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ECOLOGICAL AND BEHAVIOURAL INTERACTIONS BETWEEN FARMED AND WILD ATLANTIC SALMON: CONSEQUENCES FOR WILD SALMON

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ABSTRACT

The concentration of hatcheries and sea cages for Atlantic salmon farming in several areas of the Maritime Provinces introduces the probability that ecological interactions between farmed and wild Atlantic salmon will occur. Farmed salmon escape as fry, parr and smolts into fresh water and as smolts, post-smolts and adults in coastal marine areas, and they can move from one habitat to the other and interact directly or indirectly with wild salmon. In fresh water, the entry of escaped farmed spawners can influence natural migration and spawning, and behavioural interactions can affect mating selectivity and interbreeding that control genetic interactions and population performance. Between the fry and smolt stages, competition for food and space can increase with the intoduction of large numbers of conspecific organisms with a distinct developmental and size advantage. In addition, predator-prey relationships can potentially be altered by flooding streams with farmed fry, parr and smolts. These interactions would lead to changes in productibity of native salmon populations through processes affecting growth and survival. In the marine environment, the migratory behaviour of post-smolts and adults through areas with many closely spaced cage sites and high densities of farmed fish could be altered and wild fish could fall prey to the predators around cage sites. Exposure to many cage sites also would increase the probability of disease and parasite transmission to wild fish. These interactions could increase the marine mortality rate of wild salmon from local and distant stocks that migrated through cage site areas. The apparently large number of escaped farmed salmon remaining in the marine in the marine environment also increases the probability of dispersal and interaction with wild salmon stocks outside of aquaculture areas. Although interactions between farmed and wild salmon have been shown to occur, few of these have been investigated in the Maritime Provinces and their impacts on wild salmon remain unknown.

Résumé

La concentration d'installations piscicoles et de cages en mer pour l'élevage du saumon de l'Atlantique dans plusieurs régions des Maritimes fait naître la possibilité d'interactions écologiques entre les saumons d'élevage et les saumons sauvages. Des saumons d'élevage s'échappent sous forme d'alevins, de tacons ou de saumoneaux dans les eaux douces et sous forme de saumoneaux, de post-saumoneaux ou d'adultes dans les zones côtières. Ces poissons peuvent se déplacer d'un habitat à l'autre et interagir directement ou indirectement avec des saumons sauvages. En eau douce, l'arrivée de géniteurs d'élevage peut influer sur les migrations naturelles et le frai et des interactions comportementales peuvent influer sur la sélectivité de l'appariement reproducteur et le métissage qui régissent les interactions génétiques et le statut de la population. Entre les stades d'alevin et de saumoneau, la concurrence faite pour la nourriture et l'espace peut s'accroître suite à l'arrivée d'un nombre important d'organismes de la même espèce disposant d'avantages certains en matière de développement et de taille. Les relations prédateurs-proies peuvent aussi être modifiées par l'arrivée massive dans les cours d'eau d'alevins, de tacons ou de saumoneaux d'élevage. Ces nouvelles interactions pourraient occasionner une modification de la productivité des populations de saumons autochtones en agissant sur la croissance et la survie. En milieu marin, le comportement migrateur des post-saumoneaux et des adultes devant traverser des zones à fortes concentrations de cages rapprochées et de poissons d'élevage pourrait être modifié et les poissons sauvages pourraient devenir la proie des prédateurs se trouvant dans le voisinage des cages. Le passage à proximité d'un grand nombre de cages pourrait aussi accroître le risque de transmission de maladies et de parasites aux poissons sauvages. Ces interactions pourraient accroître la mortalité en mer des saumons sauvages de stocks locaux ou éloignés qui migrent au travers des sites d'élevage en cages. Le nombre important de saumons d'élevage échappés qui semblent demeurer en milieu marin accroît aussi la probabilité d'une dispersion et d'interactions avec les stocks de saumons sauvages de l'extérieur des zones aquacoles. Des interactions entre les saumons d'élevage et sauvages ont été démontrées, mais peu ont été étudiées dans les Maritimes et leurs incidences sur les saumons sauvages demeurent inconnues.

Introduction

Atlantic salmon escape from fish farms and commercial hatcheries in the Maritime Provinces and have access to natural bodies of water. The reasons for the escape or release into the environment are varied, and escape can occur at almost all free-swimming stages. Regrettably, the numbers of salmon escaping from sea cages and hatcheries are not reported by the industry, but indirect evidence from a river where the number of salmon of farmed origin is monitored indicates that the number of escaped fish has increased dramatically in recent years as the industry expanded (from < 40% of the salmon run in the Magaguadavic River in the early 1990s to about 70-90% of the run since 1994; Carr et al. 1997*a*). However, there is no accurate estimate of the number of farmed salmon at large at any time or of their regional distribution. Such basic information is needed to assess the potential impacts of interactions between farmed and wild salmon on the wild stocks.

Interactions between farmed and wild Atlantic salmon can be classified into two categories: ecological and genetic interactions. Ecological interactions may involve the transfer of diseases (including parasites), predation, or competition for space, food or mates between wild and escaped farm fish. Depending on the direction and strength of these interactions, growth and survival of both wild and farmed fish could be affected. They can also involve modification of the timing and pattern of natural migrations and complex interactions during spawning that can affect survival of fish of either origin. Genetic interactions result from exchange of genetic material (hybridisation) and/or the alteration of selection pressures caused by interactions between wild Atlantic salmon and farmed fish, usually of the same species, but could potentially occur between fish of different species (as rainbow trout farming increases) (reviewed in Hindar et al. 1991; Utter et al. 1993; Fleming 1995; Verspoor 1997). It should be noted that ecological and genetic interactions are not mutually exclusive. Rather, ecological interactions can alter selection pressures and the probability of hybridisation, while genetic interactions through hybridisation can influence the likelihood of ecological interactions in subsequent generations. This paper, however, will only examine the ecological and behavioural interactions that can lead to genetic interaction or the transfer of diseases and will not deal with their impacts on the wild stocks. Other workshop papers dealt with the potential genetic effects of interactions (Lacroix et al. 1998; Verspoor 1998) and the potential impacts of diseases and parasites (McVicar 1998; Olivier and MacKinnon 1998).

