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Ecological impact assessment of the use of European-origin Atlantic Salmon in Newfoundland aquaculture facilities

D. Cote[1], I.A. Fleming[2], J.W. Carr[3], and J.H. McCarthy[1]

[1] AMEC, 133 Crosbie Road, St. John’s, Newfoundland and Labrador, Canada A1B 4A5

[2] Department of Ocean Sciences, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada A1C 5S7

[3] Atlantic Salmon Federation, PO Box 5200, St. Andrews, New Brunswick, Canada E5B 3S8

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Aquaculture companies operating along the south coast of Newfoundland have requested permission to use farmed European-origin Atlantic salmon in their operations to increase their competitiveness. Canada's National Code on Introductions and Transfers of Aquatic Organisms requires that a risk assessment be conducted in evaluating requests for importation or transfers of fish. This document examines the potential ecological risks that farmed European-origin Atlantic salmon and their hybrids present to native Atlantic salmon populations through competitive and predatory interactions, as well as disease transmission.

Based on many generations of selective breeding and very distinct origins, farmed European-origin Atlantic salmon are expected to have considerable genetic and phenotypic differences compared to native wild fish. These differences may cause negative impacts through interbreeding, disease transfer, or competitive interactions but the likelihood of these to occur is very much context-dependent and, therefore, difficult to predict. Escape events from aquaculture facilities are common and should be considered inevitable for farmed European-origin Atlantic salmon. Assuming escapes originate predominantly from the marine environment, most negative interactions will be dependent on the ability of farmed European-origin Atlantic salmon to mate with wild or farmed Atlantic salmon. Negative ecological interactions of these progeny can arise through direct competition with wild fish or through outbreeding depression (e.g., reduced disease resistance, etc.).

Known interactions of wild and farmed salmon along the south coast of Newfoundland are not widespread; however, relatively little effort has been put towards monitoring farmed-wild fish interactions relative to other areas where impacts have been documented. The declining abundance of wild stocks along the south coast, however, makes populations in these rivers more vulnerable to negative impacts.

Past decisions regarding the importation of farmed European-origin Atlantic salmon in eastern North America highlighted the lack of certainty regarding the extent and severity of farmed European-origin Atlantic salmon-wild salmon interactions as the primary reason for recommending against importation. Despite many advances in the understanding of wild–farmed interactions, the uncertainties associated with this issue remain large when paired with the potential magnitude of negative effects on imperiled wild stocks.

Évaluation de l’impact écologique de l'utilisation du saumon de l'Atlantique d'origine européenne dans les installations d'aquaculture de Terre-Neuve

RÉSUMÉ

Les entreprises d'aquaculture qui œuvrent le long de la côte sud de Terre-Neuve ont demandé la permission d'utiliser des saumons de l'Atlantique d'élevage d'origine européenne dans le cadre de leurs activités afin d'accroître leur compétitivité. Le Code national sur l'introduction et le transfert d'organismes aquatiques du Canada exige qu'une évaluation des risques soit menée lors de l’évaluation des demandes d'importation ou de transfert de poissons. Ce document examine les risques écologiques potentiels que présentent les saumons de l'Atlantique d'élevage d'origine européenne et leurs hybrides pour les populations indigènes de saumons de l'Atlantique lors de leurs interactions et vu leur concurrence avec les prédateurs, ainsi que dans l'optique de la transmission de maladies.

En raison de ses nombreuses générations d'élevage sélectif et de ses origines très distinctes, il devrait exister des différences génétiques et phénotypiques considérables entre le saumon de l'Atlantique d'élevage d'origine européenne et les poissons sauvages indigènes. Ces différences pourraient entraîner des effets négatifs au chapitre des croisements, de la transmission de maladies ou des interactions concurrentielles, mais la probabilité de ces interactions dépend en très grande partie du contexte et, par conséquent, est difficile à prédire. Les évasions à partir d'installations aquacoles sont communes et devraient être considérées comme inévitables pour le saumon de l'Atlantique d'élevage d'origine européenne. En supposant que les évasions proviennent principalement de l'environnement marin, la plupart des interactions négatives dépendront de la capacité des saumons de l'Atlantique d'élevage d'origine européenne à se reproduire avec les saumons de l’Atlantique sauvages ou d'élevage. Les interactions négatives de cette progéniture avec leur écologie peuvent survenir en cas de compétition directe avec les poissons sauvages ou de dépression endogamique (p. ex., affaiblissement de la résistance à la maladie, etc.).

