# One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture

**Mart R. Gross**

**Abstract**: Today, over 94% of all adult Atlantic salmon (*Salmo salar*) are in the aquaculture niche and wild numbers continue to decline while aquaculture numbers increase. The developmental and evolutionary forces in the aquaculture or "domestic" niche are so unlike those in the wild niche that two distinct biologies are being created from the original Atlantic salmon species. We may now need to recognize a new biological entity — *Salmo domesticus* — and treat it as an "exotic" when it escapes into the wild. Escapement therefore raises important concerns about ecological and genetic impacts, both within and outside the native range of *Salmo salar*. This paper explains why escaped domestic Atlantic salmon have had an impact on wild Atlantic salmon populations and now threaten Pacific salmonids as well. A polarization of views between aquaculturists and environmentalists will not resolve the problems. The three interest groups in fisheries — aquaculture, biodiversity, and capture — must begin to work together if we are to take up the challenge of preserving biodiversity and if aquaculturists, who hold the future of Atlantic salmon in their hands, can be expected to willingly prevent further impacts from their industry.

**Résumé** : Aujourd'hui, 94 % des saumons de l'Atlantique (*Salmo salar*) adultes sont issus de l'aquaculture, et les effectifs de saumons sauvages continuent de décroître tandis que les effectifs provenant de l'aquaculture augmentent. Les forces agissant sur le développement et l'évolution des saumons d'aquaculture, ou des saumons « domestiques », sont si différentes de celles agissant sur les saumons sauvages que deux biologies distinctes se sont formées à partir du saumon atlantique d'origine. Nous pouvons aujourd'hui considérer une nouvelle entité biologique — *Salmo domesticus* — et la traiter comme une entité exotique quand elle s'échappe dans le milieu naturel. Le fait que des saumons d'aquaculture s'échappent dans le milieu naturel soulève des inquiétudes importantes au chapitre des impacts écologiques et génétiques tant à l'intérieur qu'à l'extérieur de l'aire de répartition naturelle de *Salmo salar*. Le présent article explique pourquoi les saumons atlantiques domestiques évadés ont eu un impact sur les populations sauvages de l'espèce et menacent maintenant aussi les salmonidés du Pacifique. Les problèmes ne trouveront pas de solution dans une polarisation des positions des aquaculteurs et des environnementalistes. Les trois groupes d'intérêts du secteur des pêches — les aquaculteurs, les personnes qui se préoccupent de la biodiversité, et les pêcheurs — doivent commencer à collaborer si nous voulons réussir à préserver la biodiversité et si nous voulons faire en sorte que les aquaculteurs, qui ont l'avenir du saumon atlantique en leur pouvoir, en arrivent à freiner volontairement les impacts de leur industrie.

[Traduit par la Rédaction]

## Introduction

Although the wild Atlantic salmon (*Salmo salar*) entered commercial aquaculture only 25 years ago (e.g., Boghen 1995; Saunders 1995; Anderson 1997), its biomass in aquaculture already exceeds that in its native range. This shift in abundance and distribution raises important questions about the evolutionary fate of Atlantic salmon and about the potential for ecological and genetic impacts on wild populations both within and outside the native range. The purpose of this paper is to discuss the implications of aquaculture for the future of the Atlantic salmon and other species in the wild.

My laboratory initiated studies of wild and cultured salmon in the early 1980s when government "enhancement" led to a massive hatchery program for Pacific salmon in western North America (e.g., van den Berghe and Gross 1984, 1986, 1989; Gross 1985, 1991; Fleming and Gross 1989, 1990, 1992, 1993, 1994). By the late 1980s we brought this knowledge to a Norwegian program comparing wild and cultured Atlantic salmon (e.g., Fleming et al. 1994, 1996). With Atlantic salmon now cultured in Pacific waters, we are back studying the possible impacts of escaped Atlantic salmon. Regrettably, research on wild–cultured interactions operates in a politically charged and antagonistic environment where there are those who favor aquaculture and those who favor the wild fish. Moreover, their lack of biological knowledge and the political implications of conflict have largely paralyzed government agencies with a mandate to foster both. As a consequence, the needs of specific research programs on the interactions between wild and cultured fish are often overlooked.

This paper underscores the necessity for cooperation among all interest groups in interpreting and understanding the research outcomes from such programs and in assessing how we might best manage these outcomes to foster aquaculture, natural biodiversity, and capture fisheries. The paper has four sections. By beginning with a review of the

Received February 11, 1998. Accepted November 10, 1998. J14428

**M.R. Gross.** Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada.
e-mail: mgross@zoo.utoronto.ca

abundance and distribution of wild and cultured salmon and the ecological and life history differences of their niches, we realize that cultured fish have become a distinct evolutionary lineage. Therefore, it may now be time to recognize the evolution of "*Salmo domesticus*." The second section raises and reviews the potential impacts of domestic salmon that escape into the habitats of wild Atlantic and wild Pacific salmon. For both cases it is argued that the escaped fish are an "exotic" and therefore the concerns associated with exotic introductions are important (e.g., International Union Conservation of Nature (IUCN) 1997). Section three highlights the importance of "ecorealism" in dealing with the impacts of aquaculture on salmonid biodiversity. Salmonid aquaculture brings both benefits and costs to wild fish populations and it is necessary to maintain a balanced perspective. Finally, section four provides recommendations for future directions which include the collaborative effort of all three sectors in fisheries — aquaculture, biodiversity, and capture fisheries — to solve the challenges of the novel evolutionary and ecological experiment that the recent massive culture of salmon presents.

## The evolution of "*Salmo domesticus*"

The wild and aquaculture niches differ greatly in their capacity, distribution, ecology, and life history and an appreciation of these differences is necessary to understand the future directions of the Atlantic salmon as a species.

### Niche capacity and distribution

*Wild*

The native wild niche includes the rivers and northern Atlantic Ocean bound by North America, Scandinavia, and Europe between 40° and 70°N (MacCrimmon and Gots 1979). Prior to human predation and habitat alteration, this niche may have supported 10–24 million adult individuals (50 000–100 000 mt). In the past 50 years, it is unlikely for populations to have exceeded 5–8 million adults (25 000–35 000 mt) (calculations by R. Behnke in Parrish et al. (1998)).

*Aquaculture*

By contrast, the aquaculture niche is worldwide and extends the native distribution into the Pacific Ocean and Southern Hemisphere (Heen et al. 1993). For example, net pens in the Pacific waters of British Columbia, Canada, were producing almost 4 million adult individuals in 1995 alone (17 000 mt; calculated from 1995 statistics of the BC Provincial Ministry of Agriculture, Fisheries and Food). In the Southern Hemisphere (40° and 60°S), 1995 production in Tasmania reached 1.4 million (6000 mt) and in Chile about 12 million individuals (54 000 mt).[1] Worldwide figures for 1995 estimate some 104 million adult Atlantic salmon living in commercial aquaculture (471 820 mt), with roughly 25% outside the native range. By year 2000, with predicted increases of 40–65% above year 1995 (Anderson 1997), there may be 146–172 million adults in aquaculture.

*Relative capacity and distribution*

Clearly the aquaculture niche dwarfs the wild niche in both current and historic capacity. In 1995, well over 94% of all Atlantic salmon adults were in aquaculture. Even at maximum carrying capacity, the wild niche will support only 10% of the adults projected for the aquaculture niche by year 2000. The spatial and numeric distributions in aquaculture are also unique. More than two farmed Atlantic salmon live in the Southern Hemisphere for every wild individual in the native Northern Hemisphere; about three farmed salmon are in the Pacific drainage for every one wild individual in the Atlantic drainage. Within the native range, Norway has roughly 100 000 wild spawners (Jonsson and Fleming 1993) or 1.5% of the world's wild Atlantic salmon, but 59 million or 57% of all the world's adult Atlantic salmon (wild and 1995 cultured).

### Ecology and life history

Ecological and life history differences found within the wild and aquaculture niches are summarized in Fig. 1. These differences give rise to the developmental and evolutionary forces, Fig. 2, which pry apart the biology of the species. Some of the resulting differences are summarized in Table 1.

### Evolution of *Salmo domesticus*

Genetically based evolutionary changes move the fish towards "domestication," thereby adapting the Atlantic salmon to the aquaculture niche while simultaneously maladapting it to the wild niche. The complexity and power of selection within the aquaculture niche is seen, for example, in the rapid response across generations of tameness toward human handlers, while evolving increased aggression to each other. After a few generations in the high-density niche of aquaculture, farmed juveniles aggressively out-compete wild juveniles in competition experiments and hybrids show intermediate aggression levels (Einum and Fleming 1996). Fleming et al. (1994, 1996) show other remarkable morphological and behavioral differences between first and fifth generation Norwegian farmed salmon.

Salmon breeders commonly use artificial selection to improve performance traits (Gjerde 1993). The economic benefits of selective breeding include reduced production costs, more rapid turnover time, better quality product, and thus greater market acceptance. The Norwegian program, which has successfully increased growth rate, decreased early maturity, and increased disease resistance, now provides egg stock to many countries of the world. Future production of Atlantic salmon may include more substantial genetic changes, such as the current availability of triploid and transgenic Atlantic salmon (Donaldson 1997).