The goal of this paper is to identify the ecological interactions that occur between farmed Atlantic salmon (escaped and contained) and wild Atlantic salmon in the Maritime Provinces and to outline the potential impacts of these interactions on the wild stocks. Although there is growing evidence that interactions between farmed and wild fish are intensive in some areas at the centre of the aquaculture industry such as Passamaquoddy Bay and its rivers (Carr et al. 1997*a*, 1997*b*; Lacroix et al. 1997; Stokesbury and Lacroix 1997; O'Neil 1998; Whoriskey et al. 1998), there are no studies to date linking these interactions directly to specific impacts on the wild stocks in the Maritimes. As escaped farmed salmon disperse to rivers outside the immediate area of aquaculture (see O'Neil 1998), the potential for ecological interactions may be more extensive than anticipated (Amiro 1998*a*, 1998*b*). The possible effects of these ecological interactions on wild salmon stocks will be examined. Despite the lack of Maritimes-specific data for Atlantic Canada (due to a lack of investigation), the majority of effects we report from the literature show broad geographical distributions and repeated patterns. These provide a logical basis for concern about negative ecological interactions between farmed and wild Atlantic salmon in the Maritime Provinces.

This assessment is meant to focus on the situation as it exists for most of the salmon aquaculture industry in the Maritime Provinces. To that effect, it is worth noting that the farming of Atlantic salmon in the Maritimes is similar that elsewhere in world. However, it tends to be mostly limited at the present time to a small geographic area around the Fundy Isles in Southwest New Brunswick (see Fig. 1; Chang 1998). Atlantic salmon farming in northern Maine, U.S.A. also shares the same waters and adds to the concentration of sea cages in the Fundy Isles area (Baum 1998). In Norway and Scotland, both major producers of farmed salmon with long histories, marine cage sites are more widely dispersed along coastlines with lower local concentrations than in Southwest New Brunswick. While localisation of farming in the Maritimes should limit the extent of direct interaction and impact on the wild salmon stocks, the high concentration have the potential to greatly increase the intensity of interactions with wild stocks within the immediate area compared to those observed elsewhere. Moreover, there are unique stocks of wild salmon (e.g., inner Bay of Fundy salmon; Amiro 1998*a*) that pass through the area. The potential impacts of interactions in the freshwater and marine environments will be considered separately for specific life history stages because of the potential contribution by commercial hatcheries and brackish and marine cage sites to the pool of farmed salmon at large.

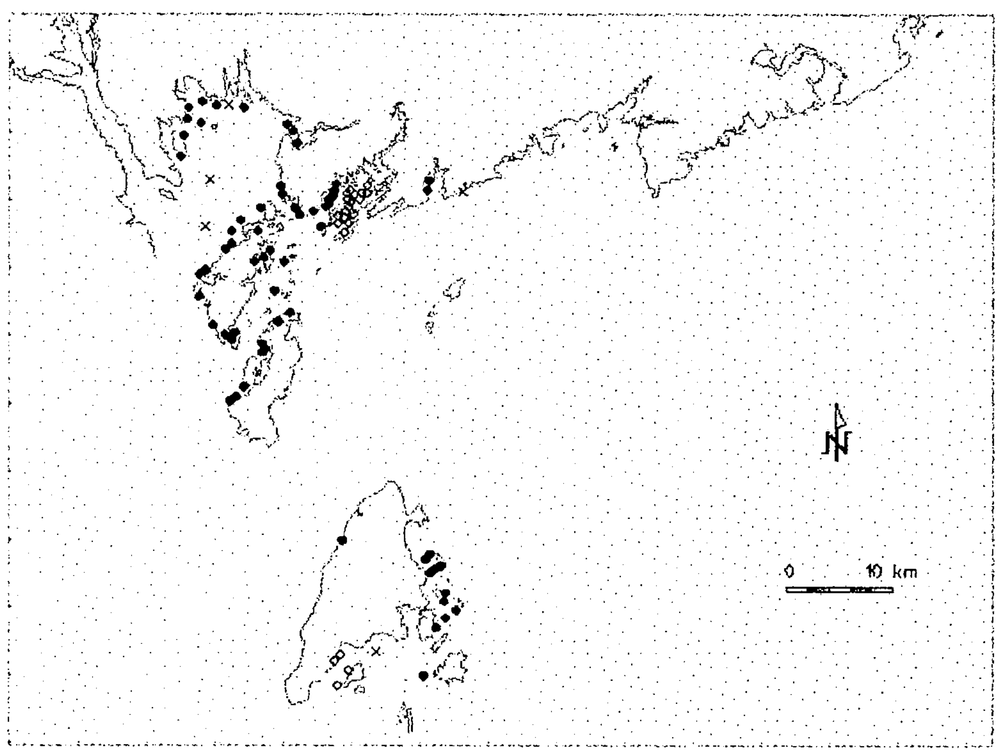

Figure 1. Map of Southwest New Brunswick showing the location of commercial marine cage sites for farmed Atlantic salmon in Passamaquoddy Bay and the Bay of Fundy.

Interactions in Freshwater Habitat

Migration

Farmed Atlantic salmon that escape from sea cages show a strong tendency to migrate into nearby rivers, particularly as they begin to mature (Hansen and Jonsson 1991; Youngson et al. 1997). This pattern also appears in the Maritimes, where the Magaguadavic River, which lies in close proximity to many marine and estuarine cage sites in Passamaquoddy Bay, has become a magnet for escaped farmed salmon. The proportion of farmed fish in the wild population, estimated at about 5% of the population in 1983 (about 50 escapees; Martin 1984), has recently increased dramatically in a short time period, from 34–39% (48 and 54 escapees) in 1992/1993 to 90% (1,200 and 712 escapees) in 1994/1995 (Carr et al. 1997*a*; Whoriskey et al. 1998). However, in a recent study, some farmed fish captured at the mouth of the Magaguadavic River, tagged and released back to the marine environment in sites up to 48 km away, were found to return to the Magaguadavic River within a short time period (Whoriskey et al. 1998). This may be an indication that these fish originated from hatcheries on the river and that they had imprinted to the river as smolts before being transferred to sea cages. Such a "homing" behaviour could have serious ecological implications for those rivers where hatcheries that supply smolts to the industry are located, especially if the river contributes a high proportion of the smolts used for farming (e.g., the Magaguadavic River). A river with a large hatchery production could essentially become a magnet for escaped farmed salmon, thereby intensifying the interaction and potential impact on the wild population in that river. However, evidence also indicates that escaped fish from throughout the general migrate to the Magaguadavic River area (as shown by the capture at the river mouth of farmed rainbow trout originating from cages in Maine; J. Carr, Atlantic Salmon Federation, St. Andrews, pers. comm.). Studies from Norway have found that smolts and post-smolts released at marine sites tend to enter nearby rivers to spawn rather than returning to their natal river (Hansen et al. 1993). They show little homing tendency or ability to their natal river. An alternative explanation for the pattern observed in the Magaguadavic River is that because large rivers, such as the Magaguadavic, can act as magnets for strays (Hindar 1992; Heggberget et al. 1993), they attract disproportionate numbers of farmed escapees even from distant sites.