Les interactions connues entre les saumons sauvages et d'élevage le long de la côte sud de Terre-Neuve ne sont pas généralisées; toutefois, relativement peu d'efforts ont été déployés pour surveiller les interactions entre les poissons d'élevage et les espèces sauvages par rapport à d'autres zones où des impacts ont été répertoriés. Cependant, la diminution de l'abondance des stocks sauvages le long de la côte sud rend les populations dans ces rivières plus vulnérables aux impacts négatifs.

Les décisions antérieures concernant l'importation de saumons de l'Atlantique d'élevage d'origine européenne dans l'est de l'Amérique du Nord soulignaient le manque de certitude quant à l'étendue et à la gravité des interactions entre le saumon de l'Atlantique d'élevage d'origine européenne et le saumon sauvage comme raison principale pour justifier la recommandation d'interdire cette importation. Malgré de nombreux progrès dans notre compréhension des interactions entre les poissons sauvages et d'élevage, les incertitudes associées à cette question demeurent importantes, surtout considérant l'ampleur potentielle des effets négatifs sur les stocks sauvages mis en danger.

BACKGROUND/RATIONALE FOR WORK

Canada’s aquaculture organizations have expressed considerable interest in gaining access to better-performing Atlantic salmon broodlines to increase Canadian aquaculture industry competitiveness. In particular, aquaculture companies operating along the south coast of Newfoundland have requested permission to use farmed European-origin Atlantic salmon in their operations. Canada’s National Code on Introductions and Transfers of Aquatic Organisms requires that a risk assessment be conducted in evaluating requests for importation or transfers of fish. To date, such requests have been denied, in part, due to the uncertainty surrounding the potential for ecological and genetic risks that escapees from farms could pose to wild Atlantic salmon and their habitat. An increased understanding and characterization of these risks is needed to help inform management on policy direction and/or decision-making and on possible mitigation measures that may alter risk profiles.

This document examines the potential ecological risks that farmed European-origin Atlantic salmon and their hybrids present to native Atlantic salmon populations in native river systems and marine habitats on the south coast of Newfoundland. Other important elements of this general assessment are covered in complimentary contributions and address the potential impacts of genetic introgression (Verspoor *et al.* 2015) and the measures available to mitigate impacts (Benfey 2015; Bridger *et al.* 2015).

Ecological risks focused on in this report include those related to competitive and predatory interactions as well as the consequences of disease transmission and consider how these interactions could be mediated by the presence of farmed European-origin x wild Atlantic salmon hybrids. The document will review existing knowledge of farmed European-origin Atlantic salmon impacts in North America, derived from historical interactions along the coast of Maine and the Bay of Fundy. It will then summarize the extensive literature of general farmed escapee impacts on wild Atlantic salmon, followed by a characterization of the proposed farmed European-origin Atlantic salmon broodstock and receiving environment along the south coast of Newfoundland. This information will be used to assess potential impacts of escapees and hybrid progeny on wild conspecifics through pathways of competition, disease transmission, reproduction, displacement, and predation. Finally, data gaps will be identified and scientific conclusions provided. Potential impacts of farmed European-origin Atlantic salmon on wild stocks will often be illustrated through comparisons with known effects of native-origin cultured Atlantic salmon and differences between farmed North American-origin Atlantic salmon and farmed European-origin Atlantic salmon. It is important to emphasize that farmed European-origin Atlantic salmon impacts on wild populations should be considered in absolute terms rather than relative to the impacts of farmed North American-origin Atlantic salmon.

EXISTING INFORMATION ON EUROPEAN-ORIGIN SALMON IN ATLANTIC CANADA

Wild populations of Atlantic salmon in North America are highly distinct from their wild European counterparts (King *et al.* 2001; Spidle *et al.* 2003; O’Reilly *et al.* 2006; Bourret *et al.* 2012) due to over half a million years of geographic isolation (King *et al.* 2007). Nonetheless, Atlantic salmon with European ancestry have been used in North America since the mid-1980’s, as eggs of several European strains (including those from Norway, Scotland, Iceland, and Finland) were imported for aquaculture in Maine (Baum 1998; Glebe 1998). By the mid-1990s, Norwegian strains (primarily Landcatch) and their hybrids represented 30-50% of the fish stocked in culture facilities, and totalled over 1 million fish (Baum 1998). Importation of live fish or eggs from Europe was banned in Maine in 1995, though the industry continued to import Norwegian-origin milt (Mowi and Bolaks strain) from Iceland through the late 1990’s (Baum 1998). As of 2003, due to concerns over the genetic integrity of declining wild populations, only genetically-screened North American broodstock are permitted for culture in Maine (National Research Council 2003).

