ◦ Ecosystem disruption ◦ Native-species genetic contamination ◦ Alien pathogen introduction • Native-species depletion ◦ Collection for aquaculture ◦ Reduction or elimination by escaped aquaculture animals (nonnative or native) or their diseases • Animal and habitat contamination by aquaculture chemicals • Genetic contamination and fitness reduction ◦ Interbreeding between wild and feral aquacultured animals ◦ Numerical overwhelming of native species by feral aquacultured conspecifics • Effects on humans • Lack of adequate industry regulation and oversight	• Continue to develop environmentally responsible aquaculture systems and procedures • Develop culture techniques for native species of low trophic levels ◦ Develop markets for those species • Produce broods for grow-out from broodstock rather than collect them from the wild • Utilize responsible stock enhancement • Utilize genetic methods to their fullest extent in all types of aquaculture • Increase research directed toward disease and parasite reduction • Emphasize development of community-based, low-technology aquaculture in a framework of integrated coastal management • Emphasize education and training about environmentally responsible aquaculture • Coordinate laws and regulations governing aquaculture to the extent that is needed ◦ Provide for accompanying enforcement and reward system
Bartley (worldwide)	• Information gaps in reporting outcome of alien-species aquaculture ◦ Absence of impact information (positive or negative) ◦ Possible bias of existing data • Ecological effects (can be cascading) ◦ Predation of alien species on native species ◦ Competition between alien species and native species ◦ Habitat alteration by alien species	• FAO member nations and other nations report all impact information, positive and negative, from aquaculture activities • Conduct risk assessments, using an ecosystems approach, prior to the introduction of aquaculture activities ◦ Include animals to be introduced, habitat sited for the introduction, and effects to stakeholders • Where possible, use native species for aquaculture

(*Continued*)

Table 1. Summary of the ecological and genetic effects of aquaculture presented in this book—cont'd.

Author (country)	Problems	Solutions

	• Genetic interactions
	  ○ Lack of baseline genetic studies
	• Disease/parasite transmission
	• Socioeconomic effects
	• Effects on the industry itself through failure to attend to ecological concerns
	• Damage that is largely unknown, in any respect
	  ○ Accumulation of small negative effects
	  ○ Unforeseen ramifications
	• Little baseline data of any type available in some regions	

Pullin, Froese, and Pauly (worldwide)	• Limited perspectives in measuring success of aquaculture
	  ○ Short-term analyses, based largely on economics and food needs
	• Finite resource capabilities that cannot withstand infinite disturbance
		• Establish integrated management of resources and ecosystems, with humans factored in as an integral component
		• Improve ecologically sound farmed-fish production
		  ○ Use genetic enhancement of farmed fish to streamline production (e.g., improve feed to energy conversion ratio)
		  ○ Culture fish low on the trophic scale
		  ○ Rely less on fish-based feeds
		  ○ Reduce effects of emissions from aquaculture farms
		  ○ Reduce fish escapes from aquaculture farms
		  ○ Reduce contaminated water output
		• Diversify products produced and maintain high quality
		• Fund research to enable ecologically sound, farmed-fish production

Chao and Laio (Taiwan)	• Land subsidence ○ Saltwater intrusion • Large-scale harvest of wild larvae or juveniles for grow-out culture • Destruction of nursery areas and coastal wetlands and mangroves • Reduction in genetic diversity[3]	• Enforce policies designed to protect the environment • Develop a public awareness program for sustainable aquaculture practices • Develop technologies that emphasize intensive, recirculating aquaculture systems • Place net pens in locations where they will not cause extensive localized environmental damage • Monitor stock-enhancement and sea-ranching activities

(*Continued*)

Table 1. Summary of the ecological and genetic effects of aquaculture presented in this book—cont'd.

Author (country)	Problems	Solutions
Hedgecock and Coykendall (USA)	• Reduction in genetic diversity from stock-enhancement activities • Lack of knowledge regarding long-term effects of stock enhancement (worldwide problem)	• Consider effective population size when conducting stock-enhancement activities ◦ Assess the effects of hatchery- based stock enhancement on the "variance effective population size" using the Ryman-Laikre (1991) model (a practical, understandable model)
Grewe, Patil, McGoldrick, Rothlisberg, Whyard, Hinds, Hardy, Vignarajan, and Thersher (Australia)	• Damage to native stocks by feral hatchery-bred populations ◦ Competition ◦ Disease and parasites ◦ Displacement ◦ Ecosystem disruption • Genetic pollution ◦ Introduction and introgression of foreign genes ◦ Disruption of locally adapted gene complexes ◦ Reduction in many fitness components	• Use genetically modified sterile (in the wild)/feral (in the hatchery) cultured organisms for aquaculture to prevent reproductive capability in the wild
Hindar and Fleming (Norway)	• Interbreeding between escaped farmed salmon (the products of decades of hatchery selection) and wild stocks ◦ Generation of hybrids with reduced fitness components ◦ Reduction in overall population fitness due to long-term interbreeding between wild and escaped hatchery fish	• Develop closed-system aquaculture • Culture sterile fish • Selectively harvest escaped hatchery fish • Restrict transport of cultured fish • Build gene banks for native stocks
Bert, Crawford, Tringali, Seyoum, Galvin, Higham, and Lund (USA/ worldwide)	• Absence of baseline data on population genetic structure of stock to be enhanced • Limitations in genetic diversity of hatchery broods used for stock enhancement ◦ Reduction in fitness of broods used for stock enhancement ◦ Genetic damage to enhanced stock through interbreeding with released hatchery fish • Selection for, and adaptation to, hatchery environment by hatchery offspring	• Conduct standard population genetics study on recipient species ◦ Include sufficiently broad geographical area to obtain information on population structuring and gene-flow patterns ◦ Use adequate broodstock numbers ◦ Guard against selection in the hatchery † Monitor using genetics † Avoid selecting particular size classes or phenotypes in routine operations † Mimic conditions in the wild as much as possible ◦ Keep ratio of hatchery fish to wild fish low (e.g., <5%) each generation

(*Continued*)

Table 1. Summary of the ecological and genetic effects of aquaculture presented in this book—cont'd.

Author (country)	Problems	Solutions
	• Release of high number of hatchery animals compared to number of wild animals in recipient population ◦ Excessive overall decrease in effective numbers of breeders (after Ryman and Laikre, 1991) ◦ Overall decrease in fitness of the admixed population ◦ Accidental overharvest of wild animals	
Ogburn (Australia)	• Farming of alien species (oysters) ◦ Translocation of alien species ◦ Loss of native species • Reduction in plant biomass • Deterioration of water quality ◦ Eutrophication • Improper aquaculture site location ◦ Self-pollution ◦ Nutrient-laden discharge and chemical release ◦ Wetlands destruction ◦ Acid soil exposure ◦ Cultured-animal escapement from facilities • Introduction of parasites • Disease • Reduction in genetic diversity ◦ Inbreeding ◦ Lowered fitness	• Conduct risk assessments for new aquaculture proposals • Quarantine zones with parasitized or diseased animals • Restrict translocation of alien aquacultured species • Locate aquaculture facilities in suitable locations that reduce operating expenses, which reduces public scrutiny • Ensure operational controls at the site ◦ Monitor water exchange ◦ Maintain operations at levels that do not exceed carrying capacity • Build with environmentally safe products • Develop regional overall development and management plans
Mustafa, Rahman, Ransangan, and Stephen (Malaysia)	• Morphological deformation of hatchery fish • Escape of cultured fish that interbreed with depleted wild stocks	• Remediate possible negative genetic effects of inbreeding ◦ Introduce a percentage of new broodstock, preferably collected from the wild, each generation ◦ Increase broodstock numbers ◦ Exchange broodstock among hatcheries ◦ Generate a gene bank for the affected species • Prevent escape of hatchery fish
Ahn and Kong (Republic of Korea)	• Farming of alien fish species in lakes and reservoirs ◦ Decline in water quality (eutrophication, nutrification) and benthic habitat	• Prohibit aquaculture in reservoirs • Develop and promote aquaculture of native species • Selectively fish alien species • Continue to study aquatic systems

(*Continued*)

Table 1. Summary of the ecological and genetic effects of aquaculture presented in this book—cont'd.