The timing of salmon runs into rivers has generally evolved to be in synchrony with natural flow or temperature regimes that favour success of the wild stock (reviewed in Fleming 1996). A change in the timing of river ascent could therefore have potentially serious implications if it introduced the population to adverse conditions. Farmed salmon often enter rivers later than wild salmon (Lund et al. 1991; Carr et al. 1997*a*; Lund 1998), and this appears to be related to a lack of juvenile experience with the river resulting in delayed entry (Jonsson et al. 1990; Fleming et al. 1997). In the Magaguadavic River, most wild fish enter the river in July and August, whereas farmed salmon usually enter the river later in September–November (Carr et al. 1997*a*; Whoriskey et al. 1998). Year-to-year changes in farmed salmon timing apparently reflect the occurrence of storms and escapes from sea cages. For example, a large number of escaped farmed fish of similar size and age (one-sea-winter) entering the river in a two-week period in 1994 coincided with severe storms in early September; this was again reflected in a large number of two-sea-winter fish entering the river early (July) the following year. Asynchrony in run timing between wild and farmed fish could result in a high degree of type-assortative mating, where interbreeding between farmed and wild fish is uncommon (Webb et al. 1991). On the other hand, delayed spawning by farmed salmon may result in the overcutting of redds built earlier by wild fish which would have a negative impact on their survival (Lura and Sægrov 1991; Webb et al. 1991). However, delayed river entry by farmed fish does not necessarily translate into delayed spawning relative to wild fish (Lura and Sægrov 1993; Fleming et al. 1996). Rather, spawning time may be more of a reflection of genetic differences between populations due to adaptation to climatic and river temperature regimes (reviewed in Fleming 1996). For example, escaped farmed salmon in southern Norway often appear to spawn before wild salmon while further north the opposite situation occurs. This appears to reflect the origin of most Norwegian farmed salmon from rivers in the mid-western regions of the country.

The migratory behaviour of escaped farmed salmon upon river entry appears quite variable among regions and seldom matches exactly that of the local wild salmon. In Norway, farmed salmon have been shown to migrate upriver as quickly as wild salmon and distribute themselves further upriver (Økland et al. 1995; Heggberget et al. 1996; Thorstad et al. 1998). The farmed females are also less stationary in a particular section of river during the breeding season than are wild females (Økland et al. 1995). This latter observation may reflect lack juvenile experience within the river (Jonsson et al. 1990) and/or inferior competitive ability (Fleming et al. 1996). In contrast to the observations from Norway, escaped farmed salmon in the River Polla, Scotland, were distributed further downstream than wild salmon during spawning (Webb et al. 1991, 1993*a*). This, however, does not appear to be a general pattern as considerable overlap exists in the spawning distribution of farmed and wild fish within other Scottish rivers (Webb et al. 1993*b*). Tracking studies from the Magaguadavic River, New Brunswick, also contrast with previous observations, suggesting that most escaped farmed salmon are relatively inactive after entry into fresh water compared to wild salmon and often remain in the lower reaches of the river (Carr et al. 1997*b*). The cumulative distances travelled by farmed salmon during the natural spawning period are about one-third of those of wild salmon, and most farmed fish do not migrate up to the spawning areas but hold positions in pools relatively close to the estuary (Carr 1995). Unlike the wild fish, they fail to move back downstream or exit the river after the spawning period (cf. Thorstad et al. 1998). Some of the tagged escapees from farms overwintered in fresh water and were captured by anglers the following spring (J. Carr, Atlantic Salmon Federation, St. Andrews, pers. comm.). It is not known if these farmed fish resumed feeding in fresh water or if they eventually matured and spawned the year after entry, but their continued presence in the river has important ecological implications. They represent new competitors and potential predators and, in large numbers, could alter the trophic dynamics of the system.

The potential effects of effluent from salmon hatcheries on the movements of migrating wild fish have not been considered. Migrating salmon are known to be attracted to pheromones and population-specific odours (Solomon 1973; Groot et al. 1986). Thus plumes at the outlets of salmon hatcheries could act as attractants, disrupting natural migration patterns of wild salmon and ultimately, affecting spawning behaviour. This remains speculative, as we are unaware of any studies documenting or refuting such effects on wild salmon. However, some of the tagged farmed escapees entering the Magaguadavic River were tracked to the outlet of two of the hatcheries on the river indicating the possibility of an attraction (J. Carr, Atlantic Salmon Federation, St. Andrews, pers. comm.). The potential effects of freshwater cage sites for grow-out of farmed smolts and post-smolts (e.g., in the Kennebecasis River where it enters the Saint John River) on the behaviour of migrating wild adult salmon should be considered.

Spawning

The vast majorities of escaped farmed fish that enter rivers along the East Atlantic coasts mature and spawn the same year (Webb et al. 1991; Lund 1998). This appears to contrast sharply with observations from the Magaguadavic River. While some of the farmed fish do mature and spawn the same year (e.g., farmed females contribute more than half of redds sampled in the river), the majority of escaped farmed salmon are immature upon river entry (Carr et al. 1997*a*). An absence of change in gonadal steroids from basal levels either during or after the spawning period in the majority (85%) of escaped adult farmed salmon entering the river indicates that these fish will not spawn later during the year of entry into fresh water (Lacroix et al. 1997). However, other farmed salmon showing signs of maturation usually have steroid profiles similar to those measured in wild salmon over the period of migration and spawning indicating that they can interbreed. Also, many (24%) farmed post-smolts entering the river after only one summer at sea are early maturing anadromous males (a pattern seldom observed in wild populations; Hutchings and Jones 1998), and high levels of androgens in these fish throughout the spawning period indicates that they can also successfully interbreed with wild fish (Lacroix et al. 1997). With the expansion of brackish water sites (e.g., in the Magaguadavic River estuary; Chang 1998), the frequency of escaped farmed salmon returning to the Magaguadavic River as post-smolts and of sexually precocious anadromous males have increased considerably (Carr and Whoriskey 1998). These may compete directly with wild males during spawning and could contribute significantly to genetic interactions.