Despite the prevalence of European-origin salmon in Maine, there has been little assessment regarding the ecological impacts these fish have had on wild Atlantic salmon populations (DFO 1999). Farmed Atlantic salmon have been detected in Maine rivers since 1990 and have been documented in 8 rivers–most in close proximity to aquaculture sites, with farmed Atlantic salmon in some rivers comprising >50% of adult returns (DFO 1999). Among these, up to 30% were sexually mature (DFO 1999). Spidle *et al.* (2003) detected 'a number' of aquaculture Atlantic salmon escapees of European ancestry during collections of wild individuals suggesting that ecological interactions have occurred. Certainly, Atlantic salmon stocks in Maine have suffered catastrophic declines, and aquaculture has been listed as one of many potential contributing factors (National Research Council 2003). However, no work has isolated the effects of farmed European-origin Atlantic salmon on wild North American Atlantic salmon populations.

Importation of farmed European-origin Atlantic salmon to Atlantic Canadian waters for commercial culture in sea cages has never been permitted, though trials have been allowed. For example, freshwater trials of Mowi strain hybrids were conducted at three commercial hatcheries in New Brunswick. These trials demonstrated poor egg fertility and fry survival (Glebe 1998). Norwegian-origin fish were also imported for evaluation in a Prince Edward Island quarantine facility in 2002 (DFO Licence No. SP-02-014), with the intent of establishing an egg supply facility for the British Columbia (BC) industry. These broodstock were required to be destroyed after the trials under the terms of the license. Atlantic Canadian commercial culture operations currently utilize St. John River strain Atlantic salmon. Since 2003, Maine facilities require pre-screening to eliminate genotypes of European-origin. Escapees of European strains have been observed among wild fish in Canadian waters. For example, O'Reilly *et al.* (2006) found European-type alleles in escaped smolt and adults in the Magaguadavic River and in escaped parr in Chamcook Stream, New Brunswick (NB). The latter were likely the result of escapes from an adjacent hatchery during approved freshwater trials. However, the collection of a pure farmed European-origin Atlantic salmon post smolt suggests at least some use of farmed European-origin Atlantic salmon in Canada or Maine were being maintained in the vicinity. These authors expressed concern that introgression from Norwegian-origin salmon might be a greater threat than introgression from local-origin salmon based on the greater number of generations that have been subject to selection for domestically desirable traits, the greater genetic divergence of farmed European-origin Atlantic salmon, and the poor survival of Norwegian-origin/wild F2 hybrid Atlantic salmon based on experimental trials (Ireland, McGinnity *et al.* 2003).

CURRENT KNOWLEDGE OF ECOLOGICAL IMPACTS RELATED TO FARMED-WILD SALMON INTERACTIONS

Concerns related to aquaculture effects on wild salmon populations are longstanding and fuelled by the analysis that occurrence of aquaculture is typically associated with declines of nearby wild stocks (Ford and Myers 2008; Dempson *et al.* 2011; Cohen 2012). Extensive study of the impacts of Atlantic salmon aquaculture escapees on wild populations has been conducted through modeling, and field, semi-natural, and laboratory studies (reviewed by Jonsson and Jonsson 2006; Ferguson *et al.* 2007; Thorstad *et al.* 2008; Leggatt *et al.* 2010; Jacq *et al.* 2011; Homarus 2012). These reviews consider potential impacts of escaped farm-origin Atlantic salmon on wild conspecifics through ecological interactions of juveniles and spawning adults in freshwater, marine competition, disease transfer, and genetic introgression. The scale of the escape event and occurrence of escaped fish in wild habitats in Canada is further considered in Leggatt *et al.* (2010) and Morris *et al.* (2008).

