

Fugitive Salmon: Assessing the Risks of Escaped Fish from Net-Pen Aquaculture

ROSAMOND NAYLOR, KJETIL HINDAR, IAN A. FLEMING, REBECCA GOLDBURG, SUSAN WILLIAMS, JOHN VOLPE, FRED WHORISKEY, JOSH EAGLE, DENNIS KELSO, AND MARC MANGEL

The farming of salmon and other marine finfish in open net pens continues to increase along the world's coastlines as the aquaculture industry expands to meet human demand. Farm fish are known to escape from pens in all salmon aquaculture areas. Their escape into the wild can result in interbreeding and competition with wild salmon and can facilitate the spread of pathogens, thereby placing more pressure on already dwindling wild populations. Here we assess the ecological, genetic, and socioeconomic impacts of farm salmon escapes, using a risk-assessment framework. We show that risks of damage to wild salmon populations, ecosystems, and society are large when salmon are farmed in their native range, when large numbers of salmon are farmed relative to the size of wild populations, and when exotic pathogens are introduced. We then evaluate the policy and management options for reducing risks and discuss the implications for farming other types of marine finfish.

Keywords: exotic species, risk assessment, genetics and evolution, general ecology, environmental policy

The aquaculture industry has become a major supplier of fish and shellfish in markets worldwide. Between 1992 and 2002, global production of farm finfish and shellfish almost tripled in weight and nearly doubled in value (FAO 2003). Roughly 40% of all fish directly consumed by humans worldwide are farmed. The growth of some aquaculture sectors has been especially dramatic. For example, global production of farm salmon (salmon reared from eggs in hatcheries and then grown to market size in marine net pens) quadrupled in weight from 1992 to 2002 and now exceeds wild salmon catch by about 70% (FAO 2003). Over 90% of this farm product is Atlantic salmon (*Salmo salar*), a species nearly depleted in the wild. With continued human pressure on marine fisheries and ocean resources, aquaculture has become one of the most promising avenues for increasing marine fish production in the future.

The rapid growth of open net-pen culture of salmon and other species, combined with well-documented escapes of farm fish into the wild, also portends a transformation in many marine ecosystems. Atlantic salmon are farmed both within their native range (e.g., northern Europe, eastern North America) and beyond (e.g., western North America, Chile, Tasmania). Atlantic salmon raised on farms now far outnumber wild Atlantic salmon returning to rivers (figure 1), and escapes occur in all aquaculture regions both through regular, low-level “leakage” and through episodic events such as storms. In the native range, an estimated two million farm salmon escape each year into the North Atlantic (Schiermeier 2003). Roughly 20% to 40% of the Atlantic salmon caught in the fisheries of the North Atlantic high seas (off the Faroes) between 1989 and 1996 was of farmed origin (Hansen et al. 1999). Farm salmon represent on average 11% to 35% of the “wild” spawn-

Rosamond Naylor (e-mail: roz@stanford.edu) is the Julie Wrigley senior fellow at the Center for Environmental Science and Policy, Stanford University, Stanford, CA 94305. Kjetil Hindar is a senior research scientist at the Norwegian Institute for Nature Research, N-7005 Trondheim, Norway. Ian A. Fleming is director of the Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland A1C 5S7, Canada. Rebecca Goldberg is a senior scientist with Environmental Defense, New York, NY 10010. Susan Williams is director of the Bodega Marine Laboratory, University of California–Davis, Bodega Bay, CA 94923. John Volpe was an assistant professor in the Department of Biological Sciences, University of Alberta, when this study was performed; he is now an assistant professor of marine systems restoration and conservation in the School of Environmental Studies, University of Victoria, Victoria, British Columbia V8W 2Y2, Canada. Fred Whoriskey is the vice president of research and environment at the Atlantic Salmon Federation, St. Andrews, New Brunswick E5B 3S8, Canada. Josh Eagle is an assistant professor at the University of South Carolina School of Law, Columbia, SC 29208. Dennis Kelso was an assistant professor in the Environmental Studies Department at the University of California, Santa Cruz, CA 95064, when this study was being prepared; he is now director of the Fisheries Program, David and Lucile Packard Foundation, Los Altos, CA 94022. Marc Mangel is a professor in the Department of Applied Mathematics and Statistics at the University of California, Santa Cruz, CA 95064.

© 2005 American Institute of Biological Sciences.

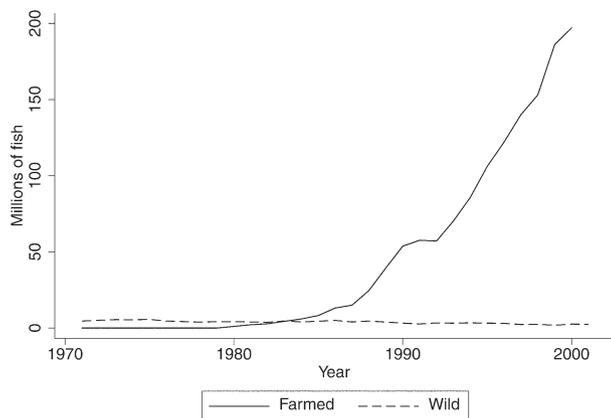


Figure 1. Atlantic salmon farmed in net pens and returns of wild Atlantic salmon to rivers (ICES Working Group on North Atlantic Salmon).

ing populations in Norway, with some populations exceeding 80% (Fiske et al. 2001). Outside the native range, millions of Atlantic salmon have escaped on the western coasts of North America (Volpe et al. 2000) and South America (Soto et al. 2001). Atlantic salmon have been found in more than 80 rivers in British Columbia alone, and they are reproducing in some locations (Volpe et al. 2000).

To what extent do escapees survive in the wild, colonize, and compete with wild fish for food and spawning resources? Does interbreeding between farm and wild salmon populations change the genetic makeup of wild salmon? Do escapes increase the incidence of diseases and parasites in the wild? In this article, we review empirical evidence on the ecological and genetic impacts of farm salmon escapes on wild fish populations and ecosystems, and assess the risks posed by salmon aquaculture for the recovery of depleted wild Atlantic and Pacific salmon populations. We then describe the economic and social consequences of escapes, and discuss government policies and management practices aimed at reducing the potential harm to ecosystems and society.

Understanding the risks associated with escapes from salmon farms is particularly relevant for management and policy as the scale of net-pen aquaculture expands. Improved technology and falling market prices for salmon have prompted aquaculture companies to begin raising numerous other marine finfish species, many of which have been overfished in the wild. New species currently being farmed include Atlantic cod (*Gadus morhua*), sablefish (*Anoplopoma fimbria*), Atlantic halibut (*Hippoglossus hippoglossus*), Pacific threadfin (*Polydactylus sexfilis*), mutton snapper (*Lutjanus analis*), bluefin tuna (*Thunnus* spp.), turbot (*Scophthalmus maximus*), sea bass (*Dicentrarchus labrax*), and sea bream (*Sparus aurata*) (Naylor and Burke 2005). In some countries, such as Norway and Canada, net cages for new species are being located in coastal waters along with salmon cages. In the United States, where the expansion of salmon farms in coastal waters has met local opposition and state-level re-

strictions, the National Oceanic and Atmospheric Administration has made it a priority to pursue the development of large offshore aquaculture operations in the exclusive economic zone, beyond the reach of state laws (Goldburg and Naylor 2005).