Author (country)	Problems	Solutions
	○ Displacement of native species ○ Spread of disease ○ Introduction of ancillary alien species ○ Transport of alien species among water bodies by humans • Lack of information on many water bodies	
Xiang (People's Republic of China)	• Self-pollution of aquaculture systems by effluents, excretions, unused feed ○ Decline in water quality and benthic habitat (eutrophication, nutrification) • Losses in genetic diversity of cultured stocks ○ Declines in fitness of cultured animals (decrease in mean scallop size, disease susceptibility)	• Use polyculture that incorporates seaweeds • Use closed systems, recycle water • Manage feeding prudently– ○ Use feed with little or no fish component ○ Maintain reasonable effective hatchery population sizes
Brummet (Cameroon/ Africa)	• Use of nonindigenous species for aquaculture ○ Displacement of native species ○ Decline in water quality and benthic habitat ○ Spread of disease ○ Poor market value • Problems with marketing aquacultured animals • Unemployment	• Develop and promote aquaculture of native species • Conduct a marketing analysis for consumer acceptance before large-scale aquaculture of alien species • Develop numerous small-scale aquaculture farms for a large number of native species • Develop markets to sellaquacultured native species
Ortega, Guerra, and Ramírez (Perú)	• Escape of alien aquacultured fish and release of alien fish into water bodies (including those in national parks) ○ Competition for food and niche space ○ Predation ○ Displacement ○ Localized extinction • Effects that compound each other ○ Further introductions of additional alien species ○ Eutrophication, which is the basis for local ecosystem change	• Allow selective fishing for alien species in national park waters and other invaded areas ○ Allow multiple, selective gear types ○ Monitor catches, evaluate result • Implement a nationwide *Tilapia* management plan ○ Monitor high-risk areas for invasions • Initiate research for employment activities alternative to aquaculture of alien species • Prohibit aquaculture of alien species • Restrict native-species transfer between different water systems

(*Continued*)

Table 1. Summary of the ecological and genetic effects of aquaculture presented in this book—cont'd.

Author (country)	Problems	Solutions
		◦ Require that people moving species adhere to international codes of conduct for aquaculture and obtain required approvals • Build aquaculture facilities that minimize the probability of escape • Produce fingerlings only at specified, properly constructed (for escape prevention) facilities ◦ Monitor production methods and facilities • Monitor water bodies bordering fish farms • Require aquaculture programs to have mechanisms for conservation of native species • Require environmental impact studies for all phases of aquaculture operations • Educate the public ◦ Inform those involved in aquaculture industries about conducting environmentally safe aquaculture ◦ Inform the general public about the hazards of releasing alien species and transferring native species among water systems • Monitor water bodies currently or potentially harboring alien species • Produce nonreproductive fish ◦ Develop technologies to generate all-male offspring or sterile fish
López-Rojas and Bonilla-Rivero (Venezuela)	• Alien-species introductions and native-species transfers ◦ Escape of cultured fish and shrimp into open waters ◦ Fish ranching in open waters ◦ Local extinctions ◦ Synergistic adverse effects exacerbated by water pollution and anthropogenic habitat destruction ◦ Rapid, significant damage to biodiversity because most native species are naturally rare • Absence of baseline information for many water systems ◦ Lack of studies on species compositions, distributions, ecologies, or life histories	• Establish regulatory controls on alien-species aquaculture[4] • Develop aquaculture of indigenous species ◦ Conduct research on native-species caged culture, closed circulations systems, genetic manipulation, feeding, health, and performance • Reduce foreign and international investments in Venezuelan aquaculture • Educate aquaculture-industry users and the general public about problems associated with alien-species aquaculture and introductions • Conduct baseline biological and ecological studies on little-studied water systems • Conduct research on employment opportunities alternative to aquaculture of alien species • View conservation of aquatic systems holistically, with humans as a component

(*Continued*)

Table 1. Summary of the ecological and genetic effects of aquaculture presented in this book—cont'd.

Author (country)	Problems	Solutions
Alves, Vieira, Magalhães, and Britto (Brazil)	• Stocking of alien fishes in water bodies ◦ Threat of hybridization with native species ◦ Loss of native-species commercial fisheries ◦ Displacement of native species ◦ Localized extinction of native species ◦ Fish community-level ecological changes ◦ Reductions in species diversity • Lack of information on species composition in water bodies	• Improve enforcement of trade laws regarding nonnative fishes • Develop aquaculture of native species • Limit the spread of nonnative species ◦ Avoid introductions of additional nonnative species • Improve habitat conditions for native species ◦ Construct fish passageways around dams and reservoirs • Develop a public educational program on the impacts of alien species • Conduct fish species and habitat surveys of water systems not yet studied • Monitor waterways for fish species composition and relative abundance
Vigliano and Alonso (Argentina)	• Division among interest groups (conservationists, those involved in the sportfishing industry, aquaculturists) regarding effects (positive and negative) of introductions of salmonids for sportfishing ◦ Debates regarding continued stocking and new species introductions ◦ Debates regarding direction of future industry development (aquaculture or sportfishing) ◦ Genetic contamination of "wild" salmonid stocks by escaped aquacultured salmonids • Undocumented stocking • Restricted access to water bodies ◦ Ownership claims to river sections • Inability to obtain baseline data on native-species composition and abundance	• Develop and enforce interprovincial policies and regulations for alien salmonid stocking and use of water bodies ◦ Study historical and current uses ◦ Consider needs and concerns of all interest groups ◦ Coordinate efforts for stocking, aquaculture, and conservation among provinces • Study fish community structure and dynamics in all water bodies ◦ Develop plans for ecologically and economically sustainable development and use of all water bodies
Pascual (Argentina)	• Predation on native species by introduced species • Effects that propagate through ecosystems in unknown ways ◦ Absence of baseline data collected prior to introductions	• Take advantage of the new ecosystem created by the establishment of alien salmonids for unique research ◦ Use the opportunity generated by multiple intra- and interspecific introductions over time to design unique ecological and genetic research on alien-species establishment

(*Continued*)

Table 1. Summary of the ecological and genetic effects of aquaculture presented in this book—cont'd.