In 1995, 94% of the world's Atlantic salmon population existed in aquaculture (Gross 1998), exceeding the abundance of wild stocks by over two orders of magnitude in some areas (DFO 1999). This disparity continues to grow as wild stocks are in decline throughout many parts of their natural range (WWF 2001; COSEWIC 2011) and aquaculture of salmon continues to expand (Thorstad *et al.* 2008).

The degree of impact of farmed salmonids depends on the frequency of escape, the scale of the escapes relative to the size of individual native populations, the survival of farmed individuals following escape, the dispersal of escaped individuals, and the capability to establish in native habitats. These factors may, in turn, vary with life history stage at escape, extent of domestication, season and area of escape, and the presence of predators and competitors. Reflecting the complex nature of effects, large scale studies that related the presence of aquaculture to the health of wild stocks have produced conflicting results. Some regional studies show negative correlations between net-pen aquaculture intensity and abundance of wild fish (Fiske *et al.* 2006; Ferguson *et al.* 2007; Ford and Myers 2008) while others indicate that aquaculture is not associated with severely depressed runs (Green *et al.* 2010; Homarus 2012). Most reviews agree that the vulnerability of wild populations is dependent on the ecosystem's health and the state of the wild population.

Large-magnitude escapes of farmed Atlantic salmon from marine cages and freshwater rearing facilities are common and widespread (e.g., Thorstad *et al.* 2008; Jensen *et al.* 2010) and are estimated to be equivalent to 50% of the wild pre-fishery abundance (Ferguson *et al.* 2007). In Nova Scotia and the Bay of Fundy, reported escapes during the 1990s (when the industry was smaller and wild populations more numerous) matched the estimated numbers of wild fish in some years (DFO 1999). The reported numbers of escapes reached their highest levels in 2005, with over 160,000 reported (Morris *et al.* 2008). The scale of escapes, however, is not accurately known in Canada (particularly regarding contributions due to frequent low magnitude events) and reported numbers of escaped Atlantic salmon are most certainly under-reported and underestimated (Leggatt *et al.* 2010). For example, in the Magaguadavic River, farmed escapes detected in the river have matched only two reported breach of containment events by industry (based on age and size), despite their detection at the counting facility in all years since the 21 year duration that monitoring has been conducted.

The fate of the vast majority of escaped Atlantic salmon is unknown, but there are several studies that indicate that escaped salmon and their hybrid progeny have poorer survival than wild counterparts (Skaala *et al.* 2012). These studies also indicate that migratory behaviour is usually irregular, taking farmed salmon well away from the point of release following their escape (hundreds and in some cases thousands of kilometres) (Whoriskey *et al.* 2006; Hansen and Youngson 2010; Skilbrei *et al.* 2010; Solem *et al.* 2012). Generally, the life history stage during escape has an important influence on homing and migratory ability, as individuals released as smolts tend to return to areas close to the release point. In contrast, pre-adults have weak homing instincts. Farmed fish are routinely found among wild individuals on marine feeding grounds (reviewed in Johannes 2006) and in rivers amongst wild individuals. In Atlantic Canada, they have been found in 87% of surveyed rivers within 300 km of aquaculture facilities comprising up to 100% of the adult salmon returning to rivers (Morris *et al.* 2008). However, data on the occurrence of farmed escapees in wild rivers remains incomplete, particularly for the relatively remote areas of the south coast of Newfoundland.

Based on available information, the greatest potential for farmed escapee ecological impacts occurs in the freshwater environment where laboratory, semi-natural, and field studies have demonstrated that domesticated Atlantic salmon juveniles use resources that are similar to those of wild salmon (Fleming *et al.* 2000; Skaala *et al.* 2012; reviewed in Ferguson *et al.* 2007). Further, farmed Atlantic salmon escapees demonstrate increased competitive abilities (Houde *et al.* 2010a; reviewed in Ferguson *et al.* 2007), faster growth (Fleming *et al.* 2000; Skaala *et al.* 2012; reviewed in Ferguson *et al.* 2007), are less risk averse (Einum and Fleming 1997; Fleming and Einum 1997; Johnsson *et al.* 2001; Houde *et al.* 2010b), and more aggressive (Einum and Fleming 1997; Fleming and Einum 1997). As freshwater production is density-dependent (e.g., Jonsson and Jonsson 2011) and farmed juveniles and hybrids show comparable survival to their wild counterparts in freshwater, such ecological interactions have the potential for severe negative consequences to wild Atlantic salmon (Ferguson *et al.* 2007). The degree of impact, however, is context-dependent, specifically reliant upon the residency status of the escapees, size differences between escaped and wild salmon, presence of predators, and the relative abundance of escaped farmed Atlantic salmon compared to that of the wild populations (Houde *et al.* 2010a). Field studies have also shown that ecological interactions between escaped farmed and wild Atlantic salmon can result in displacement and decreased productivity of wild salmon juveniles (Fleming *et al.* 2000; McGinnity *et al.* 2003).