The risks that escaped farm fish pose are a function of the probability of escape, the magnitude of each escape event, and the impact of escaped fish on wild populations, ecosystems, and society. Box 1 outlines a series of biological, socioeconomic, and technological questions that are important in assessing risks as the industry continues to grow. We provide answers to many of these questions for farm salmon escapes in the following sections. We focus on salmon as a model for assessing risks of aquaculture escapes for three reasons. First, salmon are currently the most widely farmed marine finfish for commercial markets, and much is known about their biology and the results of their escapes. Second, salmon have a number of characteristics relevant to a broader set of species. Salmon are both resident in fresh water and migratory in the oceans; they live in diverse habitats within their life cycle; both native and nonnative species of salmon are cultivated; and escapees are known to be invasive in some areas and noninvasive in others. Finally, a strong conservation ethic has evolved around wild salmon and the habitats that support them.

Potential biological consequences of farm salmon escapes

Many of the biological consequences resulting from net-pen escapes are understood well by the scientific community, yet the probabilities of their occurrence tend to be regionally (e.g., Atlantic versus Pacific) and temporally specific. Here we delineate the main biological risks and highlight the scientific uncertainties. The introduction of hatchery fish into native salmon territory for stock enhancement presents many of the same biological risks (Levin et al. 2001), although the economic, management, and regulatory issues are quite different. For this reason—and because of the recent boom in the production of marine farm fish worldwide—we focus on escapes from net-pen aquaculture.

Risks of feral stock establishment. The success of an invasive species is largely determined by fluctuating biotic and abiotic conditions that determine the window of opportunity for establishment. The probability of invasion success increases with repeated introduction and is frequently preceded by numerous failures. Repeated, unintentional releases are a by-product of large-scale industrial salmon aquaculture and increase the likelihood of escapees being present in the wild whenever conditions may favor colonization. Of 3141 introductions of aquatic species recorded by the Food and Agriculture Organization of the United Nations in 1998, 39% were a result of aquaculture (FAO 1998). The near inevitability of escapes from aquaculture facilities has led to the recommendation that introductions of species for aquaculture should be considered an introduction to the wild, even if the facility is considered a closed system (FAO 1995).

Box 1. Relevant questions for assessing risks associated with aquaculture escapes.

Ecology and genetics

- What are the chances that escaped farm fish will establish feral populations?
- To what extent will escaped farm fish compete with wild fish for prey, space, and mates?
- What is the likelihood that escaped farm fish will interbreed with and alter the genetic characteristics of wild fish?
- Will escaped farm fish transmit pathogens to wild fish?

Socioeconomics

- What are the potential long-term consequences to the fishing industry from the establishment of escaped farm fish?
- Will the presence of escaped farm fish mask any decline in native wild fish, causing unwarranted relaxation of fishery management?
- What is the potential loss to the aquaculture industry from escapes in the short and long run?
- What are the ethical aspects of permitting the potential establishment of feral farm species and any consequent decline in wild populations?
- What are the most cost-effective means to minimize the occurrence of escapes?

Technology

- What is the likelihood of escapes from the aquaculture technology proposed or in use?
- Are effective sterilization techniques available?
- Can farm fish be marked or tagged for identification in the wild?

Atlantic salmon has been one of the most intensively introduced species around the world. Despite many attempts to establish sport fisheries, Atlantic salmon have shown poor colonizing ability when introduced sporadically and have generally failed to establish self-sustaining anadromous populations beyond the native range. The situation is quite different for Atlantic salmon introduced into the wild through farm escapes within their native range. Escaped farm salmon are successfully breeding in the wild in Norway, Ireland, the United Kingdom, and eastern North America (Hansen et al. 1997). In the Pacific Ocean, incipient feral Atlantic salmon populations have been found in rivers in British Columbia (Volpe et al. 2001) and in South America (Soto et al. 2001, Pascual et al. 2002). Several feral populations of Pacific salmon have also become established in Chile and Argentina as a

result of seeding for sportfishing and escapes from aquaculture facilities (Lindbergh 1999, Pascual et al. 2002).

Although establishment is an important factor in assessing the biological impacts of escapes, it is not the whole story. Even if escaped fish fail to complete their life cycles, aquaculture operations continue to replenish them. As discussed below, escaped farm salmon can have significant impacts on wild fish whether or not escapees reproduce.

Risks of competition with wild fish for mates, space, and prey.

Although farm salmon may escape as juveniles from freshwater hatcheries, most reported escapes occur from marine net pens. Net-pen escapees can then move between marine and freshwater habitats and interact with wild salmon and other species in the ecosystem. In fresh water, they can spawn successfully in rivers in both native and nonnative ranges, though their breeding performance is sometimes significantly inferior to that of wild salmon (Fleming et al. 2000). There is little evidence to date of farm salmon directly disrupting spawning by wild salmon (Fleming et al. 2000). Spawning of wild females with farm males, however, occasionally results in poor fertilization of eggs when no wild males are involved (Fleming et al. 2000). Depending on the spawning phenology of farm and wild populations, the destruction of early nests by later-spawning farm females may cause the greatest harm during the breeding season.

Successful reproduction of farm salmon in the wild, or the escape of juveniles from freshwater hatcheries, can lead to further interactions among wild, farm, and hybrid (crossbred farm and wild) fish in fresh water. Both forms of introduction inevitably affect population density, at least initially, and can alter the frequency of competitive interactions, levels of food availability, or functional responses of predators.

The potential for competition is significant because the diet and habitat choice of farm and hybrid juveniles overlap with those of their wild conspecifics (McGinnity et al. 1997, 2003, Fleming et al. 2000) and with those of juveniles from related (Volpe et al. 2000) and unrelated species (Pascual et al. 2002, Baxter et al. 2004). Farm juveniles typically outgrow wild juveniles, even in nature (McGinnity et al. 1997, 2003, Fleming et al. 2000), reflecting artificial selection for growth (Fleming et al. 2002). Farm offspring thus have a size advantage and, potentially, a competitive edge over wild juveniles. There are also clear and consistent behavioral differences between farm and wild juveniles that are genetically based, including greater aggression and risk-taking by farm juveniles (Fleming and Einum 1997, Fleming et al. 2002). Hybrid juveniles are often intermediate in trait expression between farm and wild juveniles (McGinnity et al. 1997, 2003, Fleming et al. 2000).

Territorial and social dominance is widespread in wild salmonid populations, and the addition of cultured fish to wild populations can affect both mortality and growth of the wild fish. Aggression is an energetically costly behavior, and the increased aggressiveness of escaped juvenile farm salmon can severely stress their wild counterparts, even increasing their mortality. Displacement of native fish by larger, more

aggressive farm and hybrid fish can also result in shifts of wild counterparts to poorer habitats, again increasing mortality (McGinnity et al. 1997, 2003, Fleming et al. 2000). The outcome of such interactions is indicated by Fleming and colleagues' (2000) experimental release study, which showed that the productivity of the native juvenile salmon population was depressed by more than 30% in the presence of farm and hybrid juveniles.