The inevitable outcome of the natural and artificial selection forces within the aquaculture niche is the increasing divergence within the Atlantic salmon species into distinct biologies reflecting the distinct niches of wild and aquaculture (Fig. 2). Both intentionally and unintentionally, a new life form of Atlantic salmon is emerging from the aquaculture niche. Farmed salmon may eventually become

[1] FAO (1997*a*, 1997*b*) aquaculture statistics are in metric tons (mt) for the 14 countries producing Atlantic salmon in 1995, the most recent statistics available. Throughout this paper, tonnage is converted to the number of individuals by assuming a mean fish body weight of 4.5 kg. This provides a rough estimate that is useful for comparison purposes.

**Fig. 1.** The behavioral ecology and life history of Atlantic salmon in its two niches: wild and aquaculture.

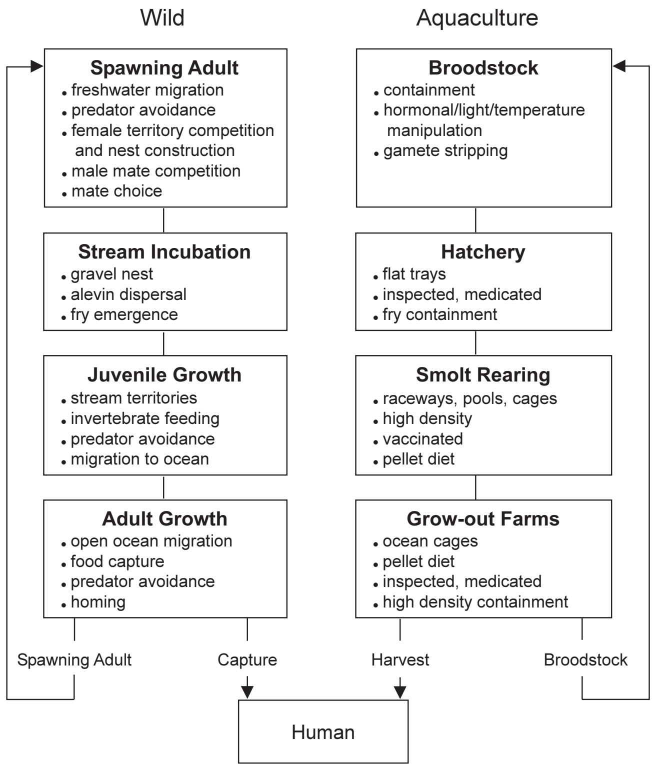
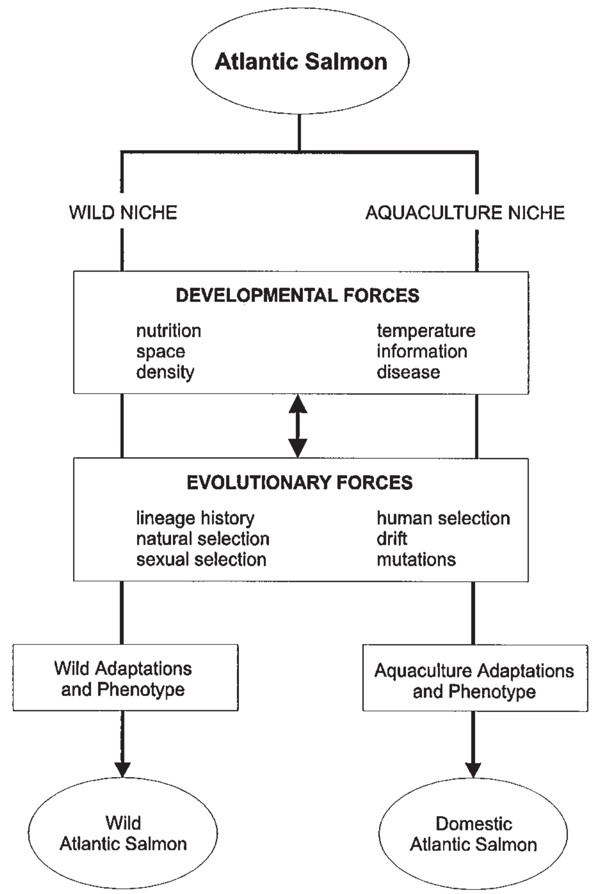



**Fig. 2.** Developmental and evolutionary forces affecting the Atlantic salmon gene pool in the wild and aquaculture eventually result in a wild and a domestic organism, with distinct evolutionary lineages.




obligate parasites, entirely dependent upon humans for survival; already humans shoot their predators, apply medicines to fight their diseases and parasites, provide special foods, and flush the niche with clean water to remove wastes, etc. The process and result are similar to the historic domestication of chickens, cows, pigs, sheep, and other animals and plants that has occurred over the past thousands of years but through technology it has become more rapid. While this paper considers two extremes in Atlantic salmon biology, wild and farmed, there are of course gradations between these two that must also be recognized (Fig. 3). In time the fisheries community may want to give new labels to these new life forms. To begin, we should recognize the existence of farmed Atlantic salmon as *Salmo domesticus*. Such a distinction will help us realize that in spite of the large biomass of *Salmo* in aquaculture, the wild species *Salmo salar* is endangered. Moreover, the domestic Atlantic salmon is an "exotic" when it leaves its aquaculture niche and enters either the native range of wild *Salmo salar* or into new areas of the globe.

## Biological implications of domestic salmon in the wild

The creation of a domestic fish species or population as well as its distribution into novel places of the world raises important concerns about potential impacts on native wild fish through a "collision of biologies" (Fig. 4). The potential for a genetic and ecological collision is related to the magnitude of escapement and the degree of direct and indirect interaction in the field. We first consider these concerns from a theoretical perspective, evaluate the magnitude of escapement, and address what is known and likely in the Atlantic and Pacific oceans.

### Theoretical concerns

The specific impacts of exotic introductions are usually difficult to predict (e.g., Moyle and Light 1996; Shigesada and Kawasaki 1997). At a global level, exotic introductions have shown many significant negative impacts and invading aliens are considered second only to habitat loss as the major threat to native biodiversity and the integrity of natural communities (IUCN 1997). The "tens rule" suggests that about 10% of introduced exotics will establish themselves (Williamson 1996). Among established exotic fish in the United States, about 50% are known to have had harmful effects, usually through ecological impacts (US Congress Office of Technology Assessment 1993). This suggests a roughly 5% probability of negative impact from escaped and invading domestic Atlantic salmon (0.10 establishment × 0.50 harm). While a 5% probability may appear low, we should not underestimate the powerful harm that can occur. Some of the greatest ecological disasters in North America have resulted from invading exotic fish including salmonids (e.g., Mills et al. 1993, 1994). Of the 86 endangered fish

**Table 1.** Some genetic and developmental differences between cultured (farmed) and wild Atlantic salmon.

| Genetic | | Developmental | |
|---|---|---|---|
| Confirmed[a] | Suspected[b] | Confirmed[a] | Suspected[b] |
| Increased growth rate | No ejaculation | Lower stamina | Gut length |
| Increased age of maturity | Reduced male courtship | Smaller eggs | Diet preference |
| Increased weight | Higher hatchery survival | More eggs | Stream knowledge |
| Increased disease resistance | Higher temperature tolerance | More fat | Body odor |
| Decreased stress response | Shallower depth preference | Smaller rayed fins (parr and adult) | |
| Lower genetic diversity | Larger testes | Smaller heads on parr | |
| Allele frequency change | Juvenile color | Narrower caudal peduncle on parr | |
| Malic enzyme allele change | Adult color | Bulkier body on adult | |
| Reduced predator response | | Distorted jaw on adult | |
| Increased juvenile aggression | | Longer head on adult | |
| Increased tameness | | Longer adipose fin on adult | |
| Lower survival in wild | | Smaller hearts in females | |
| | | Decreased juvenile color | |
| | | Decreased adult color | |

[a]Aksnes et al. 1986; Cross and King 1983; Einum and Fleming 1996; Ferguson et al. 1997; Fevolden et al. 1991, 1993; Fleming et al. 1994; Friars et al. 1990; Gjedrem 1979; Gjedrem et al. 1988, 1991; Gjerde 1984; Jonsson et al. 1996; Ruzzante 1994; Ståhl 1987; Verspoor 1988; Youngson et al. 1991.
[b]Author's observations.

**Fig. 3.** A "taxonomic picture" of the Atlantic salmon "species."

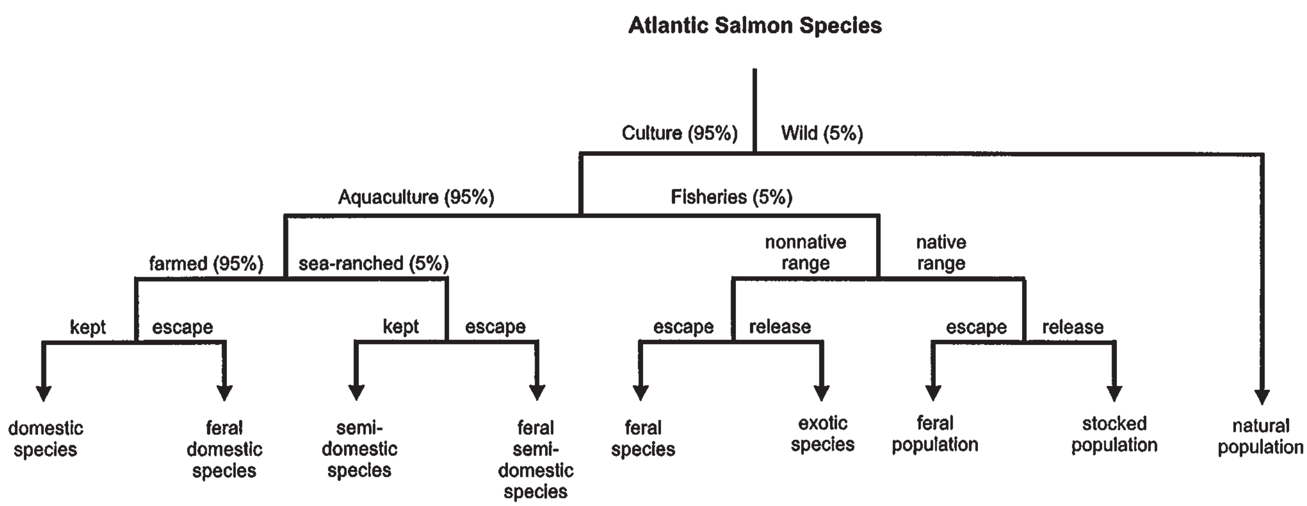



**Fig. 4.** The genetic and ecological concerns associated with domestic Atlantic salmon escaping from aquaculture and entering the wild.