Author (country)	Problems	Solutions
Stickney (USA)	• Self-induced pollution • Destruction of sensitive habitats (e.g., wetlands) • Competition between native species and alien species • Disease transmission from cultured fish to wild fish ◦ Development of disease resistance in bacteria • Water and sea floor pollution ◦ Eutrophication • Negative effects on marine mammals • Visual and sensory pollution	• Reduce stocking densities • Construct wetlands to buffer effluents • Locate marine net-pen systems offshore
Smoker and Heard (USA)	• Overfishing of wild-fish salmon fisheries ◦ Decrease in numbers of harvestable fish	• Develop statewide hatchery programs to enhance stocks in an environmentally responsible way ◦ Build and maintain hatcheries ◦ Use a public/private partnership ◦ Protect wild stocks from hatchery-stock generated displacement, predation, competition, disease, and genetic damage ◦ Prevent accidental overfishing • Evaluate contribution of hatchery fish to annual harvests
Waples, Ford, and Schmitt (USA)	• Absence of comprehensive evaluations of the outcomes of most stock supplementation programs on salmonids	• Periodically, perform a meta-analysis of the success of targeted stocking programs using a comprehensive set of questions designed to reveal where assessment information is lacking in addition to estimating the success of the program
Yokoyama, Nishimura, and Inoue (Japan)	• Local declines in water quality and benthic habitat • Reductions in species richness ◦ Azoic conditions beneath cages in sheltered embayments during summer	• Locate marine fish farms in open, deeper areas with good current flow • Assess potential fish-farm areas for assimilative capacity ◦ Survey areas cited for potential net-pen fish farms for appropriateness • Use the index "embayment degree" to evaluate appropriateness of a site for net-pen aquaculture
Hirata, Yamauchi, Matsuda, and Yamasaki (Japan)	• Self-induced pollution around marine open-water net pens	• Use polyculture to improve water quality and possibly fish growth and quality and to provide additional income

(*Continued*)

Table 1. Summary of the ecological and genetic effects of aquaculture presented in this book—cont'd.

Author (country)	Problems	Solutions
Shpigel and Neori (Israel)	• Self-induced pollution in and around aquaculture farms ◦ Nitrification from protein-based feeds	• Develop and promote integrated aquaculture that uses algae and shellfish as biofilters • Use a food-chain approach (micro- and macroalgae, detritivorous and herbivorous invertebrates, fish)
Chopin, Yarish, and Sharp (Canada)	• Coastal water nitrification	• Use integrated aquaculture with an algal component ◦ Study each system prior to introducing the integrated-aquaculture system and design a system appropriate to the site
Soto and Jara (Chile)	• Self-induced pollution around marine and freshwater net pens ◦ Eutrophication ◦ Biodiversity losses ◦ Seafloor pollution through unused fish feed	• Increase the abundance and diversity of filter- and detritus-feeding bivalves and other benthic invertebrates under and around net pens by increasing habitat structural complexity (e.g., provide artificial habitats) • Selectively fish introduced and escaped alien species and other species that grow abundantly around net pens

[1] Includes solutions that are proposed, that are in the process of being realized, and that have already been accomplished.

[2] Problems are summarized from Chapter 1, solutions from this chapter.

[3] Here defined as *genetic variability*—the alleles collectively present in the stock, population, species, or higher taxonomic unit under consideration—and *genetic composition*—the frequencies of those alleles in the same unit.

[4] Nirchio and Perez (2002) also warned against the widespread casual nature of tilapia farming in Venezuela and provide evidence that all-male tilapia culture is not a solution to unwanted reproduction.

genetic diversity. Activities involving the construction and operation of aquaculture facilities can pollute waters, change water-flow patterns, and alter landscapes. Escaped or released aquacultured animals or plants, particularly alien species, can alter trophic webs; introduce diseases, parasites, or other alien "hitchhiking" species; locally reduce numbers of native species; reduce abundance of individuals in native species; and numerically or genetically overwhelm conspecific wild populations.

Common solutions also appear, as variations on common themes, and range from national and state-of-the-art to local and simple. Many common solutions suggested here have already been suggested in various publications; their inclusion in this book further emphasizes their need and importance. Unique solutions include using oceanographic conditions and processes or the presence and location of free-living native and exotic species as factors in determining locations for net-pen aquaculture or using biotechnology to prevent genetic damage from escaped aquacultured animals.

Notably, aquaculture effects are not always perceived to be negative. In the novel Argentinean situation presented herein (see Vigliano and Alonso, 2007;

Pascual and Ciancio, 2007), ranched alien salmonids are considered by some people to be more important than the native species, regardless of environmental concerns, in part because the original ecosystem components and structure are generally not known. In this case, proposed solutions focus more on the best economic use and equitable distribution of the alien-species resource than on the restoration of ecosystems to a semblance of their presumed original state. The overall solution, in this case, seems to be widespread sanctioning and active expansion of this type of salmonid aquaculture throughout broad regions. Clearly, some unique situations require innovative and sometimes controversial solutions.

Regardless of the approach taken to reduce the environmental effects of specific aquaculture operations, solving the problems requires that both aquaculture-industry participants and those who govern or regulate the industry's activities assume responsibility and initiate action. Most effects can be minimized or prevented by proactive conduct of industry participants and those who oversee the industry.

2.2. Problems and Constraints Yet to Be Fully Addressed

Although much progress has been made toward developing aquaculture facilities, practices, and regulations that are compatible with environmental conservation, much has yet to be done. Ideas for further advancement can be synthesized from the chapters presented in this book and the many previous publications in which aquaculture effects were addressed (including the following: Pullin, 1990, 1993, 2001; CBD, 1992; Chua, 1993; Csavas, 1993; Gowen and Rosenthal, 1993; Lightfoot et al., 1993; Martínez-Espinosa and Barg, 1993; Campton, 1995; Courtenay, 1995; FAO, 1995, 1997, 2002; Prein, 1995; Thorpe et al., 1995; Bardach, 1997; Barg and Phillips, 1997; Beveridge et al., 1997; Clough and Johnston, 1997; ; Goldburg and Triplett, 1997; Thia-Eng, 1997; Williams, 1997, 1999; Yokoyama et al., 1997; Bartley and Rana, 1998; Naylor et al., 1998; Shaklee and Bentzen, 1998; Tringali and Bert, 1998; Welcomme and Bartley, 1998; Youngson et al., 1998; Abban, 1999; Ackefors, 1999; Åsgård et al., 1999; Bartley and Pullin, 1999; Bell and Gervis, 1999; Bernal, 1999; Fletcher et al., 1999; Grant, 1999; Gupta, 1999; Li, 1999; Neira et al., 1999; Phillips and Barg, 1999; Pillay, 1999; Refstie and Rye, 1999; Sandnes and Ervik, 1999; Wang, 1999; NACA and FAO, 2000; Naylor et al., 2000; Pérez et al., 2000; Bert et al., 2001, 2002a, b; GESAMP, 2001; Goldburg et al., 2001; Hernández-Rodríguez et al., 2001; Kongkeo, 2001; Belias et al., 2003; Nash, 2003; De Jesus and Kohler, 2004; Hilborn, 2004; Hossain et al., 2004; Leber et al., 2004; Walters and Martell, 2004).

The sections that follow are a synthesis of these ideas. They fall into two broad categories: (1) operations of the industry and (2) associated socioeconomic and governmental factors.