In Pacific streams, competitive interactions between native fish and Atlantic salmon for prey and space most often involve steelhead (*Oncorhynchus mykiss*) in North America and galaxiid fishes in South America (Pascual et al. 2002). Steelhead tend to be competitively superior to Atlantic salmon at a given body size (Gibson 1981). However, prior residency is a far better predictor of competitive superiority; the earlier-hatching Atlantic salmon not only have a potentially greater size at the same age, but they also have an early residency advantage that can provide a significant competitive advantage (Volpe et al. 2000). In South America, Australia, and New Zealand, the effects of Atlantic salmon introductions on the native fish fauna are poorly documented, but competitive interactions with, and predation by, other introduced salmonids have reshaped fish communities in these regions (Crowl and Townsend 1992, Pascual et al. 2002). Introductions of salmonid fishes into regions where such species have previously been absent can lead to the restructuring of stream food webs, and also the food webs of the surrounding forests, as the flow of nutrients between the interconnected ecosystems is altered (Baxter et al. 2004).

Little is known about competitive interactions in the marine environment. The presence of large numbers of escaped farm salmon in coastal ecosystems is likely to increase competition for available resources as introduced fish consume wild food items and occupy space. In the Atlantic Ocean, large numbers of escapees migrate to feeding grounds; for example, 20% to 40% of the fish off the Faroe Islands are of farm origin (Hansen et al. 1999), and these fish show feeding patterns similar to those of wild fish (Jacobsen and Hansen 2001). Feeding by farm Atlantic salmon following escape in the Pacific Ocean tends to be limited, but it still occurs in some areas (Soto et al. 2001, Morton and Volpe 2003). In the Pacific, many native wild populations of salmon are already under competitive pressure from billions of hatchery-reared fish released annually into the pelagic environment (Levin et al. 2001).

Risks associated with genetic interactions. Wild salmon populations exhibit considerable genetic differences (Stahl 1987, King et al. 2001), some of which are believed to reflect adaptations to local environments (Taylor 1991). Rapid genetic change in farm salmon has resulted from intentional and unintentional selection during domestication, and from the use of a limited number of breeders. The founding population of most farm Atlantic salmon consisted of 40 Norwegian stocks used to establish a breeding program in the 1970s. Derivatives of this breeding program produce 70% of the eggs

used in Atlantic salmon farming in Norway, and a large share of the eggs and sperm used for salmon aquaculture in most other countries. Farm salmon demonstrate genetic variability among strains, but they exhibit lower total genetic variability than wild populations (Norris et al. 1999).

An earlier review (Hindar et al. 1991) of the genetic effects following releases of nonnative salmonids reached two broad conclusions. First, the genetic effects of intentionally or accidentally released salmonids on natural populations are often unpredictable and may vary from no detectable effect to complete introgression or displacement. Second, when genetic effects on performance traits (e.g., survival in fresh water and seawater) have been detected, they appear always to be negative in comparison with the traits of unaffected native populations.

Interbreeding between escaped farm fish and wild fish has since been demonstrated in spawning arenas; in a river following the release of genetically marked fish (McGinnity et al. 1997, 2003, Fleming et al. 2000); and in wild populations in various countries where salmon farming is practiced (Hansen et al. 1997). The extent to which interbreeding of escaped farm and wild salmon leads to long-term loss of fitness and productivity in wild populations is now becoming clear. Interbreeding between wild and farm fish can result in mixing of gene pools if the hybrids can reproduce, and eventually can lead to a wild population composed entirely of individuals descended from farm escapes. In a Norwegian study (Fleming et al. 2000), 55% of farm escapes in the experimental spawning population contributed 19% of the genes to adult fish one generation later. Continued one-way gene flow at this rate would halve the genetic difference between farm and wild salmon every 3.3 generations and lead to rapid genetic homogenization. With current levels of gene flow from farm salmon to wild salmon, the amount of genetic variability that can be maintained in the total salmon population could soon depend almost solely on the limited variability present in farm fish (Tufto and Hindar 2003). The result would be an irreversible loss of the unique genetic diversity of wild salmon (Hindar et al. 1991) and hence of their capacity to adapt to environmental change.

In addition to the loss of unique gene pools, interbreeding between wild and farm fish of the same species has been shown to make offspring less fit than their parents (McGinnity et al. 2003). In McGinnity and colleagues' (2003) recent farm release study in Ireland, the lifetime success of hybrids was only 27% to 89% as high as that of their wild cousins, and 70% of the embryos in the second generation died. These results provide strong evidence of how interbreeding might drive vulnerable salmon populations to extinction.

Rapid growth rates of farm and hybrid juveniles may further speed genetic homogenization by reducing their age at maturity and thus their generation time relative to that of wild salmon (Fleming et al. 2000). It may also increase the frequency of early male maturation before seaward migration, and result in increased mating competition and breeding success for such males (Garant et al. 2003). Unlike the much larger

migratory males, these early-maturing males do not court females but rather attempt to “sneak” fertilization, sometimes with great success. Early male maturity can also promote interspecific hybridization (Garcia-Vazquez et al. 2002).

Longer-term fitness consequences depend on the extent to which natural selection in recently established feral populations will promote wild-type traits (Kinnison and Hendry 2004). Natural selection should eliminate maladapted domestic traits. Evidence of remarkable rates of genetic change in transplanted Pacific salmon populations (Kinnison and Hendry 2004) suggests that this process could occur very rapidly. However, as long as escapes from net pens continue, cumulative fitness depression, rather than readaptation, is the more likely longer-term outcome, particularly in the North Atlantic, where wild salmon populations are small (Hindar et al. 1991, McGinnity et al. 2003).

Farm escapees can also breed with wild salmon of a different species. Interspecific hybridization occurs naturally at low rates between Atlantic salmon and brown trout (*Salmo trutta*; Youngson et al. 1993). More important, an increase in the rate of hybridization between these species in Scotland (Youngson et al. 1993) and Norway (Hindar and Balstad 1994) shows associations with the presence of escaped farm salmon. The average proportion of interspecific hybrids is low (1% or less), but reaches 10% or more in some rivers. Interspecific hybrids survive well but are largely sterile, and thus may lower the productivity of local populations. Lowered productivity is of special concern where local populations are endangered. While hybrids between Atlantic and Pacific salmon are unlikely to be viable (Chevassus 1979), attempted fertilization may still result in a loss of wild gametes and hence a decline in wild populations, especially if the number of escaped farm salmon in rivers is large.

Risk of pathogen transmission. In addition to risks associated with genetic interactions, salmon aquaculture presents risks of increasing disease outbreaks, proliferating possible disease transmission routes in the environment, and decreasing the immunity of wild fish to disease. Transmission of pathogens and diseases from aquaculture to vulnerable wild fish can occur through populations that are infected at the hatchery source, through contact with wild hosts of the disease, through infected escapees, and through wild fish migrating or moving within plumes of an infected pen or disease outbreak. Dense cultures often lead to clinical expressions of disease and a shedding of pathogens into the environment, and hence to a higher prevalence of disease overall (Jones et al. 1999).

There is now sufficient evidence of the transmission of pathogens and disease from cultured salmonids to wild populations to raise concern. Recent epidemiological patterns in Ireland, Scotland, Norway, and Canada suggest that outbreaks of sea (or salmon) lice (*Lepeophtheirus salmonis*, *Caligus* spp.) in wild fish are connected with the increased concentration of aquaculture (Naylor et al. 2003, Krkosek et al. 2005). Salmon lice can also transfer highly virulent infec-

Box 2. Furunculosis in salmon farms.