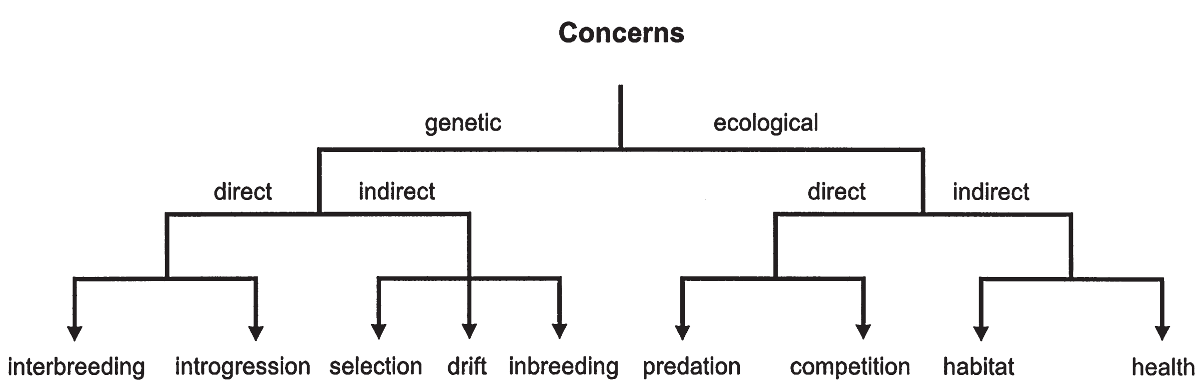


**Table 2.** Marine captures of escaped farmed Atlantic salmon in the northeastern Pacific Ocean from 1987 through 1997 (from annual reports of Thomson and McKinnell (1993–1997); and personal communication for 1997 from A. Thomson, Atlantic Salmon Watch B.C.).

| | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | Mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Alaska | – | 0 | 0 | 1 | 7 | 2 | 27 | 27 | 23 | 135 | 79 | 30 |
| B.C. | 1 | 106 | 8 | 2 | 31 | 349 | 4543 | 1037 | 648 | 671 | 2623 | 1002 |
| Wash. | – | 6 | 52 | 446 | 970 | 157 | 179 | 338 | 125 | 112 | 2172 | 456 |
| Total | 1 | 112 | 60 | 449 | 1008 | 508 | 4749 | 1402 | 796 | 918 | 4874 | 1488 |

species in the United States, 51% are impacted negatively by exotics, 9% have exotics as their major cause for endangerment, and 6% are endangered due to exotics (Lassuy 1995).

While many authors have called attention to concerns of escaped farmed fish within their native ranges (e.g., Hanson et al. 1991; Hindar et al. 1991; Krueger and May 1991; Saunders 1991; Heggberget et al. 1993; Utter et al. 1993; Allendorf and Waples 1996; Fleming et al. 1996), the potential impacts and concerns also apply outside the native wild range. Escaped farm fish can directly reduce the genetic adaptiveness of wild fish by interbreeding and thus perturbing gene complexes or by introgressing and thus replacing the wild gene pool by a cultured gene pool (Fig. 4). Escaped farmed fish can also indirectly impact the genetics of wild fish by generating new forms of selection or by reducing wild population size so that genetic drift or inbreeding decreases genetic adaptiveness. Ecologically, escaped farmed fish can reduce the adaptiveness of wild fish directly by competing for resources such as food or space, or by preying on wild fish at their early life stages, or indirectly through habitat modification such as disturbing spawning redds, or introducing new or higher intensities of disease.

## Escapement of domestic salmon

The movement of domestic individuals into the wild is not uncommon. Recent estimates from the salmon farming industry in British Columbia suggest that up to 2% may enter the wild each year (Alverson and Ruggerone 1997). Losses can occur in large pulses or through small leakages. For example, in 1988 a single winter storm along the middle coastal region of Norway released about 700 000 individuals into the Atlantic Ocean (Gausen and Moen 1991). In the Pacific, 101 000 Atlantic salmon were released into Puget Sound, Washington State, on 2 July 1996 and over 360 000 on 18 July 1997 from mishaps at single farms (Thomson and McKinnell 1997; personal communication from A. Thomson, Atlantic Salmon Watch B.C.). Escapement into the wild is known to occur at all life stages from yolk-sac fry up to and including adults (e.g., Lough et al. 1997).

### *Native range*

Within the native range of wild Atlantic salmon, significant numbers of free-living farmed fish are now found. Examples include: (1) the salmon feeding grounds in the Northeast Atlantic Ocean where 25–48% of individuals are escapees from fish farms (Hansen et al. 1993); (2) Norwegian wild rivers, where 20–30% of all breeding adults are escapees from farms; this rises to over 80% in some rivers (Skaala and Hindar 1997); and (3) the Magaguadavic River in New Brunswick, Canada, where 51–68% of the smolts migrating to the ocean are losses from three hatcheries that produce Atlantic salmon smolts for aquaculture (Stokesbury and Lacroix 1997).

### *Pacific drainage*

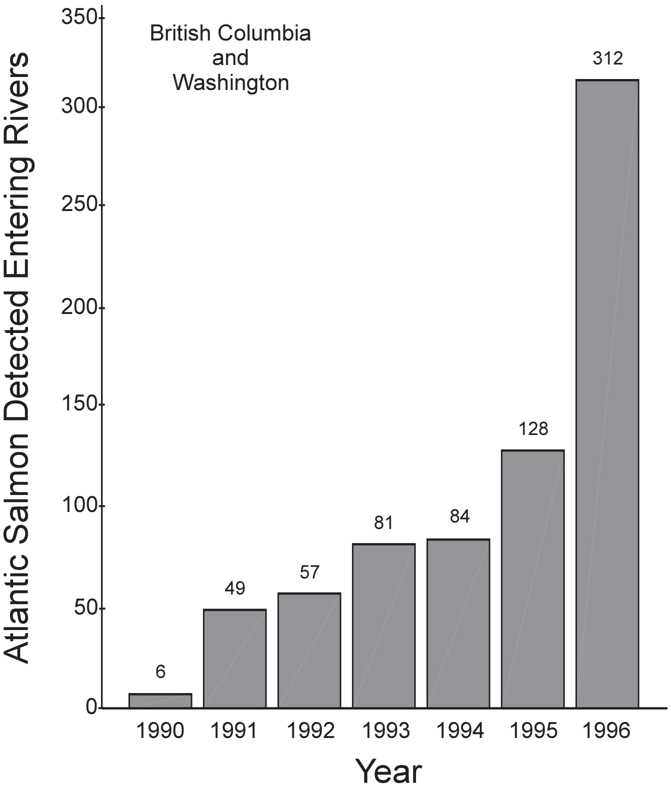
In the North American Pacific drainage, where the Atlantic salmon is farmed in only small areas of Washington State and British Columbia, the marine commercial and recreational fishery report incidental captures averaging 1488 per year over the past 10 years with a trend toward increasing numbers (Table 2; McKinnell et al. 1997). The State of Alaska prohibits Atlantic salmon farming; however, incidental captures of Atlantics are made along the coast of Alaska and the Aleutian Islands; they probably originate from farms in lower British Columbia and upper Washington State. Recently, an Atlantic salmon with a full stomach of pteropods was captured in a bottom trawl in the Bering Sea (U.S. National Marine Fisheries Service; personal communication from A. Thomson, Atlantic Salmon Watch B.C., 18 November 1997).

Escaped Atlantic salmon are also found in the freshwaters of the Pacific region. In British Columbia, two lakes are used to raise Atlantic salmon juveniles in net pens; escaped juveniles were found in both lakes and in one a variety of stages including fry, parr, pre-smolts, and smolts (Lough et al. 1997). Elsewhere, an estimated 20 000 pre-smolts were accidentally spilled into a stream from a hatchery transport truck and at a later time 860 live parr were electrofished from the stream. Some were discovered in the stomachs of cutthroat trout in a lower lake and about 55 were found the next spring in the lake and at its outlet. The number of adult Atlantic salmon that are leaving the Pacific ocean and entering freshwater rivers in Washington and British Columbia is rapidly increasing (Fig. 5) and over 50 rivers have been documented as having adult Atlantic salmon.

### *Amount*

While some movement of Atlantic salmon from the aquaculture niche into the wild will be inevitable, the amount will vary with facilities (e.g., net pen vs. land-based containment), location (e.g., ocean exposure vs. sheltered bays), and societal regulations (e.g., laws, insurance premiums). The total loss will also depend on the total number of fish in the aquaculture niche. There is, for instance, a positive 7-year correlation between the number of smolts placed into Norwegian net pens and the number of escapees that are later captured in ocean fisheries and Norwegian rivers (Lund et al. 1997).