2.2.1. Operations of the industry

Aquaculture-industry leaders and participants can facilitate environmentally sustainable development of the aquaculture industry by ensuring that, overall, natural ecosystems are maintained in the vicinities of their operations and in the areas where aquacultured organisms are released into natural ecosystems, such as areas of stock enhancement. Following are suggested directions that build on the advances that industry participants have made to further their movement toward environmentally sustainable aquaculture:

1. Continue technical and operational development of aquaculture systems that leave a minimal ecological footprint. Technical advances could continue in developing automated feeding methods that result in little wastage; designing facilities that reduce the escape of cultured animals from hatcheries and aquaculture ponds, tanks, and net pens to near-zero; locating aquaculture facilities in low-impact coastal areas; and incorporating constructed wetlands and settling ponds into land-based aquaculture facilities. The use of polyculture and integrated-aquaculture facilities that incorporate seaweeds and/or filter-feeding mollusks could be further promoted and supported. These economically efficient types of aquaculture can assist with balancing nutrients, cleaning waste water, and reducing by-products and waste products by recycling nutrients and organic matter. They also provide additional income from the sale of the ancillary products (algae, bivalves). Improvements could continue in practices such as rotating net-pen locations; adjusting densities of cultured animals in aquaculture enclosures to reduce pollution; using extensive, rather than intensive, aquaculture (but see Edwards, 1993); and ensuring that aquaculture waste products do not exceed local environmental carrying capacity and resilience. Sometimes, responsible application of operational technology means using technically simple, low-input methods (but see Boyd, 1999). Some traditional aquaculture practices—such as using manures for feeds; irrigating crops with intensive-aquaculture effluents; using fish waste products to feed cultured fish at lower trophic levels, including juvenile fish of the same species; or using aquacultural wastes to fertilize agricultural crops—are more ecologically beneficial, less complicated, and more cost-effective than some advanced techniques. Increased use of these types of methods where appropriate could be promoted.
2. Continue development of methods for aquaculturing native species. The broad diversification of aquaculture protocols required to meet this suggestion at the worldwide level involves commitments of time by people with expertise in aquaculture methods and systems and money for developing the protocols to grow numerous local species. In addition, sometimes aquaculture of numerous species must be attempted before some successes can be realized. Thus, the commitments can be difficult to justify when resources are limited and techniques for aquaculture production of alien species that

are easy to grow, such as tilapia, are readily available. Nevertheless, the worldwide environmental ramifications of globally culturing only a few species accentuate the importance of this type of research and development. Some scientists believe that some environmental problems generated by aquaculture of alien species are the most intractable, irreparable, and damaging of those associated with any source (e.g., Naylor et al., 2001).

3. Continue to expand the focus on eliminating alien-species introductions into the wild for open-water aquaculture (e.g., ranching of aquatic fishes or marine mollusks). This particularly applies to sensitive areas such as those with high incidences of endemism or important gene pools. Open-water ranching that is environmentally viable over a long term is most likely to be achieved through the use of indigenous species or strains.
4. Continue to increase the focus on reducing the use of wild aquatic animals to support aquaculture. Two categories of problems are relevant:
   a. Harvesting animals in young life stages for grow-out in aquaculture environments. This type of harvesting is usually localized, intense, and unregulated. It can locally deplete native-species wild populations and, thereby, adversely affect local fisheries for those species or those species' predators. It is tantamount to fishing the species without catch limits before individuals have had the chance to reproduce.
   b. Using aquaculture feeds that include fish protein derived from the harvest of wild fish (this problem applies to both aquaculture and agriculture). Herbivorous and planktivorous wild fish are harvested principally for use as protein components in agricultural feeds for livestock and poultry and in aquaculture feeds for carnivorous fish. The aquaculture of carnivorous fish does not relieve overall pressure on the harvest of wild fish because the cultured carnivorous fish are fed diets containing large amounts of products processed from harvested herbivorous and planktivorous fish. Nor is harvesting wild fish to feed aquacultured fish destined for human consumption efficient compared to direct human consumption of the wild fish. Nor does culturing carnivores significantly add to the food supply of rural people in developing countries. High-level carnivorous vertebrates and invertebrates are produced by people in developing countries principally for consumption by people in industrialized countries. Culturing species low in the food chain rather than carnivorous species and reducing the harvest of fish such as clupeoids (as defined in Froese and Pauly, 2006) for use in animal feeds are ideas that seem ecologically sound. Although these ideas are commonly voiced by people interested in reducing the ecological impacts of aquaculture, they should also be considered from a socioeconomic perspective. Their merits should be weighed against the following social complexities and economic factors associated with their implementation:

   1) In some cases, larval or juvenile animals are harvested for aquaculture because the culture techniques for all life stages of those species have not been fully developed. It can take a long time, much research, and considerable money to work out the details of efficiently rearing a species; and sometimes protocols cannot be developed for a critical life stage.
   2) The species aquacultured must be palatable to humans. Many types of herbivorous and planktivorous fish are not. This is why they are used in feeds for other animals.
   3) The cost and productivity of culturing a species low in the food chain must be weighed against that of fishing wild stocks of the species. Can the species be cultured? Which is more profitable and economically viable—aquaculture of the species or fishing for the species? Which causes greater damage to the species and the ecosystem? Can economic gain and environmental protection be balanced if the species is aquacultured? Can they be balanced if the species is harvested?
   4) The fisheries for many herbivorous and planktivorous species are important industries in some developing countries. Ceasing the use of these species as components of aquaculture feeds and, thereby, potentially reducing their fisheries value may have significant economic ramifications in those countries. Also, the use of these fish in agricultural feeds far outweighs their use in aquacultural feeds (Emerson, 1999), so eliminating fish protein from aquacultural feeds may do relatively little to reduce the overall use of fish in animal feeds at this time.
   5) Fish and fish products that would normally be discarded (e.g., bycatch from trawl fisheries) are also used to make aquacultural and agricultural feeds. This use of fish products that would otherwise be wasted reduces the need to use directed-fishery species for animal feeds.
   6) Feeds that do not contain fish protein may remain in the environment longer and cause more contamination problems than feeds that do contain fish. Pelagic and benthic organisms feed on and degrade fish-based feeds (see e.g., Soto and Jara, 2007 and references therein). Thus, excess fish-based feeds may have shorter residence times in waters than other types of feeds. (This seems to be a fertile area for research.)

5. Continue to improve stock-enhancement methods. Stock enhancement, if done properly, can increase the numbers of individuals in a depleted population as well as increase the effective size of the population (N_e, after Ryman and Laikre, 1991). In several areas, significant progress has been made toward conducting responsible stock enhancement (as described in Blankenship and Leber, 1995). In some cases, stock enhancement is implemented only after alternative means of restoring stocks, such as improving or expanding habitats used by the target species and improving management

of the target species' fishery, have failed. A number of stock-enhancement efforts are initiated only after a risk assessment that includes a rigorous evaluation of the biological and economic effectiveness of stocking is conducted. Some stock-enhancement efforts are planned to continue only long enough to accomplish goals set *a priori* for the stock-enhancement effort. Many stock-enhancement projects are monitored for their potential ecological and genetic effects on wild animal stocks and the supporting ecosystems. These types of advancements, which are also broadly applicable to sea ranching, should continue.