It is now well established that escaped farmed salmon can spawn successfully in the rivers they enter (Lura and Sægrov 1991; Webb et al. 1991; 1993*a*; Lura and Økland 1994). Evidence from semi-natural breeding experiments, however, indicates that the breeding performance (measured from mate and territory acquisition to egg deposition and fertilisation to egg survival) of farmed salmon can be significantly inferior to that of wild salmon (Fleming et al. 1996; Berejikian et al. 1997). Reproductive inferiority relative to wild conspecifics appears to be a pattern common to cultured fish, having also been observed to a lesser degree in sea-ranched/hatchery fish (Leider et al. 1990; Jonsson et al. 1991; Fleming and Gross 1993; Fleming et al. 1997). The breeding performance of farmed salmon appears to be positively related to the length period from escape until spawning, i.e., fish that escape early show better performance than those that escape shortly before spawning (Fleming et al. 1996, 1997). In addition to such environmental effects of farming on breeding performance, there are also likely to be genetic effects associated with the number of generations the fish have been cultured, though this has never been tested directly. Farmed fish can be competitively inferior to wild fish during spawning (Fleming et al. 1996; Berejikian et al. 1997), and this effect is likely to be density-/sex ratio-dependent as has been observed in sea ranched/hatchery fish (Fleming and Gross 1993; Fleming et al. 1997). The competitive and reproductive performance of cultured fish appears to decline as the intensity of competition for breeding resources increases (e.g., density increases or the sex ratio becomes more male-biased). This suggests that healthy, dense spawning populations of wild fish will be more resistant to intrusions by farmed fish than populations already in a poor state. The competitive inferiority of farmed fish also appears to be sex-biased, i.e., farmed females perform significantly better than farmed males (Fleming et al. 1996; Berejikian et al. 1997). This suggests that much of the gene flow that will occur between farmed and wild populations will involve farmed females and wild males. However, in populations such as in the Magaguadavic River where there is a high incidence of early maturing anadromous farmed males that have escaped as post-smolts from estuarine cages and where parr escape from commercial hatcheries and some male parr may mature, farmed males may contribute more to the gene flow than farmed females. There is also evidence that the culturing of Atlantic salmon alters female egg traits, resulting in the production of more, but smaller eggs (Jonsson et al. 1996), which may affect subsequent juvenile survival. Results from a controlled release of genetically-tagged farmed and wild fish into a natural river appear to confirm many of the above findings. Most of the fitness differences between farmed and wild fish appear to manifest themselves during spawning and early juvenile rearing and less so during later life history stages (Fleming, Mjølnerud, Hindar and Jonsson, unpubl. data; see also McGinnity et al. 1997).

There is little evidence to date of farmed salmon directly disrupting spawning by wild salmon (Fleming et al. 1996; Berejikian et al. 1997; Fleming, Mjølnerud, Hindar and Jonsson, unpubl. data). While farmed and wild males may compete for spawning females, there is little indication that this affects fertilisation rates or the performance of females. Occasionally, farmed males do exhibit inappropriate spawning behaviours that can lead to a reduction in fertilisation success of a female's eggs when no wild males are involved in the spawning event (Fleming et al. 1996). This, however, is unlikely to occur often given the superior competitive abilities of wild males and abundance of wild, early maturing male parr in most salmon rivers. The most likely negative ecological interaction during the breeding season will be the destruction of early nests by later spawning females (Lura and Sægrov 1991; Webb et al. 1991; Fleming et al. 1996). In this case, the relative spawning time of farmed to wild females, which can vary considerably among populations as discussed above, will be a critical determinant of the impact. In the Magaguadavic River, where the gonadal steroid profiles of maturing wild and escaped farmed salmon are in synchrony (Lacroix et al. 1997), the potential for destruction of nest by late spawners is minimal.

While interactions between farmed and wild fish during breeding may have minimal immediate ecological effect on wild populations (depending on relative spawning times), they are of considerable importance in terms of genetic interaction (i.e., gene flow) and subsequent ecological interaction the next generation. Successful breeding and interbreeding by farmed salmon will generate pure farmed and hybrid (farmed-x-wild) offspring that will compete directly with wild offspring the next generation. These latter genetic and ecological interactions may profoundly affect the productivity of wild populations. For example, the change in ratio of multi-sea-winter fish to one-sea-winter fish returning to spawn in the Magaguadavic River (from 2:1 to 0.4:1 over the past decade, Carr et al. 1997*a*) has greatly decreased total egg deposition within the river and is of prime importance to the dynamics of the population (Lacroix et al. 1998). The reasons for this change are unknown, but the possibility that it is the outcome of ecological and genetic interaction with farmed fish over the past two decades should not be ignored. Age- or size-specific change in marine survival is another possible cause for the change in sex ratio.

Juveniles and Smolts

Interactions among wild, farmed and hybrid juveniles in fresh water are likely to result via two main mechanisms: (1) escape from freshwater rearing stations/hatcheries; and (2) the successful spawning and production of offspring by farmed salmon. The possibility that juvenile salmon of farmed origin escape between the fry and smolt stages from hatcheries into rivers with wild stocks of salmon has generally been ignored. Yet, many hatcheries that supply smolts to salmon farms in the Maritimes are located on salmon-producing rivers (see Fig. 2).

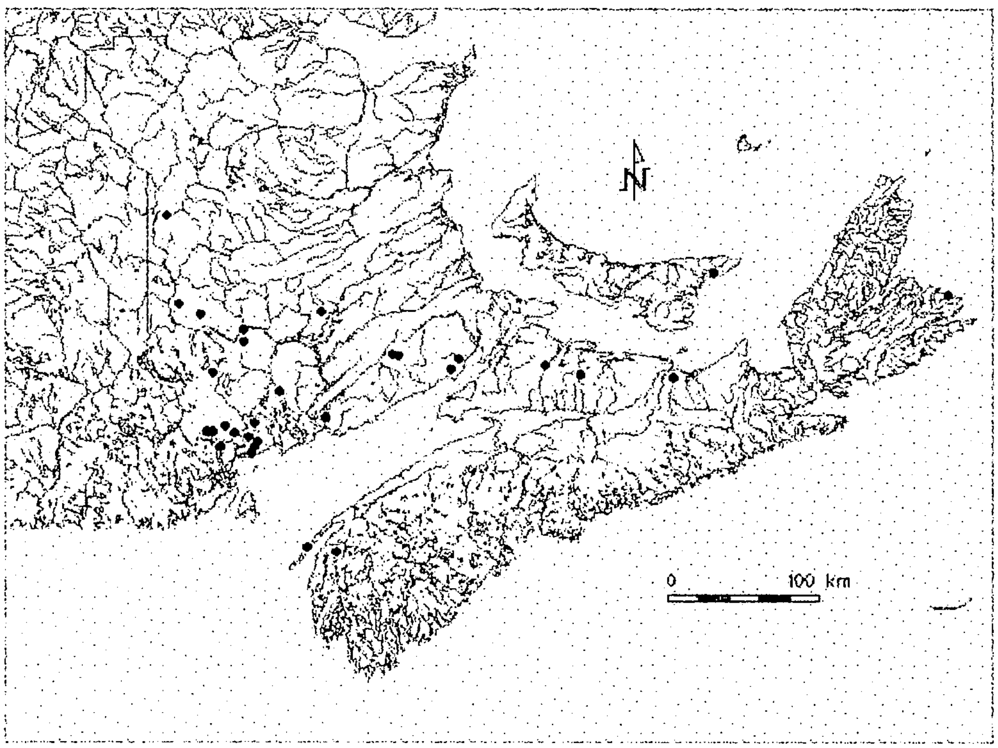

Figure 2. Map of the Maritime Provinces showing the location of commercial hatcheries/fish culture stations that produce Atlantic salmon smolts for aquaculture. Rivers that support wild salmon stocks are shown.