Furunculosis, caused by the bacterium *Aeromonas salmonicida*, was first described in brown trout culture in Germany in 1894, and in North America in 1902. Opinions differ on its geographical origin, but not on the potential of its spread through translocated and cultured fish. Outbreaks can occur several hundred kilometers from the last known outbreak, often associated with known translocation of fish. In 1985, the disease was introduced to Norwegian fish farms by transport of smolts from Scotland. The disease spread rapidly from the first few infected farms to reach 550 fish farms (70% of the total) by the end of 1992. In 1988–1989, more than 250,000 escaped farm salmon were from farms infected with furunculosis. These fish were then found among spawning salmon (both farm escapees and wild fish) the following autumn. By 1992, furunculosis had been registered in 74 Norwegian rivers. In four rivers, the disease reached epidemic proportions. The rapid spread of furunculosis after the development of Norwegian marine aquaculture contrasts with the limited spread from a natural population that was infected in the late 1960s without showing evidence of further transmission. Vaccination programs and better husbandry in the aquaculture industry seem to have eliminated the furunculosis problem in recent years.

tious salmon anemia (ISA) between fish (Nylund et al. 1999). ISA has been detected in fish farms in Norway, Canada, Scotland, and the United States, as well as other countries. In hatchery fish, molecular epidemiology has pinpointed the spread of infectious hematopoietic necrosis, or IHN (a virus affecting the kidney and often the spleen, liver, and pancreas of the fish), from steelhead raised in Idaho to wild salmonid populations in the Columbia River (Kurath et al. 2003). Dispersal of cultured salmonids is heavily implicated in the spread of whirling disease (Bartholomew and Reno 2002), a disease that can affect many anadromous salmonid species.

Various pathogens and parasites have been detected in escaped farm salmon. Infected escapees are suspected to have transmitted furunculosis disease to wild stocks (box 2; Johnsen and Jensen 1994). In 1999, the Atlantic Salmon Federation in Canada detected clinical ISA for the first time worldwide in wild Atlantic salmon, and in escaped farmed Atlantic salmon that had entered the same river (ICES 2001).

Biological risks in perspective. The fundamental question surrounding escaped farm salmon is one of risk, and how much risk society is willing to accept. This question will gain even more significance if transgenic salmon, whose genetic coding is differentiated from that of wild salmon, are introduced for commercial production into open net-pen culture

(Fletcher et al. 2000). Any ecologically competent exotic fish, including transgenic and selectively bred Atlantic salmon with genetically based traits not currently found in wild populations, poses substantial risks. Such risks include potential reductions in the genetic diversity (and resulting ability to adapt to environmental change), productivity, and fitness of wild fish, leading to possible extinctions. The biological evidence presented above suggests that farm Atlantic salmon introduced into native range are more likely to hybridize and exhibit greater competition with wild salmon than would be the case for escaped Atlantic salmon in the Pacific. This conclusion goes against the conventional wisdom that indigenous species are lesser threats for genetic modification than exotic species (Tiedje et al. 1989). The verdict is not yet in, however, on how aggressive escaped Atlantic salmon will be in the Pacific, as evidence that Atlantic salmon are reproducing and competing with wild Pacific salmon is accumulating. Some biologists believe this risk is low (Waknitz et al. 2003). In both the Atlantic and Pacific regions, biological risks to wild populations rise with the number of farm escapes and are highest when farm escapees outnumber wild salmon in a given location. One important exception is the case of exotic pathogen introductions; a very small number of fish carrying an exotic pathogen may be sufficient to cause severe mortality in wild fish populations.

Potential economic and social consequences of escapes

Net-pen escapes also increase the risk of economic and social losses, although there have been few attempts to estimate these losses to date. The most direct cost is borne by the aquaculture industry in the form of foregone revenue, lost capital invested in grow-out stock, and public perception problems. In some cases, these costs are offset by insurance payments for damage, particularly when the escapes occur during storm events. Even with chronic leakage, aquaculture firms often weigh the benefits of eliminating escapes against the financial costs of improving the strength and durability of net pens, altering harvest equipment, and other measures. The nonmarket costs of escapes (i.e., effects on wild populations and ecosystems) do not pose direct financial burdens on producers.

Escape-driven declines in wild fish populations are more likely to affect commercial fishing interests and conservationists who care about the health of wild fish and ecosystems. Although net-pen aquaculture is often regarded as a means to reduce pressure on wild fish populations, wild salmon capture is actually higher today than it was before 1990, when farmed output was negligible in international markets (Goldburg and Naylor 2005). At a global scale, salmon aquaculture is thus supplementing, not substituting for, wild catch. At the same time, escapes may have a detrimental impact on vulnerable wild salmon populations at a regional scale. If production of hatchery fish is increased to compensate for escape-driven declines in wild populations, costs to the fishing industry might increase with higher licensing

fees, or costs to taxpayers might increase with subsidies to hatcheries.

Alternatively, escapes could increase revenues for the recreational fishing industry by providing new types of sport fish. Exotics are a mainstay of many freshwater recreational fisheries in the United States and elsewhere (e.g., New Zealand). These gains must be balanced with the reduction in native fish catch resulting from escapes, since native fish are also extremely important to the recreational fishing industry in many regions. For example, Scotland's once lucrative recreational fishery for wild Atlantic salmon is now in a serious decline, due in part to ecological damage from the expanding salmon aquaculture industry (McKibben and Hay 2004).

Threats to wild salmon populations also create costs to society as a whole. Nonmarket metrics for conservation, such as memberships in conservation organizations, support for legislation, and voting behavior, can be used as indices in evaluating the risks and impacts of escapes. Privately funded conservation organizations such as the Atlantic Salmon Federation in North America and the Atlantic Salmon Trust in the United Kingdom have significant member support. These groups, along with the intergovernmental North Atlantic Salmon Conservation Organization, play leadership roles in conservation of wild salmon. Many people value the pure existence of wild salmon (whether or not they fish or ever see salmon), and many appreciate the ecosystem services that wild salmon provide, such as their roles in food webs and nutrient cycling that sustain broader wildlife populations. As a legal measure, the US Endangered Species Act (ESA) articulates the protection of species at essentially any cost to the public. Several populations of wild salmon on both the East Coast and the West Coast of the United States are currently listed, or subject to be listed, as threatened or endangered under the ESA (Waples 1995, NRC/NAS 2002). The Committee on the Status of Endangered Wildlife in Canada has also listed certain wild salmon populations in the "endangered" or "at risk" category.

Conservation values can also be measured by various economic methods, such as contingent valuation analyses that elicit people's willingness to pay (WTP) for the protection of a given species or ecosystem or their willingness to accept (WTA) a given amount of damage to a species or ecosystem. Surveys in Washington State have shown that residents' WTP is \$50–\$70 per household for wild salmon conservation through habitat restoration efforts or dam removal (Loomis 1996). Because farm salmon escapes may contribute to the extinction of certain wild salmon populations, the subjective loss value of WTA can be infinite (Naylor 2000).