6. Continue to increase the use of genetic methodologies and tools and the consideration of genetic diversity in production aquaculture.[2] The importance of genetics to production aquaculture is still not widely recognized. Population genetics and diagnostic genetics, as described for stock enhancement in Bert et al. (2007), also have broad applicability to production aquaculture. The presence of genetics in production aquaculture can be increased in several ways.
    a. Using genetics techniques and analyses to gather genetic information on native species that could be, or are, aquacultured or affected by aquaculture. Population genetics can be used to gather baseline information on the levels and hierarchical partitioning of genetic diversity; the geographic extent of genetically homogeneous populations; and the magnitude and patterns of gene flow in species that could be affected by aquacultured animals if they escaped from aquaculture facilities. Baseline genetic information about wild populations cannot be obtained after genetic changes related to aquaculture have occurred. Population genetics can also be used to ensure that broodstocks are drawn from the desired populations.
    b. Using molecular genetics to ensure that genetic diversities of hatchery populations and wild stocks are not changed by aquaculture activities. Population genetics can be used to ensure that broodstocks have sufficient genetic diversity and that breeding strategies are designed to avoid genetically based problems in hatchery broods. Diagnostic genetics can be used to determine the gametic contribution of broodstock individuals to broods and to estimate N_e of the broodstock and broods. Maintaining adequate N_e in broodstocks is important because their genetic diversity is related to their N_e, which, in turn affects the N_e (and, therefore, fitness) of their broods. Diagnostic genetics can also be used to genetically mark hatchery broodstock and broods so they can be distinguished from wild individuals if the hatchery fish escape into the wild and mix with wild conspecific populations. Population genetics can also be used to estimate

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[2] "Production aquaculture" is defined here as aquaculture that generates animals for direct harvest from an enclosure (e.g., facility or net pen), rather than aquaculture that generates animals for release into the wild for various purposes (e.g., stock enhancement or sea ranching).

   the genetic effects of escaped or released hatchery fish. Other molecular genetic techniques can be used to generate highly selected, sterile, or otherwise genetically modified aquacultured animals that have a low probability of survival and reproduction in the wild (e.g., Grewe et al., 2007; but see Youngson et al., 1998).
   c. Developing and implementing programs to conserve genetic resources of aquatic species, including establishing marine parks, reserves, and management areas. Population genetics and evolutionary genetics can be used to identify important aquatic areas that should be conserved for their genetic value. These include areas that contain populations with unusually high levels of genetic diversity; areas that act as havens for ancient or novel genetic lineages or that possess habitats conducive to speciation (e.g., transitional habitats, as exemplified by the presence of numerous hybrid zones or contact zones between closely related species); and areas that are deemed generally valuable for their diversity or uniqueness, such as the Amazon River or Congo River watersheds.
7. Continue to increase the focus on conducting basic ecological research in areas where the aquatic fauna is poorly known and development of aquaculture occurs or could occur. In some countries, the freshwater fish and invertebrate fauna has not yet been well documented for even large aquatic systems. Knowledge of the species composition and of individual species' densities and distributions, habitats, and interactions with other species are essential for determining if released or escaped aquacultured animals have significantly changed ecosystem components. As for baseline genetic information, baseline ecological information cannot be obtained after effects related to aquaculture have occurred.
8. Continue to encourage research for reducing the incidence of disease infection, parasite affliction, and pest infestation in aquacultured animals. Employing methods for avoiding these health problems, such as hatchery-based selection for resistant strains, is important because these are among the most intractable of all aquaculture dilemmas; each can decimate entire hatchery or net-pen populations and impact sympatric wild populations (e.g., Krkošek et al., 2006).

2.2.2. Socioeconomic and governmental factors

Social acceptance, reasonable economic gain, and adherence to relevant laws and regulations are necessary for the success of any industry. Regulatory entities and other stakeholders, together with aquaculture-industry leaders, need to continue their focus on expanding the industry in ways that are beneficial to people, compatible with the environment, and supportive of laws and regulations designed to protect biodiversity. Following are suggested directions that build on the socioeconomic and regulatory advances that have been made to further the movement toward environmentally sustainable aquaculture:

1. Continue to develop small- and medium-scale community-based aquaculture operations in poor areas of the world, particularly in rural areas. Although industrial aquaculture has generated substantial employment, the real potential for provision of food to people in need is in small- and medium-scale aquaculture. Governments and nongovernmental organizations often suggest aquaculture as an economic activity that can supplement or replace fishing for people in small rural nearshore villages. However, constraints such as high initial capital costs, lack of suitable sites (land, water), or lack of infrastructural support can prevent poor fishers from adopting aquaculture as an employment opportunity. Governmental officials should increase their support of small-scale rural aquaculture. Joint ventures between public and private organizations are also needed. Plans for development should be flexible and leaders' expectations should be tempered by realistic appraisals of what can be achieved without disrupting other community activities and livelihoods as well as local terrestrial and aquatic environments.
2. Continue to advocate integration of aquaculture facilities into (at the least, loosely formulated) coastal management plans that, where needed, include protected areas. Thus far, integrated coastal management has not been highly successful because it is complex, and instituting legal and community changes is difficult.
3. Continue to increase requirements for risk evaluations prior to introducing new aquaculture activities. Thorough risk evaluations include the following:
    a. predetermined standards for operating in an ecologically and genetically responsible manner;
    b. broad estimates for the probability of the aquacultured organism's survival and reproductive capacity if it escapes into the wild;
    c. estimates of the extent and nature of the potential environmental effects the organism could have if it escapes and the relationship between the number of individuals that escape and extent of the effects;
    d. acceptable impact limits and contingency plans in the event that the established standards are breached (e.g., control or monitor escape dispersion; enact penalties for environmental damage).
4. Continue to emphasize educating participants in the aquaculture industry about ecologically viable methods of aquaculture; about the environmental problems generated by poor aquaculture practices and the importance of the environment to their livelihoods and lives; and about existing rules, regulations, and policies that govern aquaculture activities. People involved in all levels of aquaculture should be included. For example, numerous scientists who specialize in stock enhancement are vigorously promoting environmentally sound stock enhancement and aquaculturists are responding (see e.g., http://www.searanching.org).

5. Continue to improve markets for aquacultured local fish. A corollary of this suggestion—develop aquaculture methods for marketable local fish—may be a more needed avenue of aquaculture improvement. It is not uncommon to develop aquaculture operations for (usually alien) species only to find that the cultured organisms are not marketable due to preferences of local inhabitants for local species. Some widely aquacultured species are unpalatable to many people in some communities. Experimental marketing on a small scale can assist decision-makers in determining which species to aquaculture or deciding whether or not to invest in large-scale aquaculture of a particular species.
6. Continue to establish, promulgate, and enforce cost-effective environmental-protection laws and regulations relevant to the types and scales of aquaculture being practiced and to foster coordination among levels of governmental and enforcement agencies to coordinate those laws and regulations, as appropriate. In many countries, jurisdiction and laws for conducting environmentally responsible aquaculture and for conserving aquatic resources, including genetic diversity, are dispersed among or uncoordinated between governmental agencies and levels. In some developing countries, regulations governing aquaculture exist, but governments lack the personnel and resources to enforce them.
7. Continue to expand public recognition of good aquaculture practices. Positive incentives nearly always result in quicker and broader acceptance of methods and ideas by user groups than do threatened punishments. Highly visible acknowledgments of good practices further encourage individuals to adhere to those practices.