Many of these rivers have historical runs of wild salmon and support juvenile salmon populations. Three of the largest hatcheries are located along the Magaguadavic River. Together, these produce in excess of two million smolts annually which represents almost one third of the total smolt production for cages in Southwest New Brunswick. Recent studies on that river indicate that large numbers of juvenile salmon escape from hatcheries into the river (Stokesbury and Lacroix 1997; Whoriskey et al. 1998). Similar situations have also been observed in other nearby rivers with hatcheries (e.g., the Waweig River, G. Lacroix, unpubl. data). Often these fish escape as young fry soon after first feeding, but they also appear to enter the river as parr too small to be one-year-old smolts. These introduced fish then remain in the river for one or more years before they smoltify. On occasions, smolts appear to enter the river from hatcheries and, if the timing is right, they will emigrate directly. Smolts of hatchery origin in the Magaguadavic River are younger and much larger than wild smolts (Stokesbury and Lacroix 1997).

The size advantage of cultured juveniles is a general phenomenon, because rapid growth and early smolting are goals of smolt production facilities for farmed salmon (e.g., Gjedrem et al. 1988; Glebe 1998). As a result, the synchrony of juvenile life history stages in hatcheries is accelerated relative to that in the wild: eggs hatch in January, more than 3 months earlier than in the wild; fry emerge and start feeding in February and are already larger than 5 cm by the time fry emerge from redds in the wild (cf. Lacroix 1985). At any time, parr of a given age that escape from hatcheries are much larger than their wild counterparts (Table 1). Hatchery fish will be ready to smoltify by March–April as large one-year-old fish compared to the smaller two- and three-year-old wild smolts that migrate in April–June (Stokesbury and Lacroix 1997). This imparts a very large size advantage to fry, parr and smolts that escape from hatcheries over that of native fish, and could give the escaped hatchery fish a competitive advantage over wild fish that lasts throughout freshwater residence (Stokesbury and Lacroix 1997). Moreover, the presence of new size classes of fish, different from those normally observed in wild populations, could thereby alter the competitive balance between age classes.

Table 1. Comparison of the timing of life history events and of the range of sizes at a given time for Atlantic salmon from the wild population in the Magaguadavic River in Southwest New Brunswick and from a commercial hatchery on that river.

	Wild	Hatchery
Spawning	Nov.–Dec.	Nov.–Dec.
Hatching	April	January
Emergence/first feeding	June	February
Age-0 parr length (cm)		
June 1	3–4	6–9
August 1	4–5	10–14
October 1	5–6	11–22
Smolt age (yr)	2–3	1
Smolt length (cm)	12–19	14–35

Successful spawning by farmed salmon in rivers will lead to the production of farmed and hybrid (farmed-x-wild) offspring that will compete directly with pure wild offspring. The outcome of this interaction will depend partly on the performance (e.g., growth, competitive ability and survival) of farmed and hybrid offspring in the river. Under artificial rearing conditions, fish of farmed/hatchery origin typically outgrow those of wild origin (e.g., Reisenbichler and McIntyre 1977; Johnsson et al. 1993, 1996; Einum and Fleming 1997). In the specific case of farmed fish, this appears to be both a function of the original origin of the fish prior to domestication and adaptation to the culture environment through intentional and unintentional domestication selection (Fleming and Einum 1997). The growth advantage of farmed over wild juveniles has also been found under natural river conditions in Norway (Einum and Fleming 1997) and Ireland (McGinnity et al. 1997), however, farmed juveniles may suffer higher mortality, particularly during early life (McGinnity et al. 1997). Interestingly, the growth results contrast with findings on hatchery/sea-ranched fish, which suffer a growth disadvantage relative to wild fish under natural conditions (Reisenbichler and McIntyre 1977). Unlike the hatchery/sea-ranched fish, the farmed fish have undergone intense, directed selection for growth. An increase in mortality of farmed relative to wild juveniles in a river was observed and found to be confined mostly to the earliest life stages (McGinnity et al. 1997). Little or no difference in survival between wild and farmed parr was found at later stages (Einum and Fleming 1997; McGinnity et al. 1997; Fleming, Mjølnerud, Hindar and Jonsson, unpubl. data). It is during the early period that overall mortality of salmon is high and, thus, there is ample opportunity for differential survival. There are clear, consistent differences in behaviour of cultured and wild juveniles (e.g., response to predation risk; Johnsson and Abrahams 1991; Berejikian 1995; Johnsson et al. 1996; Einum and Fleming 1997; Fleming and Einum 1997) that would lead to such a result. This suggests that there may be fewer but larger farmed juveniles than wild ones in the F_1 generation (of course, this also depends on relative numbers farmed and wild spawners).

The offspring of farmed-x-wild matings (hybrids) could exhibit either poorer (outbreeding depression), intermediate (blending of traits) or superior (hybrid vigour/heterosis) performance in nature relative to farmed and wild juveniles. Findings by Einum and Fleming (1997) working with farmed and two native Norwegian salmon populations indicate that hybrid juveniles are behaviourally intermediate between farmed and wild juveniles. Similarly, McGinnity et al. (1997) observed the survival of hybrid juveniles to be intermediate, though generally not significantly different from that of wild juveniles. Growth performance of hybrid parr, however, has been found to be either intermediate (McGinnity et al. 1997) or superior (Fleming, Mjølnerud, Hindar and Jonsson, unpubl. data) to that of farmed and wild parr, appearing to reflect differences in environmental conditions (Einum and Fleming 1997). These findings suggest that the parr of wild parents will be competing for resources with the larger parr resulting from pure farmed and hybrid matings.