Adult interactions between escaped and wild individuals also occur in freshwater. Compared to juveniles, escaped adults typically exhibit reduced competitive capabilities that include lower rates of aggressive and courting behaviour, mate acquisition, and sperm release in males, and higher egg retention, fewer nests, fewer fertilized nests, and altered spawning behaviour in females (Fleming *et al.* 1996, 2000; Weir *et al.* 2004). Such competitive inferiority results in consistently lower reproductive success relative to wild conspecifics (Fleming *et al.* 1996, 2000; Weir *et al.* 2004). Nonetheless, considerable evidence exists of spawning success of escaped salmon (e.g., 20% of redds in the Magaguadavic River, NB, are the product of escaped farmed salmon, Carr *et al.* 1996) and disruption of wild Atlantic salmon redds by escaped farmed salmon (Ferguson *et al.* 2007). Genetic introgression of farmed salmon into wild populations has occurred and can negatively impact wild salmon populations by diluting the river-specific adaptations expressed by wild Atlantic salmon genotypes and affecting the subsequent survival of native populations (Fleming *et al.* 2000; McGinnity *et al.* 2003; Houde *et al.* 2010a; Bourret *et al.* 2011; Skaala 2012). This introgression may also limit the capacity for future adaptation to environmental changes should escapees express reduced genetic diversity compared to that of native populations (Hindar *et al.* 2006; Ferguson *et al.* 2007; Karlsson *et al.* 2011), although Conejeros *et al.* (2011) suggested, based on a very small scale study, that pathogen resistance in farmed Atlantic salmon may remain unaffected. However, introgression does not always occur, with some populations demonstrating resistance to genetic change even after exposure for many generations (Glover *et al.* 2012). When introgression does occur, modeling suggests that multiple generations would be required for genotypes to recover to wild condition and revert to pre-disturbed states (Hindar *et al.* 2006). Escaped farmed Atlantic salmon can also exert indirect genetic effects on wild salmon, which occur in the absence of genetic introgression. This can arise when the presence of escapees alters selection processes, diverts gametes from wild fish, and/or reduces the effective size of wild populations; leaving them vulnerable to genetic drift and inbreeding depression (Ferguson *et al.* 2007). The magnitude of these impacts varies according to the health of the wild population, the salmon strains involved, and the relative abundance of farmed and wild salmon (Glover *et al.* 2012).

Evidence of competition in the marine environment has been documented for Pacific salmonids (Holt *et al.* 2008; Ruggerone *et al.* 2012), but in most cases hatchery salmon are more impacted than wild salmon (Daly *et al.* 2012; Sturdevant *et al.* 2012). Competitive interactions of Atlantic salmon in the North Atlantic Ocean are not well understood. However, Olsen and Skilbrei (2010) showed that recaptured farmed Atlantic salmon in the vicinity of the site of their escape were unable to feed effectively on wild prey. Nevertheless, as reviewed by Thorstad *et al.*

(2008), escaped salmon have been observed frequently on wild Atlantic salmon feeding grounds consuming similar prey. Field studies in the Gulf of Maine and Bay of Fundy showed no evidence of density-dependent effects for post-smolts, which would be expected if the habitat was resource-limited due to competition from escaped farmed Atlantic salmon (Lacroix and Knox 2005), nor has research shown that marine survival of Atlantic salmon in Norway is density-dependent (Jonsson and Jonsson 2004; Wertheimer *et al.* 2004). In contrast, a single study of post-smolts in the Gulf of St. Lawrence showed indirect evidence of density-dependent effects (i.e., density-dependent growth) in the first 1-2 months following entry into the marine environment (Friedland *et al.* 2009). Nonetheless, relative to freshwater environments, competitive ecological interactions in the marine environment among farmed and wild Atlantic salmon are considered to be minimal.