**Fig. 5.** The number of farmed fish documented in rivers of British Columbia and Washington State from 1990 through 1996 (Atlantic Salmon Watch Program B.C., courtesy of A. Thomson).




Assuming 146–172 million adult Atlantic salmon in the aquaculture niche by year 2000 and a 1–2% escapement, an estimated 1.5–3.4 million adults may enter the wild each year. The number of escapees therefore probably exceeds 50% of all wild adult Atlantic salmon in the world. Roughly 75% of these escapees will be in the native wild niche of the Atlantic drainage and the remainder in non-native waters of the Pacific drainage.

## The Atlantic ocean experience

There is mounting evidence that many of the concerns about a collision of biologies are materializing in the native range of Atlantic salmon in the Atlantic drainage. First, Atlantic salmon that have escaped from farms are known to be spawning throughout the native range including rivers in Norway, Scotland, Ireland, Iceland, and Eastern Canada (Table 3). Although their spawning success is less than that of wild individuals, their sheer numbers can result in a relatively high total contribution to the gene pool within rivers. For example, Crozier (1993) demonstrated a shift in the gene pool of a wild Atlantic salmon population in Ireland after escapement from a farm raising a Scottish aquaculture strain. In the River Vosso, one of Norway's historically famous wild salmon rivers, escaped farm fish now contribute about 44% of the total genes (Skaala and Hindar 1997). In an experimental study involving genetic marking of farmed and wild fish, farmed fish contributed 21% of the total genes in the River Imsa, Norway. Most of the genetic contribution was through hybridization, probably between wild males and farmed females (Fleming et al. 1997). In the Magaguadavic River, New Brunswick, Canada, an estimated 55% of the redds are from farmed fish (Carr and Anderson 1997). These significant influxes of aquaculture genes into wild populations will shift the wild populations from local optima thus disrupting life history adaptations and maladapting the populations. As the genetic differences across wild populations are homogenized, the capacity for evolution of the wild fish is reduced. While empirical observations from a number of salmonid species suggest that gene flow levels of this magnitude will result in poorer performance (Hindar et al. 1991), no direct study has yet been done on domestic and wild Atlantic salmon.

Second, ecological impacts occur through food and space competition, reproductive habitat perturbation, and disease transfer. For example, Ferguson et al. (1997) placed three lines of fish — farmed, wild, and hybrid — into an Irish river to study their behavior and growth. The farmed fish behaviorally displaced the wild fish into downriver sections where feeding rates are probably lower; the farmed fish grew fastest, the hybrids intermediate, and the wild fish slowest. In Norway, Fleming et al. (1997) found that the offspring of farmed fish that bred in the River Imsa grew faster than the offspring of wild fish, with hybrids having intermediate growth. A common reproductive habitat perturbation occurs during the spawning season when escaped farmed fish, lacking information about the wild rivers, typically arrive later at the spawning grounds. This late arrival results in farmed fish digging up the gravel that already contains the nests of wild females and replacing the wild eggs with their own (e.g., Webb et al. 1991).

The impact of disease and parasite transfer has been one of the strongest to date. For example, *Gyrodactylis salaris* was carried by farmed Swedish smolts out of the Baltic Sea drainage and into the eastern Atlantic drainage, where it is known to have extirpated over 35 wild populations in Norway (Johnsen and Jensen 1991). Atlantic salmon in the eastern Atlantic drainage are more susceptible to this disease than those in the Baltic Sea drainage, thus the Baltic aquaculture fish act as carriers of the disease, not becoming ill themselves but infecting less resistant populations. The transfer may have occurred during enhancement practices. *Aeromonas salmonicida* or furunculosis was carried by Scottish smolts to Norwegian aquaculture and probably spread through escapees to infect hundreds of wild populations (Johnsen and Jensen 1994). Finally, it is thought that sea lice are being transferred from farms where sea lice remain a common problem (Scottish Office Agriculture 1997). It was recently found that sea lice are denser on 1 sea-winter escaped farmed fish than 1 sea-winter wild fish (Jacobson and Gaard 1997). These sea lice may contribute to increased wild stock mortality, reduced seawater growth, and premature return of adults (e.g., Todd et al. 1997).

Although it is difficult to quantify or partition the impacts on wild Atlantic salmon by escapement from the aquaculture niche (e.g., Fig. 4), it can no longer be reasonably questioned that major impacts do occur. Over the last decade, the primary ecological impact on wild fish health is through the transfer of diseases and parasites. While new diseases and parasites will surely appear, the current problems are now better controlled in the aquaculture niche (e.g., Aarflot 1995; Bruno and Poppe 1996; except perhaps for sea lice; also, re-

**Table 3.** Observations on the occurrence, survival, and biology of cultured (farmed) Atlantic salmon in the wild.

| Character | Observation | Reference |
|---|---|---|
| Abundance | 25–48% of salmon on feeding grounds in NE Atlantic Ocean | Hansen et al. (1993) |
| | 50–80% of spawners in River Vosso, western Norway | Skaala and Hindar (1997) |
| | 20–30% of all Norwegian spawners | |
| | 51–68% of all smolts leaving Magaguadavic River, New Brunswick have escaped from hatcheries | Stokesbury and Lacroix (1997) |
| | Over 2000 marine captures and 140 adult freshwater captures per year in NE Pacific Ocean between 1993 and 1997 | Atlantic Salmon Watch — A. Thomson, peronal communication |
| | Postitive correlations between smolts placed into Norwegian cages and percent capture in fisheries and in Norwegian streams (7-year assessment) | Lund et al. (1997) |
| Survival | Two-fold lower marine survival (sea-ranched) | Jonsson et al. (1991) |
| | 20% lower juvenile survival in streams | Ferguson et al. (1997) |
| Size, feeding, and growth | Escaped smolts larger in size when migrating from Magaguadavic River, New Brunswick | Stokesbury and Lacroix (1997) |
| | Experimentally introduced farmed strain and hybrids grow faster than wild juveniles in rivers in Ireland | Ferguson et al. (1997) |
| | Experimentally introduced farmed strain and hybrids grow faster than natives in Norwegian river | Einum and Fleming (1997) |
| | Naturally spawned farmed and hybrid offspring grow faster than native juveniles in Norwegian river | Fleming et al. (1997) |
| | Adult farmed females entering Norwegian river are 10% smaller in size than wild females | Lura and Sægrov (1991) |
| | About 7% of marine captures of escaped farmed fish in NE Pacific Ocean have prey in stomach | McKinnell et al. (1997) |
| | About 35% of marine captures of escaped Atlantic salmon in Scottish marine waters have prey in stomach | Hislop and Webb (1992) |
| | Farmed and hybrid offspring from natural breeding are scattered throughout Norwegian river during juvenile growth | Fleming et al. (1997) |
| Reproductive behavior | **Norway** | |
| | Later maturity and spawning than wild females | Heggberget (1988) |
| | Earlier maturity and spawning than wild females (3.5 weeks) | Lura and Sægrov (1991) |
| | Utilize similar spawning habitats | Økland et al. (1995); Fleming et al. (1997) |
| | Males competitively inferior | Fleming et al. (1997) |
| | Females show less breeding behavior and are less efficient at nest covering; males are less aggressive and court less | Fleming et al. (1996) |
| | **Iceland** | |
| | Adults enter rivers later and spawn later than wild stock | Gudjonsson (1991) |
| | **Scotland** | |
| | Farmed adults stay lower in river and spawn later | Webb et al. (1991) |
| | **Eastern Canada** | |
| | Adults enter river later than wild fish | Carr et al. (1997) |
| Reproductive success | Farmed progeny hatch and initiated feeding earlier in Norwegian streams | Lura and Sægrov (1991) |
| | Females carry more unspawned eggs, have more nest destruction, greater egg mortality, and overall less than 1/3 the success of wild females (Norway) | Fleming et al. (1996) |
| | Males have fewer spawnings, often do not ejaculate, and overall have less than 3% the success of wild males (Norway) | Fleming et al. (1996) |
| | Successful spawning | Lura and Sægrov (1991) |
| | Unfertilized eggs | Lura and Sægrov (1991) |
| | Successful spawning in an eastern Canadian river in 1993 | Carr and Anderson (1997) |
| | 55% of redds are of farmed origin in an eastern Canadian river | Carr and Anderson (1997) |

**Table 3** (*concluded*).

| Character | Observation | Reference |
|---|---|---|
| Reproductive interactions | Interbreeding of a Scottish farmed strain with wild fish in an Irish river and shift in wild gene pool | Crozier (1993) |
| | Farmed fish producing over 44% of the genes in the River Vosso, western Norway demonstrating that gene pool is being replaced by farmed strain | Skaala and Hindar (1997) |
| | Farmed fish contribute 21% of the genes in River Imsa, southwestern Norway, mainly through hybridization, after experimental release | Fleming et al. (1997) |
| | Farmed fish dig up wild fish's eggs when making their own nest | Webb et al. (1991) |
| Disease and parasites | Sea lice in farms apparently contributing to increased wild stock mortality, reduced seawater growth, and premature return | Dawson et al. (1997); McVicar (1997); Todd et al. (1997) |
| | More sea lice on 1 sea-winter escaped farmed salmon than wild salmon in Norwegian sea | Jacobson and Gaard (1997) |
| | *Gyrodactylis salaris* carried into Eastern Atlantic drainage from Baltic sea drainage by smolts from Swedish farm, killing over 35 Norwegian wild populations; the latter are more susceptible | Johnsen and Jensen (1991) |
| | *Aeromonas salmonicida* (furunculosis) carried to Norwegian aquaculture from Scottish smolts, probably spread by escapees to wild populations | Johnsen and Jensen (1994) |

cent outbreaks of ISA — infectious salmon anemia). I suspect that the impact of most concern for wild fish in the future will be genetic, through interbreeding and introgression of aquaculture genes and through increasing drift and inbreeding due to reduced wild population size (due in part to increasing competition and further habitat perturbation). The resulting loss of the wild gene pool may give rise to yet less fit individuals for future evolutionary change and survival in the wild. There is a strong possibility that the magnitude of escapement combined with the biological divergence between the two niches will result in the disappearance of all wild Atlantic salmon populations within areas of aquaculture.