Competition for food and space may result from the interaction among farmed (either escaped hatchery juveniles or offspring from spawning), hybrid and wild juveniles. Territorial and social dominance behaviour in salmonids, as a result of interactions between species or between cultured and native fish, can affect both mortality and growth (e.g., Fausch and White 1986; Swain and Riddell 1990; Einum and Fleming 1997). The intensity and form of intraspecific competition may be altered when salmon from different populations that have not co-evolved interact, resulting in deleterious consequences as suggested by Fausch (1988) for interspecific competition. For example, cultured (hatchery and farmed) juveniles are known to show innate differences in aggressive behaviour and dominance relative to wild juveniles. Several studies have recorded higher levels of aggression and/or dominance in cultured fish (Moyle 1969; Swain and Riddell 1990; Einum and Fleming 1997), while others have noted the opposite (Ruzzante and Doyle 1991; Berejikian et al. 1996). These equivocal results (Ruzzante 1994) may be explained by the context-dependent nature of aggression and dominance, with cultured juveniles dominating over wild juveniles in one type of environment (e.g., pools) and the vice versa in another type of environment (e.g., riffles; Fleming and Einum 1997; see also Berejikian et al. 1996). It should be noted that any advantage that cultured fish have in terms of aggression and dominance would often be tempered by a disadvantage from lack of prior residence. The prior residence effect, whereby interactions between residents and intruders are more commonly won by the resident (Maynard Smith and Parker 1976), has been well-documented in salmonid fishes (e.g., Fausch and White 1986; Metcalfe and Thorpe 1992; Brännäs 1995; Huntingford and Garcia DeLeaniz 1997). This advantage, however, declines and is eventually overcome as the size of the intruder relative to the resident increases (Johnsson and Bohlin, unpubl. data). On the other hand, if the offspring of farmed salmon in rivers emerge earlier because their parents had spawned earlier, prior residence is likely to compound their size advantage. All of the above factors are likely to influence the outcome of competition for resources and ultimately, the productivity of the native population.

Displacement of native fish by larger, more aggressive farmed fish, both escaping from hatcheries and offspring of farmed spawners, can result in shifts in habitat use and increased mortality (Nickelson et al. 1986; McGinnity et al. 1997). The appearance of large numbers of farmed juveniles in a stream may reduce productivity of the native population because of density-dependent reductions in growth and survival rates (Nickelson et al. 1986; Heggberget et al. 1993; Flagg et al. 1995). This would be increased by the presence of fish that escape at the fry stage or are the offspring of farmed spawners because competition, after fry emerge from redds and densities are highest, can play an important role in population dynamics (Hearn 1987). An increase in hatchery fish of farmed origin in streams could intensify scramble and interference competition and result in reduced food availability to wild salmon in the same stream (Krueger and May 1991). Mature male parr competition for spawning opportunities within the river may also be altered if many of the farmed and hybrid male parr mature. The intensity of competitive interactions between wild and farmed fish will be a function of their relative densities.

Predator–prey relationships may be altered by the presence of large numbers of farmed fish in streams. Many species (fish, birds, and mammals) prey on Atlantic salmon throughout their life cycle. Flooding an area with large numbers of hatchery/farmed fish may provide native fish with a "safety in numbers" refuge from predators, but it could also attract predators and increase juvenile mortality (Ivlev 1961), especially if hatchery-reared fish were easy prey (Järvi and Uglem 1993). This would be important during the smolt migration when some schooling behaviour occurs, especially given the large numbers of large, farmed smolts escaped/released from hatcheries into streams (hatchery fish consistently make up > 60% of the smolt run in the Magaguadavic River: Stokesbury et al. 1997; Whoriskey et al. 1998). Predatory feeding rate should increase more rapidly at high than at low prey densities because of search image reinforcement and decreased availability of prey hiding places (Ivlev 1961; Ricklefs 1979). As a result, mortality of wild salmon near the source of hatchery escape or during the smolt migration could increase. The much larger hatchery fish also could outcompete the native fish and drive them from good cover (Riddell and Swain 1991), subjecting the latter to a higher rate of predation. There is little evidence for predation on wild fish species by juvenile Atlantic salmon in fresh water, other than the predation of eggs by mature male parr at the time of spawning (Ouellet 1977). The high proportion of precocious male post-smolts in the escaped farmed fish that enter the Magaguadavic River could lead to increased predation of wild salmon eggs from redds during spawning and further reduce the survival of the wild stock.

Alteration of natural predator–prey and competitive balances in rivers by the escape, release or natural breeding of large numbers of farmed juveniles can potentially be harmful to native populations. More research is clearly needed on the effects of competition and predation on native fish at different stages in fresh water.

Interactions in the Marine Environment

Migrations

A variety of ecological interactions between farmed and wild fish can occur in the coastal marine environment resulting in impacts that could act to reduce marine survival of wild stocks from rivers within the aquaculture area as well as further afield. Wild salmon smolts and post-smolts emigrating from rivers of Passamaquoddy Bay into the Bay of Fundy on their way to feeding grounds in the North Atlantic Ocean or adults returning on their spawning migration must navigate through areas where they come in close proximity to large numbers of cage sites around the Fundy Isles and high densities of salmon in captivity (see Fig. 1). For some populations (e.g., from the Magaguadavic River), this may expose the fish to a diversity of potential hazards stretching over many kilometres. These include the transmission of diseases and parasites from farmed to wild fish (MacKinnon et al. 1998; McVicar 1998; Olivier and MacKinnon 1998), an increased potential for predation by seals and other species attracted to cage sites by the salmon and/or food supply (Bailey 1998), and a potential for exposure to hazardous chemicals used to treat farmed fish or cages (Roth and Sommerville 1993; Zitko 1994).

Delay or displacement of smolts and post-smolts from their normal migration would increase their vulnerability to predators and result in an increase in early marine mortality. The possibility that the presence of feed or of large concentrations of conspecifics attract migrating post-smolts (odour or pheromone hypothesis; see Freshwater Migration) was examined in recent tracking studies of post-smolts emigrating from the Magaguadavic and St. Croix rivers in Passamaquoddy Bay (Lacroix 1996; Voegeli et al. 1998). Regardless of river of origin, the post-smolts migrated through Passamaquoddy Bay and rapidly passed by the many cage sites along their migration route (see Fig. 1). They did not congregate near cages nor were they delayed by the presence of cages with salmon either in their departure from the river estuary (i.e., by brackish cage sites in the Magaguadavic River) or during their passage from Passamaquoddy Bay into the Bay of

Fundy (i.e., by marine cage sites). Mortality over a period of 5–10 days when fish moved through Passamaquoddy Bay was 12% for 48 fish tracked emigrating from the St. Croix River and 29% for 48 fish tracked from the Magaguadavic River (Lacroix 1996). Post-smolts from the Magaguadavic River migrated counter-clockwise in Passamaquoddy Bay and passed by more cage sites than fish from the St. Croix River, which migrated straight out. Most of the early post-smolt mortality is considered to be from predation (Lacroix and McCurdy 1996), and predators potentially attracted to cage sites may have been responsible for the high mortality of post-smolts from the Magaguadavic River. The study did not follow up on the possibility or rate of disease or parasite transmission and their subsequent impact on the post-smolts once out at sea when the pathology would manifest itself. For example, even at high infection intensity, salmon lice must reach their pre-adult stages before they cause the death of Atlantic salmon post-smolts (Grimnes and Jakobsen 1996). Sea louse epidemics spread through the salmon farming industries in Canada and Europe during the 1990s (McVicar 1998), and this could have had an unseen impact on wild salmon post-smolts exposed to infective copepodids of the sea louse.