Whole-river experiments in Norway and in Ireland were used to examine the impact of escaped farmed Atlantic salmon on wild populations over a full life cycle (McGinnity *et al.* 1997, 2003; Fleming *et al.* 2000). The experiments showed that escaped farmed Atlantic salmon and farm–wild hybrids exhibited reduced lifetime success (fitness; reproduction and survival) compared to wild Atlantic salmon, as well as demonstrating that there were negative impacts on wild salmon population productivity. In the River Imsa (Norway), farmed-origin and wild adult salmon were screened genetically, monitored, and the fate of their resulting offspring followed for a full generation (Fleming *et al.* 2000). The results support previously mentioned studies that collectively indicated that farmed Atlantic salmon have inferior performance in the wild. Specifically, farmed-origin salmon had 16% the lifetime fitness (reproduction and cumulative survival) compared to that of the native wild salmon. Reproductive success was the major bottleneck impeding fitness in the wild, with farmed salmon being competitively and reproductively inferior, with total recruitment of only 19% of that of wild salmon to the 0+ stage (Fleming *et al.* 2000). Moreover, there was evidence of resource competition and competitive displacement, as the presence of the farmed salmon depressed the river's wild smolt production by more than 30% compared to what was expected from the number of eggs produced. The depression in smolt production was thought to reflect fluctuating selection on offspring type, with competition from the farmed and hybrid offspring depressing the wild offspring survival during one or more life-history episodes and maladaption depressing the farmed reproduction and survival (including that of hybrid offspring) at other times. One-way gene flow of this magnitude ($m = 0.19$) would be sufficient to halve the genetic difference between a farm and a recipient (native) population every 3.3 generations, though this will be highly dependent on the fitness of hybrids and backcrosses during subsequent generations.

The independent, large-scale experiment conducted in the Srahrevagh River of the Burrishoole system, Ireland, was designed to quantify the genetic impact to a wild population from breeding with escaped farmed salmon (McGinnity *et al.* 1997, 2003). The performance (i.e., growth and survival) of wild, farmed, hybrid (F1, F2) and backcrossed (BC1) salmon progeny was examined, whereby specific crosses were created experimentally and the embryos planted in the experimental river. The experiment was designed to eliminate behavioural differences among spawning adults and to examine the effect of genetic differences on survival and growth at various life stages to adulthood. The genetic differences manifested into mortality differences and were greatest in the period from the eyed egg stage to first summer. Offspring of farmed parents and 'hybrids' (i.e., all F1, F2, and BC1 groups) showed reduced survival compared with wild salmon, but grew faster as juveniles and displaced wild parr, which as a group were significantly smaller (i.e., similar to the observations by Fleming *et al.* 2000). The farmed salmon consistently showed the lowest freshwater and marine survival in all cohorts. The relative estimated cumulative survival ranged from 2% (farm) to 89% (BC1 wild) of that of wild salmon, indicating additive genetic variation for survival. There was no evidence for hybrid vigour, with F1 and BC1 hybrids being intermediate between wild and farmed salmon in survival, growth, and parr maturity. There was evidence of outbreeding depression in the F2 hybrids.

Hindar *et al.* (2006) used the data from the two experiments to model the future of wild salmon populations experiencing invasions of escaped farmed salmon. Simulations with a fixed intrusion rate of 20% escaped farmed salmon at spawning (only slightly higher than that observed in Norway) suggest that substantial changes take place in wild salmon populations within ten salmon generations (*ca*. 40 years). Low-invasion scenarios suggest that farmed offspring are unlikely to become established in the populations, whereas high-invasion scenarios suggest that populations are eventually mixtures of hybrid and farmed descendants, with recovery being slow at best.

The evidence of disease transfer from farmed escapees to wild fish has caused concern (Naylor *et al.* 2005) and has been reviewed by Raynard *et al.* (2007) in the eastern north Atlantic. Of 18 diseases noted for farmed salmon, five showed evidence of transmission from farms to wild populations (sea lice, *Gyrodactylus salaris*, Furunculosis, *Lepeophtheirus salmonis*, and infectious pancreatic necrosis). No evidence was available for transmission of Infectious Salmon Anemia from farmed salmon to wild populations but it was considered likely. In many cases, diseases are thought to originate from wild populations. However, movement of aquaculture fish has been implicated in the spread of *Gyrodactylus salaris* and Furunculosis to wild European fish populations (Raynard *et al.* 2007). In Scandinavia, *Gyrodactylus* had co-evolved with salmon in the Baltic region but its presence was devastating to many populations outside its native range, particularly in Norway.