## The Pacific Ocean experience

In North America there is strong concern over the increasing numbers of escaped Atlantic salmon discovered in marine and freshwater habitats and their potential impact on native Pacific salmonids. Unlike the situation in the Atlantic native range, no impact has been clearly documented to date (Environmental Assessment Office of British Columbia 1997). This may be because there is only limited research being conducted to study impacts. One significant program is the Atlantic Salmon Watch, which primarily documents the volunteered reportings of the number of marine and freshwater sightings and provides limited biological information (McKinnell et al. 1997).

Additional research on several key concerns should become an immediate priority if net-based fish farming is to continue (Fig. 4). First, direct genetic impacts are possible through hybridization with Pacific species. Four pieces of evidence supporting this contention are (1) European studies show that farmed female Atlantic salmon have increased hybridization rates with salmonids in the wild possibly as a consequence of decreased mate discrimination (e.g., Sægrov 1993; Youngson et al. 1993; Hindar and Balstad 1994); (2) most Pacific salmonids overlap to some degree in spawning season and breeding habitat with those of the Atlantic; (3) experimental crosses by R. Devlin (Department of Fisheries and Oceans, Vancouver, B.C., Canada, personal communication) show that survival to at least the hatch of F1 progeny occurred in 10 of 14 possible crosses between male, or female, Atlantic salmon, and seven native Pacific salmonid species; and (4) precociously mature Atlantic salmon parr have extended breeding seasons and may lack conspecific mates (about 10% of escaped parr collected in a BC river had precociously mature gonads; parr represent alternative breeding tactics — Gross (1996)). While some hybridization is therefore probable, the production of "hybrid swarms" is less likely since the genetic differences between Atlantic salmon and most Pacific salmonids result in low survivorship of F1s.

Second, and of more serious concern, is the indirect genetic impact of Atlantic salmon males attempting to hybridize with females in populations of native salmonids that are locally endangered and close to extinction (e.g., Slaney et al. 1996). Each Pacific salmonid female that has her eggs fertilized by an Atlantic salmon parr or other male has those eggs removed from the gene pool. A population with only a few native females may therefore loose a significant proportion of its reproductive output with even minor hybridization events.

Third, Atlantic salmon may compete extensively with native salmonid species for food and space. Fausch (1998) found that all co-evolved and non-native salmonids experimentally tested had interspecific effects with Atlantic salmon juveniles that were at least as strong as intraspecific effects due to the more aggressive nature of aquaculture salmon. Of special concern are any size differences among juveniles. For example, it has been shown that coho typically dominate Atlantic salmon juveniles because of a size advantage resulting from the coho's earlier hatch (see Fausch 1998). Thus, Atlantic salmon, which hatch earlier than steelhead, may be expected to dominate steelhead. The primary impact of interspecific competition was displacing competitively smaller individuals into less preferable habitats (e.g., from pools into riffles or reverse) (also, Gibson 1981; Beall et al. 1989).

Fourth, perturbation of the habitat would be likely because the Atlantic salmon are an "ecological novelty in a naive community" (Townsend 1996) and would most certainly utilize the habitat in ways different from native salmonids.

Fifth, the Atlantic salmon may carry and harbor diseases or parasites to which Pacific salmonids are vulnerable. One possibility is exotic diseases, although in a recent review of the aquaculture industry in British Columbia this was not regarded to be of particular concern (Stephan and Iwama 1997). The greater concern may lie in the loading of disease on Atlantic salmon relative to native species, due to the confines of aquaculture and selection programs for genetic resistance and disease tolerance. Disease amplification through exotic carriers, followed by transmission to and health reduction of native species, is not uncommon in the biological world.

*Recipe for successful invasion*

An important question is whether the escaped Atlantic salmon could colonize and invade the Pacific region. The establishment of self-reproducing populations of Atlantic salmon may magnify the impact concerns for native salmonids (Fig. 4). A recent analysis by Alverson and Ruggerone (1997) suggests that colonization is unlikely because historical attempts to introduce anadromous populations of Atlantic salmon around the world, including British Columbia and Washington State in the 1920s, have failed (e.g., MacCrimmon and Gots 1979).

I believe, however, that the invasion of the Pacific region by Atlantic salmon is now probable for at least six reasons: (1) ability to survive in the wild — we have discovered that escaped Atlantic salmon are capable of feeding and migrating thousands of kilometres in the Pacific ocean (Table 3). Furthermore, juvenile Atlantic salmon are able to grow and survive in coastal rivers and lakes (e.g., Lough et al. 1997); (2) reproductive capacity in the wild — we know that at least some escaped Atlantic salmon become reproductively mature and enter freshwater rivers. For example, of 20 adult Atlantic salmon that were sampled in British Columbia rivers between 1991 and 1995, 17 (85%) had mature or maturing gonads (McKinnell et al. 1997). Unlike historic attempts at introductions, where human breeders chose the places and times to release embryos or fry, today's Atlantic salmon are free to choose their own habitat and spawning times and make breeding decisions that maximize reproductive success. Since female Atlantic salmon produce several thousands of eggs, it is possible for a single female to initiate a population (although inbreeding may reduce fitness). An anadromous female may find a mate since mature male parr are resident in at least some coastal rivers; (3) naturalization of brood stock — through successive generations of selection and local rearing, the aquaculture industry has developed local brood stocks. Thus, unlike historic introductions, escapees today are probably at least somewhat genetically and developmentally adapted to the Pacific environment. This adaptation should markedly increase the potential for colonization; (4) magnitude, frequency, and geographic extent of seeding — thousands of Atlantic salmon, young and old (fry with yolk sacs to almost mature fish), are escaping annually and throughout the year into both marine and freshwater habitats, in repeated episodes, and over a large geographic range. This means that all combinations of life history stage, seasonal timing, genetic constitution, and environmental conditions are being experienced by escaped Atlantic salmon, increasing the likelihood of a successful fit; (5) open niches — many open niches now exist for Atlantic salmon because native salmonids, especially chinook, coho, steelhead, and cutthroat, the species that seem most similar to the Atlantic salmon, have been dramatically reduced in number and in many cases are locally extirpated (Walters 1995; Slaney et al. 1996). Thus, historically productive salmon streams are unoccupied and large amounts of food and space for rearing and habitat for spawning, exist without competitors; and (6) new niches — the extensive changes brought by humans to the structure of Pacific river systems may result in Pacific salmonids being less competitive and Atlantic salmon better adapted to the new wild niches. Atlantic salmon have a much longer evolutionary history of coexistence with humans and human technology-influenced habitats and therefore may be preadapted to colonize the perturbed niches for which Pacific salmonids are maladapted.

Introducing Atlantic salmon into Pacific waters is an experiment that few conservation-minded biologists would willingly perform today. Historically, eggs or fry were shipped and released into environments where it was not obvious that they could survive. The introduced stock was neither developmentally nor genetically prepared, the releases were relatively small, and the local environment often presented severe biotic competition. Today, the opportunity for invasion is unprecedented and success is probable at the current state of domestication of Atlantic salmon. Whether a new salmonid species in the Pacific drainage would result in a net decrease to all salmonid biodiversity through negative impacts, or instead increase total biodiversity through the addition of a new species, remains an open question.

## Ecorealism

Concerns about the interactions between the aquaculture and wild niches of salmon have tended to polarize viewpoints between "developers" of the aquaculture niche and "defenders" of the wild niche (e.g., contrast Kenney's (1997) report "Net Gain" with Ellis' (1996) report "Net Loss"). Developers are often reluctant to accept impacts, while defenders rarely put impacts into a perspective that permits acceptance of any potential benefits. Needham (1995) has thus suggested the need for a touch of "ecorealism" in any aquaculture vs. wild debates.

This paper explains why the escapement of Atlantic salmon from their aquaculture niche presents a concern for the wild niche of Atlantic salmon and for species biodiversity beyond their native range. Historically, the two greatest negative forces on the Atlantic salmon have been the capture fisheries, both commercial and recreational, and habitat alteration and destruction. These forces, expressed through overfishing, misguided stocking, dams, clear-cutting, pulp mills, log booms, terrestrial agricultural, mines, cities, storm-water runoff, etc., have resulted in widescale extirpations, depletions, and loss of biodiversity, in both Atlantic and Pacific salmonids, long before commercial salmon aquaculture appeared in the 1970s. While capture fisheries and habitat manipulations will continue to have a negative impact, the concern of many conservation-minded biologists today and into the next century will be the emergence of aquaculture as a third force that impacts on the wild species. Since any one of these three forces can lead to the complete loss of the remaining wild remnants of Atlantic and possibly other salmonids, the three forces combined are cause for significant concern.