We are unaware of work on the potential effects of the concentration of cage sites on the migratory behaviour and homing success of wild salmon returning to rivers. This likely reflects the difficulty of undertaking such a study, in part, because there are seldom base line data prior to the initiation of cage culture and moreover, it is difficult to establish "controls". The best approach may be to compare several affected and unaffected populations, where hopefully other effects become randomised. A decrease in the proportion of returning salmon that enter their natal rivers would have serious implications to population maintenance in a river. Predators such as seals are apparently attracted to cage sites and have been identified by the industry as the prime factor responsible for the escape of farmed salmon from cages (Bailey 1998). Seals could also have an impact as predators of adult salmon migrating by the many cage sites on their return to rivers to spawn. The transmission of diseases and parasites from cage sites to wild salmon migrating through areas with high cage site densities during their spawning migration should also be of concern (McVicar 1998; Olivier and MacKinnon 1998). For example, the incidence of sea louse infestations or an increase in the numbers of lice on wild salmon and sea trout entering some rivers has increased in recent years in Europe and Canada (Birkeland 1996; Whelan and Poole 1996; Whoriskey et al. 1998; P. Amiro, Department of Fisheries and Oceans, Halifax, pers. comm.; B. Finstad, pers. comm.).

As the Canadian aquaculture industry has expanded and the number of sites and farmed fish increased, more farmed fish have escaped to the marine environment (Carr et al. 1997*a*; Bailey 1998; Chang 1998). This parallels what occurred earlier in Norway during the rapid expansion of the farming industry (Lund et al. 1991; Lund 1998). A continued increase in abundance of farmed salmon in coastal areas may attract predators such as seals, which could increase pressure on the wild stocks. The high densities of escaped farmed salmon remaining at large may also condition predators to prey on salmon through image reinforcement. This has been postulated as a potential factor indirectly contributing to the loss of the inner Bay of Fundy salmon (Amiro 1998*a*, 1998*b*). An increase in the numbers of escaped farmed fish could further increase their dispersal to rivers outside of the immediate aquaculture area and introduce ecological interactions to other populations (see O'Neil 1998 for observed distribution of escapees in the Maritimes).

Salmon from the Saint John River have been used almost exclusively as broodstock for salmon farming in New Brunswick (Glebe 1998). As a result, farmed salmon in New Brunswick are considered to be genetically closely related to salmon endemic to rivers in the immediate area of aquaculture (Verspoor 1997; Glebe 1998). This may reduce some potential genetic impacts of interbreeding with salmon of non-indigenous origin (e.g., influx of mal-adaptive genes), but the similarities in life history (e.g., spawning time, migration, breeding behaviour) result in increased ecological interaction and interbreeding (Fleming 1995; Lacroix et al. 1997, 1998). Dispersal of escaped farmed salmon does increase the possibility that they will interbreed with native stocks that show very different reproductive strategies and migration routes than the farmed stock (e.g., salmon of the inner Bay of Fundy rivers; Amiro and Jefferson 1998). This could result in serious ecological impacts as shown by the failure of past attempts to introduce non-native stocks with different migration characteristics to inner Bay of Fundy rivers (Ritter 1975; Jessop 1975, 1976).

Post-smolt and Adult Survival

The larger size of farmed smolts, particularly those escaped from hatcheries but also those that are offspring of farmed spawners and have grown in the river (also hybrid offspring), could influence the early marine survival of post-smolts. The larger smolts may benefit from greater early marine survival (Ward and Slaney 1988). Their greater return as spawners would then accelerate the rate of extinction of native genomes (Hutchings 1991; Lacroix et al. 1998). However, the nature of this smolt size–adult survival relationship remains uncertain, and the opposite may also occur (i.e., reduced overall return for large hatchery smolts because of domestication leading to reduced returns to rivers; Ritter 1977). Effectively, interbreeding would then result in offspring that go out to sea and never return, thereby greatly diluting the natural reproductive success of wild stock. However, preliminary results from a study in Ireland suggest that while the survival and homing of farmed salmon at sea is less than that of hybrid (farmed-x-native) and pure native salmon, that of the latter two groups appears similar (McGinnity et al. 1997). Furthermore, results from a study in Norway where genetically-tagged native and farmed adult salmon were released indicate little difference in the marine survival of their native, farmed and hybrid offspring or in the proportion of returning salmon that enter natal rivers (Fleming, Mjølnerud, Hindar and Jonsson, unpubl. data).

There is a possibility that some distant salmon stocks (e.g., from inner Bay of Fundy rivers) remain within the Bay of Fundy and migrate to the Fundy Isles area (where cage sites are concentrated) during their marine stage (Jessop 1976; Amiro 1998). These post-smolts and adults would then become exposed to a variety of potential interactions with farmed fish that could reduce their marine survival (Amiro 1998*a*, 1998*b*)). These include the potential transfer of diseases and parasites to the wild stocks, a high predation rate on the wild stocks by seals and other predators that congregate in the aquaculture areas, and competition with escaped farmed fish for food.

Little is known about the behaviour of salmon immediately after they escape from sea cages and most studies have addressed this issue indirectly or with simulated releases and tag returns

(Eriksson and Eriksson 1991; Hansen and Jonsson 1991; Heggberget et al. 1991). Yet, more detailed knowledge of behaviour after escape from sea cages is required if effective mitigative measures are ever to be applied successfully. Escaped farmed fish are reported to remain near their cages for a period from several hours to several weeks (Carss 1990). A similar site fidelity has been observed for farmed steelhead trout released from sea cages in Bay d'Espoir, Newfoundland (R. Booth, Lotek Marine Technologies Inc., St. John's, pers. comm.). Some escaped fish are probably lost to predators during this time, others migrate to fresh water, but the majority of escaped fish potentially remain in the marine environment (Hansen et al, 1987*a*, 1987*b*; Hansen and Jonsson 1991; Lund et al. 1991). The large difference between the numbers of salmon that escape and the numbers that show up in rivers would indicate that the majority remains at sea. The presence of large numbers of escaped farmed salmon at large in the coastal marine environment could increase competition with smolts and post-smolts for available resources. After smoltification and entry into the marine environment, post-smolts have a low condition factor and probably need access to a food supply along their migration. The presence of many large salmon in the same coastal environment could lead to increased competition for food. Marine recoveries of escaped Atlantic salmon suggest that an unknown number of fish, particularly immature post-smolts, move into offshore feeding areas (Hansen et al. 1993, 1997*a*, *b*). Escaped fish that migrated to the traditional feeding grounds used by Atlantic salmon in the Bay of Fundy or North Atlantic (Reddin and Friedland 1993) could increase competition for food in the marine environment and result in reduced body sizes and abundance of wild populations.