High density conditions in cages can act as pest and pathogen reservoirs, cause outbreaks and/or create conditions that allow new strains to rapidly evolve (e.g., *Flavobacterium columnarae*; Homarus 2012) and can increase infestation pressure even in the face of declining wild stocks (Krkosek *et al.* 2005; Finstad *et al.* 2007; Krkosek *et al.* 2013). Proper disease control can mitigate these effects, however, outbreaks can spread into wild populations and may have substantial impacts (e.g., sea lice; Bergh 2007; Raynard *et al.* 2007; Krkosek *et al.* 2013). Pests and pathogens can spread from sea cages through direct interactions of wild fish with farming sites or through escapees which carry disease away from sites. The potential of farmed escapees as carriers depends on their survival in the wild and the degree of contact with wild salmon. It remains unclear if most diseased fish survive outside cages long enough to spread disease but infected escapees have been captured in rivers (e.g., ISA in Atlantic Canada; Olivier 2002). Leggatt *et al.* (2010) postulated that the overall effects of disease might be minimal in cases where disease agents and cultured strains are sympatric with wild populations compared to non-native strains and disease agents. This contention is supported by a general absence of evidence for detected population level impacts, save for a few notable examples where disease was likely introduced through movement of fish outside their native range (*Gyrodactylus* and Furunculosis). However, the difficulty in confirming disease-induced mortality (i.e., wild salmon mortality may not be detected) or loss of fitness in salmon severely limits the robustness of this conclusion. A recent meta-analysis study of tagged smolts (Krkosek *et al.* 2013), indicated the potential importance of disease-induced mortality in affecting recruitment of wild Atlantic salmon as individuals treated with parasiticide and released in areas with high levels of aquaculture showed higher levels of survival.

There are also notable consequences of genetic introgression that relate to disease. Important local adaptations to disease resistance are related to major histocompatability complex (MHC) alleles (Dionne *et al.* 2007; de Eyto *et al.* 2007; Dionne *et al.* 2009). Impacts on local adaptation or MHC allelic diversity arising from genetic introgression could have significant consequences to the persistence of salmon populations evolved to deal with local pathogen environments, future pathogen environments under climate change scenarios (de Eyto *et al.* 2007) or emergence of new strains (Raynard *et al.* 2007). While selective breeding for disease resistance is possible (Gjedrem *et al.* 1991), this is unlikely to be done at spatial scales that match wild adaptation or occur in timeframes necessary to protect populations.

ECOLOGICAL COMPARISONS OF WILD NORWEGIAN AND NEWFOUNDLAND SALMON

The extensive range of wild Atlantic salmon and the diverse life history is a testament to the adaptive capacity of the species. Anadromous and resident life histories, coupled with a tendency to return to natal spawning grounds has created a scenario that facilitates local adaptation. Not surprisingly, this species is characterized by hierarchical genetic structuring in which recolonization from glacial refugia and local adaptation play key roles. Several studies have highlighted the considerable genetic differences of salmon that occur on different sides of the Atlantic (King *et al.* 2001, Koljonen *et al.* 2002; Spidle *et al.* 2003, Bourret *et al.* 2012), with divergence occurring 600 thousand years before present (King *et al.* 2007). With advancing techniques, the differences have proven to be greater than previously thought and are now estimated to explain 41% of the genetic variation observed across the range (Bourret *et al.* 2012). Within continents, regional (Koljonen *et al.* 2002; Verspoor 2005; Dionne *et al.* 2008; Bourret *et al.* 2012) and local (Adams 2007; Palstra *et al.* 2007) genetic structuring is apparent. Operating in concert with the environment, genetic structuring creates varying phenotypic responses that are population-specific (Verspoor *et al.* 2015).