**Saints or sinners?**

Are there any benefits to the wild niche from developing Atlantic salmon in an aquaculture niche? An important potential benefit that is often overlooked is the change that aquaculture is bringing to world salmon markets. First, consumption of farmed Atlantic salmon has now greatly surpassed that of wild Atlantic salmon. Japan, which consumes about 1/3 of the world's salmon, is replacing consumption of many wild salmonid species with fresh-farmed Atlantic salmon (Herrmann 1994). This switch in consumer preference may well occur in other world markets (Harris 1995) resulting in decreasing harvest pressure on wild stocks (Ridler 1995). Second, the increased availability of salmon has dropped the price for wild salmon, thus reducing profitability in the commercial fishery. In western Canada, for example, the value of farmed salmon, of which some 70% are Atlantic salmon, has exceeded the landed value of all commercial wild Pacific salmon harvests since 1995 (British Columbia Ministry of Agriculture, Fisheries and Food 1995, 1996, 1997). Declining harvest values may thus reduce the pressure on wild stocks. Finally, the reduction in commercial value of wild Atlantic salmon has allowed conservation groups and conservation-oriented groups to press forward with further preservation methods. One step has been the purchase of commercial rights. For example, in the north-eastern Atlantic, the buy-out of coastal netting stations around Britain by environmentalists and sport fishers may have resulted in the 30-year high of wild salmon returns to rivers in Scotland during 1995 (Needham 1995). In the northwestern Atlantic, several conservation organizations (North Atlantic Salmon Fund, Atlantic Salmon Federation, National Fish and Wildlife Foundation) were able to purchase the Greenland fishery quotas in 1993 and 1994 (Speer et al. 1997). The North Atlantic Salmon Conservation Organization (NASC), the international scientific body governing salmon fishing with responsibilities for making recommendations concerning Atlantic salmon conservation, was able to recommend in 1996 that all commercial fisheries cease. This recommendation was precipitated by the depleted state of the resource and was politically acceptable due to the reduced commercial value of the resource.

Other potential benefits exist as well. In some cases, the domestic salmon may contribute to conservation through stocking programs (e.g., Shackley et al. 1992). However, this benefit is mitigated by the divergence in biology that has taken place in aquaculture. In addition, the knowledge base being developed about salmon, including their genetics, development, and nutritional needs, may in future be applied to the conservation of the wild niche.

In summary, the creative and productive management of salmonid species and populations will lie in recognizing and accepting four key points. (1) Aquaculture is presenting a serious threat to wild populations and negative impacts are being documented in the native range and may yet occur outside of that range. (2) Aquaculture will not disappear — it is an industry for the future. (3) Aquaculture is not the root cause of the current dismal state of salmonid fisheries and conservation: mismanaged capture fisheries and habitat destruction are the principal culprits. (4) Aquaculture does offer some benefits for wild populations — the most important being the diversion of commercial economic interests.

## Recommendations

The development of a new salmonid niche and the evolution of a new lineage present important challenges both today and for the future. The following three recommendations may help us meet those challenges.

*1. Develop a new vision for fisheries research and management*

We need to develop a new vision for fisheries research and management which recognizes the interdependence of resource usage among all three stakeholders: aquaculturists, the biodiversity community, and those involved in capture fisheries. Aquaculture, the world's fastest growing agribusiness, is necessary to meet the 30% increase in global fish production required for year 2010 (FAO 1997*c*) and can contribute to both biodiversity and capture fisheries if well managed. The biodiversity sector is a relatively new yet rapidly growing segment of society focused on appreciation and preservation of genetic, population, species, and community diversity for both intrinsic and extrinsic values. It preserves the raw material needed by the capture fisheries and the gene pools that are the genetic resources for aquaculture. Capture fisheries are evolving away from an unsustainable commercial harvest to a new optimization based on sustainability and recreational gains (FAO Code of Conduct for Responsible Fisheries 1995), a process encouraged by aquaculture. Developing a vision of interdependence among sectors encourages cooperation rather than conflict and efforts to maximize benefits and minimize costs become a shared goal.

*2. Minimize the impact of aquaculture*

There is a false sense that aquaculture is "natural" and may look after itself. Instead, it is a complex and technical agribusiness which, like any new industry, is having larger environmental impacts than need occur over the long run. The industry must acknowledge these impacts and take immediate action on a number of issues including stopping the escapement of farmed fish. The FAO Aquaculture Code of Practice (FAO 1997*c*) provides some helpful direction for aquaculture leaders which, when combined with the vision outlined above, could chart a new course for the future. In turn, governments should be willing to support the development of appropriate aquaculture technology including: closed-containment systems to minimize the escapement of fish (and other pollutants); disease assessment and prevention; nutrition; and brood stock development. The economic and cultural benefits of such investments are likely to be high.

*3. Establish significant biological research programs*

We need to launch significant biological research programs to monitor and control the impact of escaped domestic Atlantic salmon. Current support by government agencies and the industries and public they represent are paltry in comparison to the size of the challenge. For example, the Atlantic Salmon Watch program in British Columbia, a valuable source of monitoring data, lacks a significant budget and is partly dependent on a commercial capture industry that is now largely closed. The situation throughout the rest of the world is not any better. It is time for governments to cease minor, poorly funded research initiatives and begin empowering their staff and other scientists to conduct meaningful studies at the scale necessary for the issues.

## Acknowledgments

I wish to thank the many thoughtful people in aquaculture, biodiversity, and capture fisheries who have influenced my views on wild and cultured salmon. I especially thank R. Behnke, E. Black, H. Breen, J. Brown, A. Castledine, S. Crawford, J. Darling, B. Dempson, B. Devlin, L. Dill, J. Dodson, D. Ellis, I. Fleming, T. Fleming, B. Harrower, K. Hindar, G. Iwama, B. Jonsson, A. Keitlah, B. Nowell, R. Peterman, T. Quinn, H. Regier, A. Thomson, E. van den Berghe, B. Ward, and R. Ydenberg. Joe Repka, Nancy Gerrish, and Bryan Neff provided many helpful discussions, Nancy Gerrish edited the text, Bryan Neff drew the figures, Andrew Ecker helped with tables, and two anonymous journal reviewers provided instructive comments. Financial support came from the Natural Sciences and Engineering Research Council (NSERC) of Canada. I appreciate the invitation from Martha Mather and Carol Folt to attend the 1997 Atlantic salmon workshop in Braemar, Scotland and the support and initiative of Richard Degraaf, Robert Lewis, and Keith Jensen of the United States Forest Service.

## References

Aarflot, L. 1995. Management of furunculosis in Norway. Bull. Aquacul. Assoc. Can. **95**(3): 20–23.

Aksnes, A., Gjerde, B., and Roald, S. 1986. Biological, chemical and organoleptic changes during maturation of farmed Atlantic salmon, Salmo salar. Aquaculture, **53**: 7–20.

Allendorf, F.W., and Waples, R.S. 1996. Conservation and genetics of salmonid fishes. *In* Conservation genetics: case histories from nature. *Edited by* J.C. Avise and J.L. Hamrick. Chapman and Hall, New York. pp. 238–280.

Alverson, D.L., and Ruggerone, G.T. 1997. Escaped farm salmon: environmental and ecological concerns. Discussion Paper Part B. *In* Salmon aquaculture review. Technical Advisory Team Discussion Papers Vol. 3. Environmental Assessment Office, Victoria B.C. pp. B-i–B-100.

Anderson, J.L. 1997. The growth of salmon aquaculture and the emerging new world order of the salmon industry. *Edited by* E.L. Pikitch, D.D. Huppert, and M.P. Sissenwine. *In* Global trends: fisheries management. Am. Fish. Soc. Symp. **20**. pp. 175–184.

Beall, E., Heland, M., and Marty, C. 1989. Interspecific relationships between emerging Atlantic salmon, *Salmo salar*, and coho salmon, *Oncorhynchus kisutch*, juveniles. J. Fish Biol. **35**(Suppl. A): 285–293.

Boghen, A.D. (*Editor*). 1995. Cold-water aquaculture in Atlantic Canada, 2nd ed. The Canadian Institute for Research on Regional Development, Moncton, N.B.

British Columbia Ministry of Agriculture, Fisheries and Food. 1995–1996–1997. Annual reports — British Columbia seafood industry year in review. Queen's Printer, Victoria, B.C.

Bruno, D.W., and Poppe, T.T. 1996. A colour atlas of salmonid diseases. Academic Press, London, U.K.

Carr, J.W., and Anderson, J.M. 1997. Documentation of escaped female cultured Atlantic salmon (*Salmo salar*) spawning in a Canadian river. *In* Final abstracts: ICES/NASCO Symposium. Interactions between salmon culture and wild stocks of Atlantic salmon: The scientific and management issues. NASCO, Bath, England, U.K.

Carr, J.W., Lacroix, G.L., Anderson, J.M., and Dilworth, T. 1997. Movements of non-maturing cultured Atlantic salmon (*Salmo salar*) into a Canadian river. *In* Final abstracts: ICES/NASCO Symposium. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. NASCO, Bath, England, U.K.

Cross, T.F., and King, J. 1983. Genetic effects of hatchery rearing in Atlantic salmon. Aquaculture, **33**: 33–40.

Crozier, W.W. 1993. Evidence of genetic interaction between escaped farmed salmon and wild Atlantic salmon (*Salmo salar* L.) in a Northern Irish river. Aquaculture, **113**: 19–29.

Dawson, L.H.J., Pike, A.W., Houlihan, D.F., and McVicar, A.H. 1997. Comparison of the susceptibility of salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.) to sea lice (*Lepeophtheirus salmonis*) (Krøyer 1837) infections. *In* Final abstracts: ICES/NASCO Symposium. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. NASCO, Bath, England, U.K.