Nevertheless, many people place positive values on farm salmon, and the social losses from escapes must be balanced to some degree against the gains from increased aquaculture production. Farm salmon now comprise 60% of fresh and frozen salmon sold in international markets (FAO 2003) and provide a protein source for many consumers who may not have eaten salmon in the past because of the high cost and lack of year-round availability. Between 1988 and 2002, the price

of farm Atlantic salmon fell by 61%, and ex-vessel prices for the Pacific salmon species that compete most directly with Atlantic salmon (sockeye, coho, and chum) fell by 59%–64% (Naylor et al. 2003). In addition to relatively low prices and year-round availability in markets, consumers derive health benefits from the high levels of omega-3 polyunsaturated fatty acids in salmon. These health benefits must be balanced against health risks from organic contaminants, such as PCBs (polychlorinated biphenyls) and dioxins, that bioaccumulate to a larger extent in farm salmon than in wild salmon (Hites et al. 2004). An appropriate goal is to maximize net benefits from farm salmon to consumers with improved aquaculture technology and management that also reduce escapes. There is an important role for public policy to ensure that economic, social, and ecological benefits from aquaculture are jointly achieved.

The role of public policy

Despite risks to ecosystems and society resulting from farm salmon escapes, policy initiatives to prevent or mitigate escapes remain relatively weak in most major salmon-farming regions. Reporting of escapes varies widely, with some regions, such as Chile, Scotland, New Brunswick, the Faroe Islands, and Tasmania, having no reporting requirements. Where reporting is required, the extent of compliance is unknown.

Table 1 summarizes specific regulations for escaped salmon from marine aquaculture facilities in the major salmon-producing countries in 2003. The United States (regulated separately in Washington and Maine) and British Columbia have the strictest regulations on the books in terms of facility design, prevention and response plans, and monitoring and enforcement. Norway also mandates relatively strict reporting and contingency plans and, under Norwegian Standard 9415, adopted strict new technical requirements for fish farms (effective 1 April 2004 for new farms and 1 January 2006 for existing farms). Even in these regions, however, regulations tend to focus on larger escape events as opposed to chronic leakage, although the latter contributes significantly to the numbers of fugitive fish. Iceland has the strongest penalties for the failure to comply with escape-related regulations (possible loss of license), and producers without contingency plans in Norway face fines. Fines for major escape events are also levied in British Columbia, particularly if the events are not reported promptly, although such fines are rarely sufficient to induce a change in practice (Naylor et al. 2003).

Overall, the evidence indicates that where penalties for escapes exist, they generally provide an insufficient incentive to prevent escapes and are incommensurate with the ecological and socioeconomic risks described in earlier sections. Moreover, with uneven regulation across countries, “get-tough” policies in one country could drive aquaculture production into countries with more lenient regulations (Naylor et al. 2003).

Recapture and identification. As indicated in table 1, mandated recapture efforts are commonly encouraged to reduce the number of fugitive salmon in the wild. Most farm escapes

occur in coastal waters, however, and it has proved virtually impossible to recapture farm fish that escape during extreme weather conditions (Hansen and Lund 1992). Recapture of fish that escape during daily operations depends on knowledge about when and how escapes occur, gained from underwater video surveillance. Farm escapees can also be harvested at a later stage (e.g., when they approach the coast and enter fresh water to spawn). In rivers, farm escapees can be removed by allowing fishers to take farm fish while requiring them to release any wild salmonids that they catch, a practice currently encouraged in some rivers of Norway and Newfoundland. However, all recapture approaches involve some risk of reducing wild populations.

In some regions, regulations requiring fish identification—a system recently put in practice in Washington and Maine—are used to hold aquaculture producers accountable for fish that escape from their farms. Iceland requires that 10% of the fish sent to sea cages have coded wire tags in them (ICES 2003). In addition, wild Atlantic salmon can be reliably distinguished from escaped farm salmon by examining the differences in the growth rings deposited on their scales. The feasibility of providing site-specific marks for individual hatcheries and farms is being explored in North America and Norway; for example, Norwegian authorities are currently evaluating different mass marking techniques, including “bar-code” and genetic marks. Induced thermal signatures on otoliths, and on other structures that can be manipulated easily by temperature treatment, could permit virtually unlimited marking (Blick and Hagen 2002).

Despite the benefits of using markers to increase accountability, there is still resistance to such measures within the industry. Currently available markers have some downsides (e.g., infections in wire-tagged fish), but new technologies, such as genetic markers, may minimize such difficulties. Without markers, high catch levels resulting from the capture of escaped farm fish within their native range might suggest that wild stock status is better than it actually is.

Mitigation approaches. A variety of infrastructure, veterinary, and breeding approaches based on analyses of risks and critical control points also exist for reducing the number of escapes and their potential harm to ecosystems and society. To their credit, salmon-farming companies have adopted a number of measures to reduce the incidence of escapes, including the use of stronger net materials, tauter nets that deter seals from grabbing fish, and covers on boat propellers to avoid net tears. A more secure, but also more costly, method of restricting escape events and disease transmission is to isolate farm fish from the natural environment in land-based tanks or closed-wall sea pens (Naylor et al. 2003).

Sterilization of farm fish is used in some locations, such as Tasmania (Sadler et al. 2001). At present, induced triploidy is the only effective method for mass production of reproductively sterile salmonids for aquaculture (Benfey 2001, Sadler et al. 2001) and could be used to prevent genetic

Table 1. Regulations of aquaculture escapes, 2003.

Country	Facility design	Prevention and response plans	Monitoring and enforcement
United States (Maine)	Each aquaculture facility must employ a containment management system to prevent the escape of fish. Starting in May 2004, all Atlantic salmon placed in net pens must be of North American origin. The use of transgenic fish is prohibited. Timeline established for marking all new fish placed in net pens to identify the facility owner and confirm that the fish are from Maine.	Each facility must report known or suspected escapes of more than 50 fish with an average weight of at least 2 kg each within 24 hours.	Certain agencies are authorized to inspect aquaculture facilities for compliance with general permit. Each containment management system will be audited at least once per year and within 30 days of a reportable escape.
United States (Washington)	All marine finfish hatched after 31 December 2003 must be marked so that they are individually identifiable to the aquatic farmer. The use of transgenic fish is prohibited.	Aquaculture facilities must have an escape prevention plan and an escape reporting and recapture plan.	Aquaculture facilities must have procedures for monitoring the implementation of the escape prevention plan. Employees of the Washington Department of Fish and Wildlife are authorized to conduct inspections at aquaculture facilities.
Canada (British Columbia)	Regulations exist for construction, installation, inspection, and maintenance, including comprehensive regulations for net cages and related structures.	Aquaculture facilities must have written escape response plans. Facilities must verbally report any escapes within 24 hours of the discovery of an escape or evidence suggesting an escape.	Inspectors are authorized to investigate facilities' compliance with aquaculture regulations. No requirement for monitoring by license holder. Monitoring only via Atlantic Salmon Watch reporting system.
Canada (New Brunswick)	No escape regulations exist.	No escape regulations exist.	No escape regulations exist.
Chile	No escape regulations exist.	No escape regulations exist.	No escape regulations exist.
Faroe Islands	No escape regulations exist.	No escape regulations exist.	No escape regulations exist.
Iceland	No specific requirements, but escape prevention is a general condition of aquaculture operating licenses.	Aquaculture operating licenses must specify plans to catch escaped fish. Escaped fish must be reported immediately.	Compliance with regulations is monitored twice annually. Failure to comply with regulations can result in loss of operator license. No system of public reporting on compliance.
Ireland	No specific requirements, but escape prevention is a general condition of aquaculture operating licenses.	Facility owners must immediately report fish escapes and have contingency plans for fish escapes.	No systematic collection of data on contingency plans for fish escapes or plans for escape prevention. On-site audits of wear or fatigue on key elements of aquaculture system.
Norway	No specific requirements for escape prevention, although regulations are under development. Farms are required to have nets in the sea around each site in winter for monitoring escaped farm fish.	Aquaculture facilities must keep contingency plans for limiting the size of escapes and recovering escaped fish. Escapes must be reported immediately.	Government operates "national program of action against escapes" and examines contingency plans and record keeping on operational procedures.
Scotland	For existing sites, a voluntary code of practice for stock containment addresses the design and construction of aquaculture equipment and procedures that could affect escapes. New sites must have escape prevention plans.	For existing sites, a voluntary code of practice requires contingency plans for recapturing escaped fish. New sites must have contingency plans.	No evidence of government monitoring of escape prevention procedures or of contingency plans for escapes.
Tasmania	No escape regulations exist.	The holder of a marine farming license must take reasonable precautions to prevent the release, deposit, or escape into state waters of any introduced fish.	No escape regulations exist.