2.3. Responsibilities

Addressing the suggestions described above involves conducting aquaculture so that genetic diversity and natural ecological systems are maintained; socioeconomic needs are met; and reasonable, effective rules and regulations are applied. These needs should be met in ways amenable to economic gain. The responsibility for developing this type of environmentally sustainable aquaculture needs to be shared by all levels of stakeholders and all involved people, extends to resources not yet used (Bartley and Pullin, 1999), and involves cooperation at appropriate levels that range from local to international. However, distributing the responsibility for this development among individuals and groups of people can be complicated and politically or socially delicate. Nevertheless, the realm of aquaculture is sufficiently defined and contained to make cooperation possible from the local to the international level through the ecosystems approach (CBD, 2003). In this approach, all population sectors with actual or potential vested interests that can be influenced positively or negatively by proposed aquaculture operations provide input, as appropriate, into facility location and design, operational procedures, and plans for workable solutions to problems. The objective is to accommodate all interests as well as possible while maintaining standards for the conservation of natural systems. This approach allows conservation and human needs to be balanced in a realistic perspective regarding development of aquaculture that is compatible with the environment (Pullin, 1993). Aquaculture-industry leaders and the governmental, institutional, and scientific groups that provide guidance for the industry are responsible for directing the industry toward environmentally responsible aquaculture production.

2.3.1. The aquaculture industry

Responsibilities of the aquaculture industry include the following:

1. Develop affordable aquaculture practices and systems that can be built and run by local people in areas with limited modern technology (Goldburg and Triplett, 1997). Integrated, low-technology agriculture/aquaculture systems are particularly applicable here (FAO et al., 2001). This direction is essential for realizing the potential in food production and poverty reduction that aquaculture has for poor people; and it is consistent with a stated goal of the World Aquaculture Society (WAS; see http//www.was.org).
2. Expand the industry using the ecosystems approach. As suggested above, aquaculture expansion may have adverse social effects as well as adverse environmental effects (e.g., Hossain et al., 2004) or it may bring only short-lived benefits (e.g., Pullin, 1993; D'Abramo and Hargreaves, 1997). More comprehensive approaches that consider both environmental issues and socioeconomic needs should prove to be more resilient and beneficial for industry expansion in the long term.
3. Campaign for research on expanding aquaculture of native species. Attaining capacity for aquaculture of all life stages of more native species could solve two problems. First, the collection of immature life stages of native-species individuals harvested from the wild for grow-out in aquaculture facilities could be reduced. If immature wild individuals must be used for aquaculture, their harvest should be regulated. Second, aquaculture of alien species could be reduced. Although culturing alien species for which aquaculture techniques have been established is expedient, these species should not be aquacultured unless identified, potentially harmful consequences can be justified by the guarantee of equivalent, sustainable benefits (Pullin, 1993). If alien species must be used for aquaculture, their introduction should be limited, well regulated, and well monitored. More species diversity in aquaculture is widely needed.
4. Conduct stock enhancement and sea ranching in ways that do not harm the stocked population, other species in the community, and local ecosystem processes.
    a. Enhance the target stock only as long as needed, using hatchery populations that will not significantly harm wild populations (Thorpe et al., 1995).

   b. Use adaptive management for stock enhancement, with defined benefits to the fishery being enhanced (Blankenship and Leber, 1995).
   c. Avoid damage to the health of the recipient wild stock (Bert et al., 2003).
   d. Ensure that the hatchery broods used have genetic diversity compatible with that of the wild stock to be augmented (see Bert et al., 2007).
   e. Adjust the contribution of hatchery fish so that they do not genetically overwhelm the wild stocks they are supposed to supplement; some population abundances wax and wane by an order of magnitude or more (see Finney et al., 2000).
   f. Monitor populations supplemented by hatchery fish and their associated ecological communities for maintenance of genetic diversity and health (Bert et al., 2003).
5. Follow published codes of practice for all aquaculture activities. Numerous codes and guidelines exist (see Bert, 2007). A number of these were constructed through the cooperative efforts of aquaculture managers and industry leaders. Therefore, many are reasonably applicable to most types and levels of aquaculture.
6. Be proactive in evaluating the environmental effects of all aquaculture activities and in taking actions to mitigate the effects when necessary. By positively and aggressively dealing with negative environmental effects, the industry will be seen as environmentally responsible. Aquaculture organizations will need to cooperate with each other in dealing with environmental issues because many of the issues crosscut multiple types of aquaculture. They will also need to become involved with environmental management groups and regulatory agencies to assist the agencies with identifying and managing environmental effects.
7. Widely publicize all efforts to conduct sustainable, biologically and environmentally responsible aquaculture. Public perception of the aquaculture industry as an environmentally aware entity will enhance acceptance of new or expanding aquaculture activities in neighborhoods.
8. Promote the development of closed-system aquaculture, polyculture, and integrated aquaculture (e.g., Hossain et al., 2004; Chopin et al., 2007; Shpigel and Neori, 2007). These are widely accepted as less environmentally damaging than other types of aquaculture.

2.3.2. Leadership entities

Responsibilities of the groups that guide the aquaculture industry, influence its activities, or promote its advancement (e.g., governmental and other regulatory agencies and departments, nongovernmental organizations, scientific organizations, and institutions) include the following:

1. Coordinate the oversight of aquaculture activities and the regulations that govern them from the local to the international level (Hernández-Rodríguez et al., 2001), as appropriate; in this activity, consider adopting or incorporating the comprehensive guidelines that exist. This coordination may involve

cooperation among governmental agencies at different organizational levels (local, regional, national, international).

2. Encourage and support aquaculture of species that will have low- or zero-environmental impact if they escape or are released from the aquaculture facility.
    a. Discourage the aquaculture of alien species with likelihoods of generating adverse environmental effects and the expansion of aquaculture of high-level carnivorous species. Adopt, promulgate, and enforce stringent, comprehensive plans that limit the potential for introduction of potentially problematic alien species into the wild. When considering alien-species introductions, the cost of potentially detrimental effects to native species, habitats, and communities should be balanced against perceived social and economic benefits of the introductions. If alien species or strains are ranched, setting aside compensatory preserved populations and their ecosystems in locations immune to the possibility of invasion by the introduced species should be considered.
    b. Encourage and financially support the aquaculture of native species and species low in the food chain (Goldburg and Triplett, 1997; Li, 1999; Pérez et al., 2000). If hatchery breeding protocols of native species are genetically sound, aquaculture of those species is less likely to cause genetic damage and, in some cases, more likely to be successful than aquaculture of alien species. However, developing the technology to aquaculture native species may be daunting compared to cultivating hearty, adaptable species such as the tilapias. Because the proportion of protein from harvested fish can be significantly lower in feeds for herbivores than in feeds for carnivores, culturing herbivores can be less expensive, both monetarily and environmentally. Culturing these types of species requires that aquaculture techniques be developed for a broad diversity of species on a global scale, which requires many aquaculture research programs and projects. Funding the research needed to develop these techniques can be difficult. With few exceptions, the countries that most need to develop aquaculture of native species and strains are the countries that can least afford it. Financial assistance should come not only from local sources but also from regional, national, and international public and private funding agencies and organizations.
3. Conduct and fund research to domesticate aquacultured species and improve culture technologies for those species (Pillay, 1999). In theory, highly domesticated aquacultured species will not reproduce or, possibly, survive in the wild. Thus, they will generate few or no genetic alterations in wild populations or ecological alterations in habitats. In general, domestication of aquaculture species lags far behind that of terrestrial species, so adequate field testing of this hypothesis has yet to be done.