Donaldson, E.M. 1997. The role of biotechnology in sustainable aquaculture. *In* Sustainable aquaculture. *Edited by* J.E. Bardach. John Wiley & Sons, Inc., New York. pp.101–126.

Einum, S., and Fleming, I.A. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. J. Fish Biol. **50**: 634–651.

Ellis, D.W. 1996. Net loss: the salmon netcage industry in British Columbia. *A report to* The David Suzuki Foundation, Suite 219, 2211 West Fourth Avenue, Vancouver, B.C. V6K 4S2, Canada.

Environmental Assessment Office of British Columbia. 1997. Salmon aquaculture review. Vol. 1. British Columbia Government Publications, Victoria, B.C.

FAO. 1995. Code of conduct for responsible fisheries. FAO, Rome.

FAO. 1997*a*. FAO yearbook: fishery statistics, catches and landings, for 1995. FAO, Vol. 80.

FAO. 1997*b*. Fishery Information, Data and Statistics Unit. 1995. Aquaculture production statistics 1986–1995. FAO Fisheries Circular. No. 815, Rev. 9. Rome, FAO.

FAO. 1997*c*. Aquaculture development. FAO technical guidelines for responsible fisheries. No. 5. Rome, FAO.

Fausch, K.D. 1998. Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 218–231.

Fergusen, A., McGinnity, P., Stone, C., Taggart, J., Cooke, D., Cotter, D., Hynes, R., and Cross, T. 1997. Will interbreeding between wild and cultured fish have negative consequences? *In* Final abstracts: ICES/NASCO Symposium. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. NASCO, Bath, England, U.K.

Fevolden, S.E., Refstie, T., and Røed, K.H. 1991. Selection for high and low stress response in Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*). Aquaculture, **95**: 53–65.

Fevolden, S.E., Refstie, T., and Røed, K.H. 1993. Disease resistance in Atlantic salmon (*Salmo salar*) selected for high or low responses to stress. Aquaculture, **109**: 215–224.

Fleming, I.A., and Gross, M.R. 1989. Evolution of adult female morphology and life history in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution, **43**: 125–140.

Fleming, I.A., and Gross, M.R. 1990. Latitudinal clines in clutch size: a trade off between egg number and size in Pacific salmon. Ecology, **71**: 1–11.

Fleming, I.A., and Gross, M.R. 1992. Reproductive behavior of hatchery and wild coho salmon: does it differ? Aquaculture, **103**: 1–21.

Fleming, I.A., and Gross, M.R. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competion. Ecol. Applicat. **3**: 230–245.

Fleming, I.A., and Gross, M.R. 1994. Breeding competition in a Pacific salmon (Coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution, **48**: 637–657.

Fleming, I.A., Jonsson, B., and Gross, M.R. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. Can. J. Aquat. Sci. **51**: 2808–2824.

Fleming, I.A., Jonsson, B., Gross, M.R., and Lamberg, A. 1996. An experimental study of the reproductive behavior and success of farmed and wild Atlantic salmon (*Salmo salar*). J. Appl. Ecol. **33**: 893–905.

Fleming, I.A., Hindar, K., Mjølnerød, I., Jonsson, B. 1997. The simulated escape of farmed salmon in a Norwegian river: breeding success, hybridisation and offspring traits. *In* Final abstracts: ICES/NASCO Symposium. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. Bath, England, U.K.

Friars, G.W., Bailey, J.K., and Coombs, K.A. 1990. Correlated responses to selection for grilse length in Atlantic salmon. Aquaculture, **85**: 171–176.

Gausen, D., and Moen, V. 1991. Large-scale escapes of farmed Atlantic salmon (*Salmo salar*) into Norwegian rivers threaten natural populations. Can. J. Fish. Aquat. Sci. **48**: 426–428.

Gibson, R.J. 1981. Behavioural interactions between coho salmon (*Oncohynchus kisutch*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), and steelhead trout (*Salmo gairdneri*) at the juvenile fluviatile stages. Can. Tech. Rep. Fish. Aquat. Sci. 1029. 116 p.

Gjedrem, T. 1979. Selection for growth rate and domestication in Atlantic salmon. Z. Tierz. Zuchtungsbiol. **96**: 56–59.

Gjedrem, T., Gjerde, B., and Refstie, T. 1988. A review of quantitative genetic research in salmonids at AKVAFORSK. *In* Proceedings of the Second International Conference on Quantitative Genetics. *Edited by* B.S. Weir, E.J. Eisen, M.M. Goodman, and G. Namkoon. Sinauer, Sunderland, Mass. pp. 527–535.

Gjedrem, T., Gjøen, H.M., and Gjerde, B. 1991. Genetic origin of Norwegian farmed Atlantic salmon. Aquaculture, **98**: 41–50.

Gjerde, B. 1984. Response to individual selection for age at sexual maturity in Atlantic salmon. Aquaculture, **38**: 229–240.

Gjerde, B. 1993. Breeding and selection. *In* Salmon aquaculture. *Edited by* K. Heen, R.L. Monahan, and F. Utter. Halsted Press, Toronto, Ont. pp. 187–208.

Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. Nature, **313**: 47–48.

Gross, M.R. 1991. Salmon breeding behavior and life history evolution in changing environments. Ecology, **72**: 1180–1186.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends Ecol. Evol. **11**: 92–98.

Gudjonsson, S. 1991. Occurrence of reared salmon in natural salmon rivers in Iceland. Aquaculture, **98**: 133–142.

Hansen, L.P., Håstein, T., Nævdal, G., Saunders, R.L., and Thorpe, J.E. 1991. Interactions between cultured and wild Atlantic salmon. Aquaculture, **98**: v–x.

Hansen, L.P., Jacobsen, J.A., and Lund, R.A. 1993. High numbers of farmed Atlantic salmon, *Salmo salar* L., observed in oceanic waters north of the Faroe Islands. Aquacult. Fish. Manage. **24**: 777–781.

Harris, R. 1995. A strategic approach to marketing aquaculture products. *In* Cold-water aquaculture in Atlantic Canada. 2nd ed. *Edited by* A.D. Boghen. The Canadian Institute for Research on Regional Development, Moncton, N.B. pp. 583–615.

Heen, K., Thorpe, J., Ridler, N., Monahan, R.L., Mahnken, C., and Lindbergh, J. 1993. The distribution of salmon aquaculture. *In* Salmon aquaculture. *Edited by* K. Heen, R.L. Monahan, and F. Utter. Halsted Press: an Imprint of John Wiley & Sons, Inc., Toronto, Ont. pp.10–58.

Heggberget, T.G. 1988. Timing of spawning in Norwegian Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **45**: 845–849.

Heggberget, T.G., Johnsen, B.O., Hindar, K., Jonsson, B., Hansen, L.P., Hvidsten, N.A., and Jensen, A.J. 1993. Interactions between wild and cultured Atlantic salmon: a review of the Norwegian experience. Fish. Res. **18**: 123–146.

Herrmann, M. 1994. Salmon markets. J. Aquat. Food Prod. Technol. **3**: 5–21.

Hindar, K., and Balstad, T. 1994. Salmonid culture and interspecific hybridization. Conserv. Biol. **8**(3): 881–882.

Hindar, K., Ryman, N., and Utter, F. 1991. Genetic effects of cultured fish on natural fish populations. Can. J. Fish. Aquat. Sci. **48**: 945–957.

Hislop, J.R., and Webb, J.H. 1992. Escaped farmed Atlantic salmon, *Salmo salar* L., feeding in Scottish coastal waters. Aquacult. Fish. Manage. **23**: 721–723.

International Union Conservation of Nature (IUCN). 1997. Conserving vitality and diversity. *In* Proceedings of the World Conservation Congress Workshop on Alien Invasive Species. *Compiled by* C.D.A. Rubec and G.O. Lee. Published in partnership with the IUCN Species Survival Commission and the North American Wetlands Conservation Council (Canada). Canadian Wildlife Service, Environment Canada, Ottawa, Ont. 96 p.

Jacobsen, J.A., and Gaard, E. 1997. Open ocean infection by salmon lice (*Lepeophtheirus salmonis*): comparison of wild and escaped farmed Atlantic salmon. *In* Final abstracts: ICES/NASCO Symposium. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. NASCO, Bath, England, U.K.

Johnsen, B.O., and Jensen, A.J. 1991. The *Gyrodactylus* story in Norway. Aquaculture, **98**: 289–302.

Johnsen, B.O., and Jensen, A.J. 1994. The spread of furunculosis in salmonids in Norwegian rivers. J. Fish Biol. **45**: 47–55.

Jonsson, B., and Fleming, I.A. 1993. Enhancement of wild salmon populations. *In* Human impact on self-recruiting populations. An International Symposium, Kongsvoll, Norway. *Edited by* G. Sundnes. Tapir Press, Trondheim, Norway. pp. 209–242.

Jonsson, B., Jonsson, N., and Hansen, L.P. 1991. Differences in life history and migratory behavior between wild and hatchery-reared Atlantic salmon in nature. Aquaculture, **98**: 69–78.

Jonsson, N., Jonsson, B., and Fleming, I.A. 1996. Does early growth cause a phenotypically plastic response in egg production of Atlantic salmon? Funct. Ecol. **10**: 89–96.

Kenney, E.A. 1997. Net gain: the salmon farming industry in B.C. *Report for* The B.C. Salmon Farmers Association, 506 – 1200 West Pender St., Vancouver, B.C. V5E 2S9, Canada.