dilution of wild populations by farm escapes. Triploids have a number of disadvantages in commercial culture, however, and are not commonly raised. They tend to have a poorer grow-out performance and survival than diploids, and are prone to the development of a characteristic lower-jaw deformity that affects growth and marketability (Benfey 2001, Sadler et al. 2001).

Domesticating cultured fish to the point where they are unable to breed successfully in nature, or even to survive in nature, could be another effective means of reducing or eliminating genetic and ecological threats to wild populations in the future. Directed domestication has been prevalent in

farm salmon as breeding programs have selected for a variety of desired traits. Although farm salmon thus differ genetically from wild salmon, there is no aquaculture fish species to our knowledge that has yet been thoroughly domesticated, and there have been no successful efforts to breed a fish that is unable to reproduce or survive in the wild.

For disease and parasite control, regionalized production practices can be enforced to divide a region (e.g., a country or marine ecosystem) into epidemiological zones with restrictions on the transport of exotic organisms. This strategy has been used in Norway since the mid-1990s for categorizing different zones on the basis of the local status of ISA in

fish farms and hatcheries, and has been recommended more broadly by a government-appointed group investigating the causes of declining wild salmon populations (NOU 1999).

A more common method for controlling the potential consequences of disease transmission between farm and wild fish is through vaccination programs for farm fish. Veterinary certification of aquaculture stock is important in minimizing the spread of fish disease (Amos et al. 1998, Bartholomew and Reno 2002), but not fail-safe. Chemicals can also be used to control sea lice and other pathogens, but there are some risks of harm to surrounding marine organisms.

Dealing with uncertainty. Although aquaculture companies are pursuing some of these mitigation approaches in order to reduce private costs associated with disease and physical loss of fish, public policy has not provided sufficient incentives to improve practices extensively in many salmon-farming countries. The lack of strong policy measures reflects, in part, the inherent uncertainty associated with the magnitude and impact of escapes. Even when large numbers of fish escape in a region, there is typically a delay from the time of an escape to the time it is reported (if it is reported) and to the time of establishment (if establishment occurs). These time periods vary considerably among regions, species, ecological settings, and climatic conditions. In addition, while the effects of escapes on wild salmon are becoming clearer, the ecosystem-level impacts remain speculative in many cases. For some policy-makers, the absence of immediate measurable impacts from escapes may lead to the erroneous conclusion that there is no risk, especially if reducing the risks comes at a large cost to the industry. A recent legal review (Firestone and Barber 2003) concluded that the ecological, cultural, and legal implications arising from even low numbers of escaping Atlantic salmon are sufficient for escapees to be considered legally as pollutants. Unlike many effluents that can be cleaned up, the “biological pollution” resulting from farm fish escapes can be irreversible in its ecological impact.

Implications for the farming of additional marine species

The inadequacy of efforts to prevent or reduce impacts of farm salmon escapes is worrisome in the face of growing farm production of other marine finfish species. Escapes of all farm species raised in open net cages appear inevitable, and many new farm species share important characteristics with farm salmon. Wild populations of some of these fish are small in projected farming areas. Examples include Atlantic cod and Atlantic halibut for farming in the United States and Canada. The questions raised in box 1 should be reviewed as these species are farmed on larger scales. For instance, if the scale of their production becomes large and results in a concomitant number of escapes, will interbreeding of wild and escaped farm fish reduce the fitness of wild populations, making it harder for the wild populations to recover? One potential mitigating factor is that some new farm fish species are less genetically differentiated and lack the

local genetic adaptations common in wild anadromous salmon populations. This difference would lessen, although not eliminate, the genetic impact on wild populations. Most marine fish have distinct subpopulations. Atlantic cod, for example, have distinctive aggregations that are genetically differentiated and appear to have little gene flow among them (Ruzzante et al. 2001). Cod are also known to produce fertilized eggs in ocean enclosures. Although ocean cages used for offshore farming are more secure than salmon net pens, neither pens nor cages can contain fish eggs (Goldburg and Naylor 2005).

Rising production of new farm species is likely to occur to some extent in areas where the fish are not indigenous. Production of Atlantic salmon now dominates salmon farming in the Pacific as well as the Atlantic, largely because production techniques are well developed for the species and they grow well in captivity. Similarly, a handful of marine fish species may come to dominate world production. Atlantic cod and Atlantic halibut—two marine species now being farmed—could, for example, dominate future farmed cod and halibut production. They may be grown in the Pacific, even though Pacific cod (*Gadus macrocephalus*) and Pacific halibut (*Hippoglossus stenolepis*) are important commercial species and share ecological attributes with their Atlantic congeners, such as overlapping habitat and prey preferences.

Aquaculture and capture fisheries are linked through their common reliance on marine ecosystems and through the potential for escaped farmed fish to hinder the recovery of depleted wild fish populations. The experience with farm salmon clearly indicates that more attention needs to be paid to the certainty of marine fish escapes and their ecological and socioeconomic consequences as marine fish farming expands. Without a firm mandate for risk assessment in policy formulation, aquaculture activities will almost certainly lead to extensive competition between wild fish and continuously released farm fish—or widespread establishment of exotic fish species—and thus to a further decline in wild fish stocks.

Aquaculture policy is at a critical juncture, as more and more ocean resources become devoted to farming of marine fish. The expansion of marine aquaculture presents an opportunity to implement a new perspective on ocean policy recently called for by the US Commission on Ocean Policy: a perspective that focuses, not on development alone, but on precautionary, sustainable development (USCOP 2004). New policies concerning the escapes of farm fish are an excellent way to begin to act on the basis of this new perspective.

Acknowledgments

We thank Marshall Burke, Matthew Hollander, and Whitney Smith for research assistance, and Walter Falcon, Peter Vitousek, Ashley Dean, Ashley Simons, and three anonymous reviewers for helpful comments on the manuscript.