The marine behaviour of escapees probably is partly a function of the life stage and time of year at which they escape. Maturing adults would presumably behave differently than post-smolts or immature one-sea-winter fish. However, many non-maturing adult escapees (post-smolts and one-sea-winter fish) have been found to migrate to the Magaguadavic River and enter fresh water soon after they escaped from farms in Passamaquoddy Bay (Carr et al. 1997*a*; Lacroix et al. 1997). This behaviour, typical of the migration of maturing wild salmon, is unusual for salmon that will not mature in the year of entry into fresh water. Some escaped farmed salmon captured at the mouth of the Magaguadavic River and transported and released back in the marine environment, at sites up to 48 km away from the river mouth, returned back to the Magaguadavic River (22% of 144 displaced fish returned; Whoriskey et al. 1998). This "homing" affinity for the river increased after fish were displaced a second and third time. This behaviour suggests that they either had some initial affinity to that system, i.e., they originated from hatcheries on the river, or acquired it after the first return. This introduces the possibility that rivers with hatcheries that produce smolts for the aquaculture industry may be much more vulnerable to the impact of escaped fish than rivers without hatcheries. Rivers with hatcheries also tend to be located in or near the area where sea cages are concentrated (see Figs. 1 and 2). This may partly explain why the Magaguadavic River, with the largest hatchery smolt production used for aquaculture, has apparently been acting as a magnet for escaped farmed fish.

The presence of high densities of farmed salmon in captivity in coastal areas and the large numbers of escaped farmed fish potentially at large in the marine environment could be detrimental to the success of wild salmon stocks. Their impact on the natural balance, e.g., predator–prey cycle, in the marine environment may prove to be as detrimental to wild populations as the direct interaction between wild and farmed fish. More research is clearly needed on the behaviour of farmed and wild salmon in the marine environment to evaluate the potential effects on both local and distant salmon stocks.

Summary

The documented and potential ecological interactions (direct and indirect) that we identified between farmed and wild Atlantic salmon in the freshwater and marine environments are summarised in Table 2. This includes an assessment of the degree of risk posed to the native stocks and the potential influence of density in mediating a response.

Table 2. Potential ecological interactions between farmed and wild Atlantic salmon (excluding disease and parasite transfer). Based on information from the East Atlantic with some input from the Maritime Provinces.

Interaction	*Has it been examined?*	*Has it been demonstrated?*	*What is risk to native stocks?*	*Is risk likely to be density-dependent?*
(1) Direct				
Competition in the ocean	No	---	Unknown	Unknown
Disruption of migration by interference	No	---	Unknown	Unknown
Disruption of breeding behaviour	Yes	No, but unknown for F_1 & later generations	Low	Yes, negative association
Nest superimposition	Yes	Yes	Medium	Yes, negative association
Competition for food and space in fresh water	Yes, mostly in the laboratory	Yes	High	Yes, negative association
Habitat displacement in fresh water	Yes, but indirectly	Yes, but appropriate controls lacking	High	Yes, negative association
(2) Indirect				
Altered predator-prey relations	Yes, evidence from hatchery releases	Yes	High	Unknown
Disruption of migration by cages and hatcheries	Yes	No	Unknown	No
Hybridisation	Yes, but only at the 1st generation	Yes	Medium-High	Yes, negative association

Management Considerations

- Review and revise containment codes and practices for sea cages and for hatcheries using a precautionary approach. Escapes of domesticated, farmed salmon into the environment must be reduced and releases must be eliminated.
- Require that information on escapes (e.g., date of escape, number, size and age of escapees) be a condition of the licence for farming salmon. There is a large data gap here.
- Enforce existing policy to prevent and eliminate the release of juvenile farmed salmon into rivers (conservation measure).
- Review and revise policy for the siting of salmon hatcheries that rear domesticated stock. Hatcheries should be located on rivers and bodies of waters that do not have a run of wild salmon to prevent interactions with wild stocks (precautionary approach). However, caution should be taken to avoid exposing other fish species to unnecessary threat.
- Prevent access of escaped farmed salmon to fresh water and to known spawning grounds for wild salmon, and remove escaped farmed salmon where possible (conservation measure).
- Review and revise policy for siting of aquaculture cages using a precautionary approach. The use of freshwater sites for grow-out should be eliminated and prevented in rivers with wild salmon stocks. The use of brackish water sites in estuaries with wild salmon stocks should be reviewed. The use of narrow passages around the Fundy Isles for cage sites should be reviewed, and suitable migratory corridors for wild salmon stocks should be maintained to reduce possibilities of predation and transfer of diseases and parasites.
- The density of cage sites allowed in any area used by wild salmon should be reviewed to reduce the potential for ecological interaction.
- The effectiveness of methods used for predator control (e.g., seals) at cage sites should be reviewed, and an appropriate management plan devised.

Research Recommendations

Very little research has been directed at determining the impacts of interactions between farmed and wild Atlantic salmon (Table 2), especially in the Maritime Provinces. Specific hypotheses related to the following questions need to be tested:

- Do interactions during the F_1 generation alter natural selection and survival of wild salmon? What are the determinants of gene flow between farmed and native salmon populations? What is the potential for reproductive interactions at the F_1 generation and what is the impact on genetic introgression?
- Do farmed salmon fry and parr escaped from hatcheries and offspring of farmed spawners (including hybrid offspring) competitively displace native salmon? What is the impact on the freshwater production of salmon?
- Do hatcheries, cage sites and farmed salmon at large alter the migratory behaviour or decrease the survival of native salmon? Do hatcheries, cage sites and farmed salmon at large increase the incidence of diseases and parasites or the mortality of native salmon? If so, what are the requirements for safe migratory corridors? There is a need to identify the migratory

routes and destination at sea of wild salmon stocks in the Bay of Fundy to determine cause-and-effect, and to effectively manage cage site location.

- Does the behaviour of escapees from marine cages differ from that of wild salmon? There is a need to understand the behaviour of farmed fish after they escape from sea cages to determine their role in disease and parasite transmission, changes in predator–prey balance, and to find solutions to eliminate reproductive interactions.
- Do predators such as seals and birds around cage sites prey on wild salmon migrating through aquaculture areas? There is a need to understand the behaviour of predators around cage sites, and to determine if cage sites increase the density of potential predators in an area.
- What are the mechanisms controlling wild salmon population and their genetic structure? Modelling studies are needed to understand the mechanisms of interaction and impact, to identify the important factors, and to evaluate management actions.

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