Krueger, C.C., and May, B. 1991. Ecological and genetic effects of salmonid introductions in North America. Can. J. Fish. Aquat. Sci. **48**(Suppl. 1): 66–77.

Lassuy, D.R. 1995. Introduced species as a factor in extinction and endangerment of native fish species. Am. Fish. Soc. Symp. **15**: 391–396.

Lough, M., Law, B., Lewis, B., and McCulloch, M. 1997. The occurrence of Atlantic salmon in coastal streams of southern British Columbia during 1996. *Report for* British Columbia Conservation Foundation Project 712048. British Columbia Ministry of Environment, Lands and Parks. Fisheries Branch, 2080-A Labieux Road, Nanaimo, B.C.

Lund, R.A., Hansen, L.P., and Økland, F. 1997. Geographical and temporary distribution of escaped farmed Atlantic salmon, *Salmo salar* L, in relation to farming activity. *In* Final abstracts: ICES/NASCO Symposium. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. NASCO, Bath, England, U.K.

Lura, H., and Sægrov, H. 1991. Documentation of successful spawning of escaped farmed female Atlantic salmon, *Salmo salar*, in Norwegian rivers. Aquaculture, **98**: 151–159.

MacCrimmon, H.R., and Gots, B.L. 1979. World distribution of Atlantic salmon, *Salmo salar.* J. Fish. Res. Board Can. **36**: 422–457.

McKinnell, S., Thomson, A.J., Black, E.A., Guthrie, C.M., III, Wing, B.L., Koerner, J.F., and Helle, J.H. 1997. Atlantic salmon in the North Pacific. Aquaculture, **28**: 145–157.

McVicar, A.H. 1997. The co-existence of wild and cultured populations — disease and parasite implications. *In* Final abstracts: ICES/NASCO Symposium. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. NASCO, Bath, England, U.K.

Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. J. Great Lakes Res. **19**(1): 1–54.

Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1994. Exotic species and the integrity of the Great Lakes. Lessons from the past. Bioscience, **44**(10): 666–676.

Moyle, P.B., and Light, T. 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biol. Conserv. **78**: 149–161.

Needham, T. 1995. Farmed Atlantic salmon in the Pacific northwest. Bull. Aquacul. Assoc. Can. **95**(4): 38–41.

Økland, F., Heggberget, G.T., and Jonsson, B. 1995. Migratory behavior of wild and farmed Atlantic salmon (*Salmo salar*) during spawning. J. Fish Biol. **46**: 1–7.

Parrish, D.L., Behnke, R., Gephard, S.R., McCornick, S.D., Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 281–287.

Ridler, N.B. 1995. The economics of aquaculture. *In* Cold-water aquaculture in Atlantic Canada. 2nd ed. *Edited by* A.D. Boghen. The Canadian Institute for Research on Regional Development, Moncton, N.B. pp. 557–582.

Ruzzante, D.E. 1994. Domestication effects on aggressive and schooling behavior in fish. Aquaculture, **120**: 1–24.

Sægrov, H.L. 1993. Timing of spawning in cultured and wild Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in the River Vosso, Norway. Ecol. Freshwater Fish, **2**: 167–172.

Saunders, R.L. 1991. Potential interaction between cultured and wild Atlantic salmon. Aquaculture, **98**: 51–60.

Saunders, R.L. 1995. Salmon aquaculture: present status and prospects for the future. *In* Cold-water aquaculture in Atlantic Canada. 2nd ed. *Edited by* A.D. Boghen. The Canadian Institute for Research on Regional E. Development, Moncton, N.B.

Scottish Office Agriculture. 1997. Report of the Scottish salmon strategy task force. Environment and Fisheries Department, Pentland House, Robb's Loan, Edinburgh, EH14 1TY. pp. 35–81.

Shackley, P.E., Donaghy, M.J., and Hay, D.W. 1992. An experiment in the planting of Atlantic salmon, *Salmo salar* L., fry. Aquacult. Fish. Manage. **23**: 385–392.

Shigesada, N., and Kawasaki, K. 1997. Biological invasions: theory and practice. Oxford University Press, New York.

Skaala, O., and Hindar, K. 1997. Genetic changes in the R. Vosso salmon stock following a collapse in the spawning population and invasion of farmed salmon. *In* Final abstracts, ICES/NASCO Symposium. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. NASCO, Bath, England, U.K.

Slaney, T.L., Hyatt, K.D., Northcote, T.G., and Fielden, R. J. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries: Am. Fish. Soc. **21**(10): 20–35.

Speer, L., Garrison, K., Lonergan, K., Notthoff, A., Pulling, W., Powell, K., Chasis, S., Stokstad, P. 1997. Hook, line, and sinking. The crisis in marine fisheries. Natural Resources Defense Council, New York.

Ståhl, G. 1987. Genetic population structure of Atlantic salmon. *In* Population genetics and fishery management. *Edited by* N. Ryman and F. Utter. University of Washington Press, Seattle, Wash. pp. 121–140.

Stephen, C., and Iwama, G. 1997. Fish health. *In* Salmon aquaculture review. Technical Advisory Team Discussion Papers Vol. 3, Part C. Environmental Assessment Office, Victoria, B.C. pp. C-i–C-140.

Stokesbury, M.J.W., and Lacroix, G.L. 1997. High incidence of juvenile Atlantic salmon (*Salmo salar*) escaped from hatcheries in the smolt output of a Canadian river. *In* Final abstracts: ICES/NASCO Symposium. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. NASCO, Bath, England, U.K.

Thomson, A.J., and McKinnell, S. 1993. Summary of reported Atlantic salmon (*Salmo salar*) catches and sightings in British Columbia and adjacent waters in 1992. Can. Manuscr. Rep. Fish. Aquat. Sci. 2215.

Thomson, A.J., and McKinnell, S. 1994. Summary of reported Atlantic salmon (*Salmo salar*) catches and sightings in British Columbia and adjacent waters in 1993. Can. Manuscr. Rep. Fish. Aquat. Sci. 2246.

Thomson, A.J., and McKinnell, S. 1995. Summary of reported Atlantic salmon (*Salmo salar*) catches and sightings in British Columbia and adjacent waters in 1994. Can. Manuscr. Rep. Fish. Aquat. Sci. 2304.

Thomson, A.J., and McKinnell, S. 1996. Summary of reported Atlantic salmon (*Salmo salar*) catches and sightings in British Columbia and adjacent waters in 1995. Can. Manuscr. Rep. Fish. Aquat. Sci. 2304.

Thomson, A.J., and McKinnell, S. 1997. Summary of reported Atlantic salmon (*Salmo salar*) catches and sightings in British Columbia and adjacent waters in 1996. Can. Manuscr. Rep. Fish. Aquat. Sci. 2407.

Todd, C.D., Walker, A.M., Wolff, K., Northcott, S.J., Walker, A.F., Ritchie, M.G., Hoskins, R., Abbott, R.J., and Hazon, N. 1997.

Genetic differentiation of populations of the copepod sea louse *Lepeophtheirus salmonis* (Krøyer) ectoparasitic on wild and farmed salmonids around the coasts of Scotland: evidence from RAPD markers. J. Exp. Mar. Biol. Ecol. **210**: 251–274.
Townsend, C.R. 1996. Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. Biol. Conserv. **78**: 13–22.
U.S. Congress, Office of Technology Assessment. 1993. Harmful non-indigenous species in the United States, OTA-F-565. U.S. Government Printing Office, Washington, D.C.
Utter, F., Hindar, K., and Ryman, N. 1993. Genetic effects of aquaculture on natural salmonid populations. *In* Salmon aquaculture. *Edited by* K. Heen, R.L. Monahan, and F. Utter. Halsted Press, Toronto, Ont. pp. 144–165.
van den Berghe, E.P., and Gross, M.R. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **41**: 204–206.
van den Berghe, E.P., and Gross, M.R. 1986. Length of breeding life in coho salmon. Can. J. Zool. **64**: 1482–1486.
van den Berghe, E.P., and Gross, M.R. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution, **43**: 141–157.
Verspoor, E. 1988. Reduced genetic variability in first-generation hatchery populations of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **45**: 1686–1690.
Walters, C. 1995. Fish on the line: the future of Pacific fisheries. *A report to* The David Suzuki Foundation, Fisheries Project Phase I, 219 – 2211 West Fourth Avenue, Vancouver, B.C. V6K 4S2, Canada.
Webb, J.H., Hay, D.W., Cunningham, P.D., and Youngson, A.F. 1991. The spawning behavior of escaped farmed and wild Atlantic salmon (*Salmo salar* L.) in a northern Scottish river. Aquaculture, **98**: 97–110.
Williamson, M. 1996. Biological invasions. Chapman & Hall, New York.
Youngson, A.F., Martin, S.A.M., Jordan, W.C., and Verspoor, E. 1991. Genetic protein variation in Atlantic salmon in Scotland: comparison of wild and farmed fish. Aquaculture, **98**: 231–242.
Youngson, A.F., Webb, J.H., Thompson, C.E., and Knox, D. 1993. Spawning of escaped farmed Atlantic salmon (*Salmo salar*): hybridization of females with brown trout (*Salmo trutta*). Can J. Fish. Aquat. Sci. **50**: 1986–1990.

**Note added in proof**: My prediction, page 139, that escaped farmed Atlantic salmon will produce progeny in Pacific waters has apparently now been confirmed (T. Down, B.C. Ministry of Fisheries, observation and collection of free-living juveniles in Tsitika River, B.C., August 1998).