4. Ensure that aquaculture producers, managers, and stakeholders are fully educated about the importance of conducting ecologically and genetically sound aquaculture and are fully trained in such methods and technologies.
    a. Educate aquaculturists and other stakeholders about the importance of maintaining the health of the environment and about maintaining adequate genetic diversity in hatchery populations, in wild populations of the species they culture, and in all species in the ecosystems in which the cultured species live (Thorpe et al., 1995; Abban, 1999; Bartley and Pullin, 1999). Scientists and lawmakers should make promulgating this information a high priority. They should work with professional groups that are able to communicate directly with aquaculturists (e.g., extension services, outreach programs, and nongovernmental organizations such as the World Aquaculture Society, WorldFish Center, Global Aquaculture Alliance). They should particularly seek out people in remote areas who are interested in aquaculture or are practicing aquaculture. Ultimately, this is the only way that sound ecological and genetic practices will spread throughout the industry.
    b. Ensure that information about new technologies that do not harm the environment (see e.g., Subasinghe et al., 2003) is equitably distributed (Sundli, 1999). This type of information transfer also requires offices or services recognized for communicating and distributing scientific, technical, and legal findings to users and industry representatives. Extension services and outreach organizations are well positioned to perform this task.
5. Sponsor public-relations programs to educate people about the importance of aquaculture (Boyd, 1999). Governmental and institutional publications, displays, and websites are important avenues for promulgating knowledge about the relevance of aquaculture to the quality of human life.
6. Fund and conduct basic biological, ecological, and population genetic research on species currently or potentially affected by aquaculture activities and on the ecosystem components with which they interact.
    a. Conduct basic research to advance understanding of the life cycles, ecological requirements and roles, genetic diversities, and population structures of aquacultured species, closely related species, and their predators and prey. Environmentally responsible aquaculture is difficult to practice if baseline information about natural systems and wild species are not known. Basic biological research and surveys that increase knowledge of ecosystems potentially vulnerable to the effects of aquaculture should be priorities for funding at all governmental levels. Using volunteer programs that provide assistance to researchers for field work could expedite the collection of some types of biological and ecological data and of samples.
    b. Increase research on the ecological and genetic effects of aquacultured organisms that have escaped from aquaculture facilities or have been

released for stock enhancement. Although some ecosystems affected by aquaculture activities have been relatively well studied (e.g., those associated with salmonid sea ranching and stock enhancement in the North American Pacific Northwest region), little is known about the effects of aquacultured organisms or operations in many countries. Where possible, long-term studies comparing natural systems with those affected by aquaculture operations or aquacultured organisms should be conducted.

7. Improve the oversight of antibiotics and other pharmaceuticals and chemicals used in aquaculture. The long-term health of many species can be affected by the incorrect use of drugs, antifoulants, and other chemicals that are water soluble or that remain particulate, especially substances that are transported and concentrated through the food chain (Beveridge et al., 1997). Much research needs to be done on the effects of these compounds on aquatic animals and on species that feed on those animals (e.g., piscivorous birds; reptiles; mammals, including humans).
8. Develop clearly advantageous incentive programs to reward those conducting aquaculture that is compatible with the environment. Incentives such as economic benefits, codes or labels that bring recognition, or other types of rewards can be used to foster interest in and development of ecologically and genetically sound aquaculture. In addition, penalties sufficient to compensate for the environmental damage and cleanup (if cleanup is possible) should be imposed on those who pollute.

2.4. Accomplishments

Although the progress made by the aquaculture industry and its supportive governmental workers and scientific institutions in advancing environmentally sustainable aquaculture is sometimes tentative, significant accomplishments have been achieved by these groups toward making aquaculture of all types sustainable and environmentally benign.

1. First and most notably, aquaculture-industry leaders and personnel in many areas of the world have become aware of the broad and constant focus on the ecological and genetic effects of aquaculture, and they are responding.
   a. Aquaculture-facility architects and managers are considering ecological, genetic, and biodiversity issues when designing and operating aquaculture facilities.
   b. Industry has recommended that research on the compatibility of all types of aquaculture with the environment be increased (e.g., Hossain et al., 2004).
   c. Industry leaders have sponsored workshops focusing on ways to improve environmental awareness within the industry and to facilitate development of low-impact aquaculture operations that are integrated into coastal communities. Industry participants recognize that the industry's image

   may be diminished unless its members deal effectively with environmental issues. In one workshop (Stead et al., 2002), participants focused on developing stronger interdisciplinary communication between the aquaculture industry and other relevant sectors. Their objectives were to improve the scientific information and general knowledge used in integrated coastal-zone management and to develop new perspectives on the sustainable use of coastal areas and their natural resources. In another workshop, industry leaders examined the status of the fish-plant industry, the environmental effects of that industry, the regulations controlling those effects, and the technologies available that, if implemented, could improve the industry's environmental profile (Morry et al., 2003). They made firm commitments to improve their environmental image and vigilance.

   d. Industry leaders recognize the importance of managing genetic diversity and its organization within and between species and of the importance of genetic diversity to aquaculture itself (e.g., the WAS was a sponsor of the workshop upon which this volume is based).

2. Some authoritative organizations have promoted the idea of decreasing the number of alien-species introductions for aquaculture (Bartley and Subasinghe, 1996). (However, the problem of unauthorized, accidental, or inadvertent species introductions remains.)
3. Polyculture and integrated agriculture–aquaculture are already widely practiced in some countries (e.g., Cong et al., 1999).
4. The aquaculture industry and aquaculture scientists recognize the importance and contribution of small-scale aquaculture to local economies (Kongkeo, 2001). Numerous projects and programs exist to develop aquaculture as an activity that provides additional income, protein, and supplemental benefits for people in poor communities (e.g., Tembo, 1999; Subasinghe et al., 2001). Many of these programs and projects involve the local people in the development of aquaculture in their communities (see e.g., WorldFish Center activities; http://www.worldfishcenter.org).
5. Authorities have issued trade embargos against imports of specific aquaculture products (e.g., shrimp) if their culture is not seen as environmentally viable (Nambiar, 1999).
6. Some countries, and some regional and local entities, have developed legislation for environmental management of aquaculture; others have aquaculture-monitoring programs already in place (e.g., Tasmania, Australia [Crawford, 2003; Ogburn, 2007]). Some integrated coastal management that includes aquaculture and consideration of environmental capacity has been initiated. The objectives of this management have included optimal resource allocation, conflict resolution, environmental impact minimization, and resource conservation.
7. Methods for reducing many aspects of the environmental effects of aquaculture waste production have been developed and are available (e.g., Prein,

1995; Piedrahita, 2003). One program (Olsen, 2002) includes an "ecosystems approach" strategy to investigate more sustainable ways to remove nutrient wastes from coastal zones through a more holistic ecological view in which humans are treated as integral components of ecosystems.