References cited

- Amos K, Thomas J, Hopper K. 1998. A case history of adaptive management strategies for viral hemorrhagic septicemia virus (VHSV) in Washington State. *Journal of Aquatic Animal Health* 10: 152–159.
- Bartholomew J, Reno P. 2002. The history and dissemination of whirling disease. *American Fisheries Society Symposium* 29: 3–24.
- Baxter C, Fausch K, Murakami M, Chapman P. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85: 2656–2663.
- Benfey TJ. 2001. Use of sterile triploid Atlantic salmon (*Salmo salar* L.) for aquaculture in New Brunswick, Canada. *ICES Journal of Marine Science* 58: 525–529.
- Blick D, Hagen P. 2002. The use of agreement measures and latent class models to assess the reliability of classifying thermally marked otoliths. *Fishery Bulletin* 100: 1–10.
- Chevassus B. 1979. Hybridization in salmonids: Results and perspectives. *Aquaculture* 17: 113–128.
- Crowl T, Townsend C. 1992. The impact of introduced brown and rainbow trout on native fish: The case of Australasia. *Reviews in Fish Biology and Fisheries* 2: 217–241.
- [FAO] Food and Agriculture Organization of the United Nations. 1995. *Precautionary Approach to Capture Fisheries and Species Introductions*. Rome: FAO. FAO Technical Guidelines for Responsible Fisheries, no. 2.
- . 1998. *FAO Yearbook: Fishery Statistics*, vol. 86, no. 2. Rome: FAO.
- . 2003. *FishStat—Fishery Information, Data and Statistics Unit*. Rome: FAO.
- Firestone J, Barber R. 2003. Fish as pollutants: Limitations of and crosscurrents in law, science, management, and policy. *Washington Law Review* 78: 693–756.
- Fiske P, Lund RA, Ostborg GM, Floystad L. 2001. Escapes of reared salmon in coastal and marine fisheries in the period 1989–2000. *NINA Oppdragsmelding* 704: 1–26.
- Fleming IA, Einum S. 1997. Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. *ICES Journal of Marine Science* 54: 1051–1063.
- Fleming IA, Hindar K, Mjølnerod I, Jonsson B, Balstad T, Lamberg A. 2000. Lifetime success and interactions of farm salmon invading a natural population. *Proceedings: Biological Sciences* 267: 1517–1523.
- Fleming IA, Agustsson T, Finstad B, Johnsson JI, Björnsson BT. 2002. Effects of domestication on growth physiology and endocrinology of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 33: 893–905.
- Fletcher GL, Goddard S, Hew C. 2000. Current status of transgenic Atlantic salmon for aquaculture. Pages 179–184 in Fairbairn C, Scoles G, McHughen A, eds. *Proceedings of the 6th International Symposium on the Biosafety of Genetically Modified Organisms*. Saskatoon (Canada): University Extension Press.
- Garant D, Fleming I, Einum S, Bernatchez L. 2003. Alternative male life-history tactics as potential vehicles for speeding introgression of farm salmon traits into wild populations. *Ecology Letters* 6: 541–549.
- García-Vázquez E, Moran P, Perez J, Martínez J, Izquierdo J, de Gaudemar B, Beall E. 2002. Interspecific barriers between salmonids when hybridisation is due to sneak mating. *Heredity* 89: 288–292.
- Gibson RJ. 1981. Behavioral Interactions between Coho Salmon (*Oncorhynchus kisutch*), Atlantic Salmon (*Salmo salar*), Brook Trout (*Salvelinus fontinalis*) and Steelhead Trout (*Salmo gairdneri*) at the Juvenile Fluvial Stages. Ottawa (Canada): Government of Canada, Minister of Fisheries and Oceans. *Canadian Technical Report of Fisheries and Aquatic Sciences* no. 1029.
- Goldburg R, Naylor R. 2005. Future seascapes, fishing, and fish farming. *Frontiers in Ecology and the Environment* 3: 21–29.
- Hansen LP, Lund RA. 1992. Results of experimental fishing for Atlantic salmon in the outer Nordfjord in January 1992. *NINA Oppdragsmelding* 1001: 1–10.
- Hansen LP, Windsor ML, Youngson AF. 1997. Interactions between salmon culture and wild stocks of Atlantic salmon: The scientific and management issues. *ICES Journal of Marine Science* 54: 963–1225.
- Hansen LP, Jacobsen JA, Lund RA. 1999. The incidence of escaped farmed Atlantic salmon, *Salmo salar* L., in the Faroese fishery and estimates of catches of wild salmon. *ICES Journal of Marine Science* 56: 200–206.
- Hindar K, Balstad T. 1994. Salmonid culture and interspecific hybridization. *Conservation Biology* 8: 881–882.
- Hindar K, Ryman N, Utter F. 1991. Genetic effects of cultured fish on natural fish populations. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 945–957.
- Hites R, Foran J, Carpenter D, Hamilton M, Knuth B, Schwanger S. 2004. Global assessment of organic contaminants in farmed salmon. *Science* 303: 226–229.
- [ICES] International Council for the Exploration of the Sea. 2001. *Report of the Working Group on North Atlantic Salmon*. Copenhagen (Denmark): ICES.
- . 2002. *Report of the Working Group on North Atlantic Salmon*. Copenhagen (Denmark): ICES.
- . 2003. *Report of the Working Group on North Atlantic Salmon*. Copenhagen (Denmark): ICES.
- Jacobsen JA, Hansen LP. 2001. Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. *ICES Journal of Marine Science* 58: 916–933.
- Johnsen BO, Jensen AJ. 1994. The spread of furunculosis in salmonids in Norwegian rivers. *Journal of Fish Biology* 45: 47–55.
- Jones SR, MacKinnon AH, Gorman DB. 1999. Virulence and pathogenicity of infectious salmon anemia virus isolated from farmed salmon in Atlantic Canada. *Journal of Aquatic Animal Health* 11: 400–405.
- King TL, Kalinowski ST, Schill WB, Spidle AP, Lubinski BA. 2001. Population structure of Atlantic salmon (*Salmo salar* L.): A range-wide perspective from microsatellite DNA variation. *Molecular Ecology* 10: 807–821.
- Kinnison M, Hendry A. 2004. From macro- to micro-evolution: Tempo and mode in salmonid evolution. Pages 208–231 in Hendry A, Stearns S, eds. *Evolution Illuminated: Salmon and Their Relatives*. Oxford (United Kingdom): Oxford University Press.
- Krkosek M, Lewis M, Volpe J. 2005. Transmission dynamics of parasitic sea lice from farm to wild salmon. *Proceedings: Biological Sciences* 272. Forthcoming.
- Kurath G, Garver KA, Troyer RM, Emmenegger EJ, Einer-Jensen K, Anderson AD. 2003. Phylogeography of infectious hematopoietic necrosis virus in North America. *Journal of General Virology* 84: 803–814.
- Levin PS, Zabel RW, Williams JG. 2001. The road to extinction is paved with good intentions: Negative association of fish hatcheries with threatened salmon. *Proceedings: Biological Sciences* 268: 1153–1158.
- Lindbergh J. 1999. Salmon farming in Chile: Do the benefits exceed the costs? *Aquaculture Magazine* 25: 32–37.
- Loomis J. 1996. Measuring the economic benefits of removing dams and restoring the Elwha River: Results of a contingent valuation survey. *Water Resources Research* 32: 441–447.
- McGinnity P, Stone C, Taggart J, Cooke D, Cotter D, Hynes R, McCamley C, Cross T, Ferguson A. 1997. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: Use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES Journal of Marine Science* 54: 998–1008.
- McGinnity P, et al. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings: Biological Sciences* 270: 2443–2450.
- McKibben M, Hay D. 2004. Distributions of planktonic sea lice larvae *Lepeophtheirus salmonis* in the inter-tidal zone in Loch Torridon, Western Scotland in relation to salmon farm production cycles. *Aquaculture Research* 35: 742–750.
- Morton A, Volpe J. 2003. A description of Atlantic salmon *Salmo salar* captured in the Pacific salmon fishery in British Columbia, Canada, in 2000. *Alaska Fishery Research Bulletin* 9: 102–110.

- Naylor R. 2000. The economics of alien species invasions. Pages 241–259 in Mooney H, Hobbs R, eds. *Invasive Species in a Changing World*. Washington (DC): Island Press.
- Naylor R, Burke M. 2005. Aquaculture and ocean resources: Raising tigers of the sea. *Annual Review of Environmental Research* 30. Forthcoming.
- Naylor R, Eagle J, Smith W. 2003. Salmon aquaculture in the Pacific Northwest: A global industry with local impacts. *Environment* 45: 18–39.
- Norris A, Bradley D, Cunningham E. 1999. Microsatellite genetic variation between and within farmed and wild Atlantic salmon (*Salmo salar*) populations. *Aquaculture* 180: 247–264.
- [NOU] Norges Offentlige Utredninger. 1999. Til laks åt alle kan ingen giera? Norges Offentlige Utredninger 1999: 9. Oslo (Norway): Statens Forvaltningstjeneste.
- [NRC/NAS] National Research Council/National Academy of Sciences. 2002. Genetic Status of Atlantic Salmon in Maine. Washington (DC): Committee on Atlantic Salmon in Maine, National Research Council/National Academy of Sciences.
- Nylund A, Krossoy B, Devold M, Aspehaug V, Steine NO, Hovlund T. 1999. Outbreak of ISA during first feeding of salmon fry (*Salmo salar*). *Bulletin of the European Association of Fish Pathologists* 19: 70–74.
- Pascual M, Macchi P, Urbanski J, Marcos F, Rossi C, Novara M, Dell'Arciprete D. 2002. Evaluating potential effects of exotic freshwater fish in incomplete species presence-absence data. *Biological Invasions* 4: 101–113.
- Ruzzante DE, Taggart CT, Doyle RW, Cook C. 2001. Stability in the historical pattern of genetic structure of Newfoundland cod (*Gadus morhua*) despite the catastrophic decline in population size from 1964–1994. *Conservation Genetics* 2: 257–269.
- Sadler P, Parkhurst P, King H. 2001. High prevalence of skeletal deformity and reduced gill surface area in triploid Atlantic salmon (*Salmo salar* L.). *Aquaculture* 198: 369–386.
- Schiermeier Q. 2003. Fish farms' threat to salmon stocks exposed. *Nature* 425: 753.
- Soto D, Jara F, Moreno C. 2001. Escaped salmon in the inner seas, southern Chile: Facing ecological and social conflicts. *Ecological Applications* 11: 1750–1762.
- Stahl G. 1987. Genetic population structure of Atlantic salmon. Pages 121–140 in Ryman N, Utter F, eds. *Population Genetics and Fishery Management*. Seattle: University of Washington Press.
- Taylor EB. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98: 185–207.
- Tiedje JM, Colwell RK, Grossman YL, Hodson RE, Lenski RE, Mack RN, Regal PJ. 1989. The planned introduction of genetically engineered organisms: Ecological considerations and recommendations. *Ecology* 70: 298–315.
- Tufto J, Hindar K. 2003. Effective size in management and conservation of subdivided populations. *Journal of Theoretical Biology* 222: 273–281.
- [USCOP] US Commission on Ocean Policy. 2004. *An Ocean Blueprint for the 21st Century*. Washington (DC): USCOP.
- Volpe J, Taylor E, Rimmer D, Glickman B. 2000. Evidence of natural reproduction of aquaculture-escaped Atlantic salmon in a coastal British Columbia River. *Conservation Biology* 14: 899–903.
- Volpe J, Glickman B, Anholt B. 2001. Reproduction of Atlantic salmon in a controlled stream channel on Vancouver Island, British Columbia. *Transactions of the American Fisheries Society* 130: 489–494.
- Waknitz FW, Iwamoto RN, Strom MS. 2003. Interactions of Atlantic salmon in the Pacific Northwest IV: Impacts on local ecosystems. *Fisheries Research* 62: 307–328.
- Waples E. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. *American Fisheries Society Symposium* 17: 8–27.
- Youngson AF, Webb JH, Thompson CD, Knox D. 1993. Spawning of escaped farmed Atlantic salmon (*Salmo salar*): Hybridisation of females with brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* 50: 1986–1990.



TC5000

New from Meiji Techno

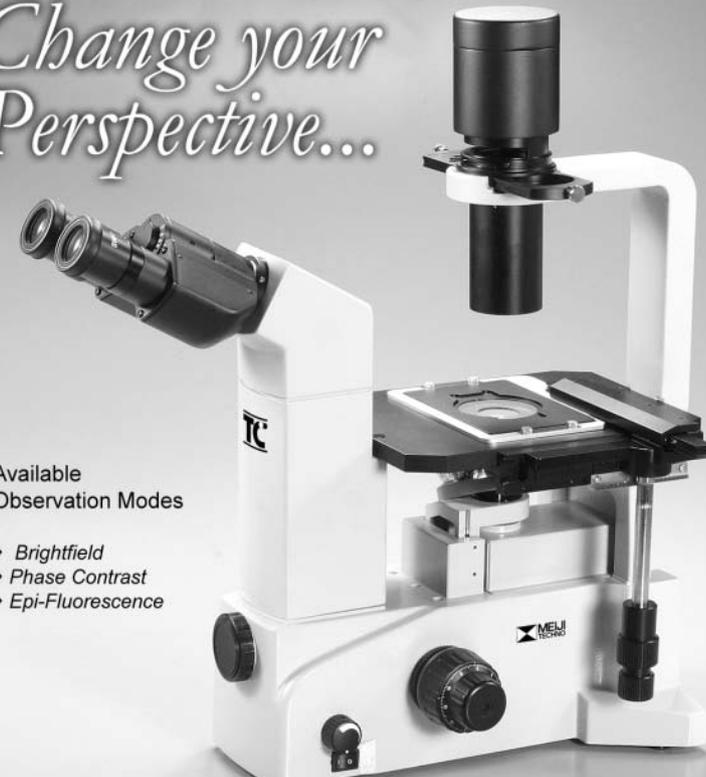
Designed with Meiji's ICOS Infinity Corrected Optical System - the new TC Series of Inverted Microscopes by Meiji Techno incorporates world class optics in a cost effective platform offering a higher standard in specimen observation.

With a host of new features and options, the TC Series makes cell checking faster, clearer and easier than ever before.

Ask your Meiji dealer for a demonstration today!

www.meijitechno.com

Change your Perspective...



Available Observation Modes

- Brightfield
- Phase Contrast
- Epi-Fluorescence






Meiji Techno America 2186 Bering Drive San Jose, California 95131
408-428-9654 - 408-428-0472 FAX - 1-800-832-0060 toll free