Supporting these broad efforts are regional demonstrations of environmental and biodiversity awareness, led by industry participants, researchers, or governmental groups and distributed throughout the world. In Pacific Ocean island nations, there is a growing awareness that aquaculture needs to be balanced with conservation of ecosystems (Bell and Gervis, 1999). The widespread failure of shrimp farms in Ecuador, Taiwan, Thailand, Bangladesh, Vietnam, and elsewhere has been attributed to deteriorated environmental conditions, directly demonstrating to shrimp farmers that financial sustainability can be achieved only through environmental sustainability (Hossain et al., 2004). In Norway, Atlantic cod (*Gadus morhua*) and European lobster (*Homarus gammarus*) stock-enhancement programs include genetic characterization of local wild stocks, broodstocks used, and juveniles produced and released; they also include monitoring programs in which the researchers use genetic tags (see Bert et al., 2002b, 2007) and collect samples for genetic characterization and comparison with local wild populations (Jørstad, 2004). In the southeastern USA, several genetic monitoring programs for red drum (*Sciaenops ocellatus*) stock enhancement are ongoing (Bert et al., 2003, 2007; O'Malley et al., 2003; R. Chapman, South Carolina Department of Natural Resources, USA and J. Gold, University of Texas, USA, personal communications). In the North American Pacific Northwest region, Allendorf et al. (1997) developed a system to prioritize the more than 300 Pacific salmonid populations (*Oncorhynchus* spp.) at risk of extinction for developing conservation and recovery efforts. Amarasinghe et al. (2001) described an international collaborative project in which researchers integrated limnological, fisheries, and socioeconomic data in order to define the trophic structure of five Asian tropical lakes. They also evaluated the capacity of the lakes to sustain the existing levels of fisheries and aquaculture and to withstand aquaculture expansion. In Brazil and Canada, several levels of government support fish gene-banking projects to supplement genetic diversity in broodstocks used for stock enhancement and intensive aquaculture and to guard against severe reduction in the aquacultured species' genetic diversity (e.g., NASCO, 1994). Lastly, in Russia, Norway, Finland, Iceland, Canada, India, and the USA, established fish genetic conservation programs of some type exist (Harvey, 1999).

Overall, aquaculture-industry participants and leaders have made significant strides in working with relevant oversight, management, and scientific entities to bring forward the industry's image being as environmentally aware. Sometimes, this has been accomplished through the industry's initiative and other times through regulation of the industry. Many aquaculture-industry participants have become aware of the significance of ecological and genetic guidelines, rules, and laws put forth by management agencies and have integrated them into their practices without undue consternation. This is an important first step toward full integration of ecological and genetic awareness into the practice of aquaculture.

3. WHAT'S NEXT?

Certainly, on more or less a worldwide basis, much attention has been given during at least the past 10 years to ameliorating the ecological and genetic effects of aquaculture. Many books, articles, and other public documents have been written; symposia, workshops, and conferences have been held; and guidelines, regulations, policies, and laws have been established (see Bert, 2007). Clearly, leaders and formal organizations associated with the aquaculture industry are aware of the constant and sometimes very public (e.g., Masood, 1997; Naylor et al., 1998, 2000, 2001) pressure to conduct operations in the industry in ways that minimize damage to neighboring environments and maintain biodiversity at all levels. But, has this attention resulted in change in the practice of aquaculture? The answer seems to be a qualified "yes." It takes a long time to convince people that change is needed, to find ways to implement change, and to gain acknowledgment of problems and their solutions at all relevant social, cultural, and political levels. But, progress is being made, although perhaps not always in the most important locations.

One of the most common recommendations of many aquaculture scientists, NGOs, and governmental organizations is integrating various types of aquaculture into comprehensive coastal-zone management plans (e.g., Chua, 1993; Gowen and Rosenthal, 1993; Beveridge et al., 1997; FAO, 1997; Thia-Eng, 1997; Phillips and Barg, 1999; Pillay, 1999; GESAMP, 2001; Paez-Osuna et al., 2003; Moksness, 2004). The benefits of this approach are numerous and powerful (e.g., Thia-Eng, 1997). Ideally, governments should have comprehensive, regional or national planning and management programs for aquaculture development (Chua, 1993). This level of cooperation requires a high degree of organization by the human community; knowledge about local ecosystem components, environmental interactions, and animal and plant community structure; and adequate regulatory infrastructure to make and ensure adherence to needed regulations. In some countries, such as those with unstable governments or with large, sparsely populated, relatively wild regions, this may be a difficult step because the necessary oversight, regulatory, and enforcement framework does not exist (King, 1993). However, aquaculture development plans that work toward the components needed for integrated coastal management can be initiated even at the local level. These plans should include the following:

1. mechanisms for coordinating governmental and institutional departments and stakeholders;
2. established regulations for responsible aquaculture that are appropriately enforced;

3. a licensing system for aquaculture activities and species to be aquacultured;
4. equitable distribution of resources;
5. an established capacity-building program (Sundli, 1999).

By cooperatively developing environmentally responsible aquaculture operations and then monitoring them for problematic effects, local community and aquaculture groups can demonstrate that aquaculture can be conducted in ways that are not environmentally damaging. Environmental management frequently works best when it is conducted locally and is community-based (Abban, 1999). Proof that environmentally conscientious aquaculture is being practiced locally should foster acceptance of aquaculture as an economic activity compatible with other demands on local resources. Individually, these types of proofs do not have major effect, but together, they can have cumulative effects (NRC, 1999). Responsible aquaculture generated through stakeholder- and government-based involvement at the community level could spread upward to the regional, national, and international levels.

Aquaculture is so integrally linked to the surrounding environment that if sustainable practices are not employed, degradation of the surrounding environment will ultimately lead to degradation of the industry itself. Ideally, aquaculture operations would be planned with background knowledge of the ecosystems in which facilities will operate as well as knowledge of the potential environmental, social, and economic effects (both positive and negative) that could be incurred and the cost:benefit ratio associated with operating, given that knowledge background. Regular, comprehensive monitoring programs should be planned and be ready to be set into motion when aquaculture operations are initiated. However, the reality is that few aquaculture developers will have this foundation in place prior to developing their operations. Nor will most of these components be included during the operations unless the aquaculturists are required to implement these activities, and for some components (e.g., gathering baseline environmental data), it will be too late. So, what, then, are the most basic elements needed for environmentally sound aquaculture? A reasonable approach that minimizes the probability of environmental damage—preventative maintenance—is the only environmentally sound alternative. This includes culturing species that have a low probability of incurring environmental damage in facilities that are well situated to minimize environmental damage and using techniques that are least likely to cause environmental damage. It also includes a monitoring program designed to detect at least the aquaculture effects with potential for substantial environmental effect and contingency plans that includes actions to stop the effects and mitigate for them as much as possible. These elements do not necessarily involve high expenses, complex facilities, or large numbers of employees. Basically, any conservation effort is better than no conservation effort.

Biodiversity conservation at all levels—from genetic to ecosystem—is a vital element in sustaining natural processes, including those that immediately or ultimately benefit humans, but it involves many tradeoffs with other management goals (NRC, 1999). Most aquaculture is conducted in the world's 25 biodiversity hotspots (as defined by Myers et al., 2000). These include much of the Indo-west Pacific (including the Philippines and Japan), Central America (including Ecuador), Southeast Asia (including Malaysia, Thailand, Indonesia, Micronesia, Polynesia, and south-central China), and coastal subtropical and tropical South America (including central Chile and Brazil's Mata Atlantica region). Thus, many countries that could gain the most from aquaculture have the most to lose in biodiversity, and losses in these regions are losses to all world heritage. The world's governments and the aquaculture industry have a continuing collective responsibility to work toward conducting ecologically and genetically sustainable aquaculture for all time, not just for the present. As is made clear by the chapters in this book, restoring the environment and its biodiversity (if it can be done) is much more expensive and time consuming than managing it wisely in the first place (World's Scientific Academies, 1994).

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