Wild Norwegian salmon differ from Newfoundland salmon particularly in traits related to sea-age, growth at sea, percent grilse (early-maturing Atlantic salmon), sex ratios, freshwater residency, and survival at sea. While life-history is population-specific, Norwegian salmon tend to grow faster at sea, have older sea-ages and lower grilse percentages, lower proportions of female grilse, and lower survival at sea (Table 1; Hutchings and Jones 1998). Norwegian salmon also rarely establish freshwater resident populations and when these occur they are under land-locked situations. Use of lakes by salmon is common in Newfoundland but it is not clear if this is a genetic adaptation or a result of relaxed competition in these habitats due to the relatively poor fish diversity on the Island. Multi-sea winter salmon, common in Norway, are present in only one river along the south coast of Newfoundland (Chaput *et al.* 2006). Adult size is negatively correlated with the ability to repeat spawn (and consequently larger Norwegian fish show lower rates of repeat spawning relative to Newfoundland—where repeat spawning rates have been increasing since the fishing moratorium (DFO and MNRF 2009).

Table 1. Comparative life history parameters of Atlantic salmon in Norway and Newfoundland (modified from Hutchings and Jones 1998).

Life History Parameter	Norway (mean ± SD)	Newfoundland (mean ± SD)
Parr size-age 1 (cm)	8.3 ± 0.9	7.9 ± 0.7
Smolt age (years)	3.01 ± 0.74	3.36 ± 0.45
Smolt length (cm)	13.1 ± 1.2	15.5 ± 1.4
Grilse length (cm)	59.5 ± 4.3	53.2 ± 1.6
Sea age (years)	1.83 ± 0.51	1.15 ± 0.17
Percent grilse	44 ± 27	86 ± 15
Percent female grilse	20 ± 0.26	67 ± 15
Smolt to grilse survival (%)	3.8 ± 0.3	7.3 ± 2.7
Age at maturity (years)	5.71 ± 0.81	5.58 ± 0.46

CHARACTERISTICS OF NORWEGIAN BROODSTOCK

The Norwegian broodstock program produces a large portion of the Atlantic salmon eggs and sperm used in aquaculture throughout the world (Naylor *et al.* 2005). While selective breeding of Norwegian Atlantic salmon began as early as the late 1960's (Jacq *et al.* 2011), the National Breeding Program began in 1971 (Gjedrem 2000), when broodstock was collected from 40 rivers in Norway (Gjoen and Bentsen 1997; Naylor *et al.* 2005) and resulted in the creation of four broodstock populations (Gjedrem *et al.* 1991). The high fecundity of salmon allowed for swift selection of attractive traits relative to other domesticated livestock (Ferguson *et al.* 2007), and genetic improvements were occurring at 10–15% per generation (Gjedrem 2000). Traits related to growth were selected in the first two generations, while improvements to age at maturity, disease resistance, flesh quality, temperature and stress tolerance, and egg quality followed in subsequent generations (Gjedrem 2000; Ferguson *et al.* 2007). Despite the broad base of the initial broodstock, selection for commercially favourable traits rapidly decreased the contributions of many stocks. For example within three generations, one population only maintained genetic contributions from six of its original 15 doner populations; one of which contributed 70% of the remaining genetic content (Gjoen and Bentsen 1997). Gjedrem *et al.* (1991) indicate that none of the four broodstock populations are dominated by more than three rivers.

In recent times, after only eight generations of selective breeding, some Norwegian farmed Atlantic salmon were 10 times more genetically distinct from conspecifics in the source rivers than those source rivers were from each other (Ferguson *et al.* 2007; see also Karlsson *et al.* 2011). These differences are attributed to intentional selection, as well as founder effects and genetic drift that are associated with small populations (Skaala *et al.* 2005). Domesticated fish show morphological and physiological differences including deformities, shorter fins, reduced streamlining, higher fat content, reduced swimming performance, and altered heart shape (Thorstad *et al.* 2008) and egg hatching time (Berg and Moen 1999). Additionally, selection for growth has resulted in associated changes in the quantity of growth hormone produced in farmed Atlantic salmon—an attribute linked to several behavioural elements (e.g., increased appetite, aggression, activity, dominance, and risk tolerance; Fleming *et al.* 2002). These changes are thought to play a large role in the decreased survival and performance of domesticated Atlantic salmon in the wild (Ferguson *et al.* 2007). The genetic and ecological departures have become so great that some have suggested that a new species, *Salmo domesticus*, is being formed (Gross 1998). Nonetheless, little information exists related to the qualitative genetic variation, the differences among the domesticated strains, and temporal changes in these strains (Skaala *et al.* 2005; Karlsson *et al.* 2011).

CHARACTERISTICS OF RECEIVING ENVIRONMENT (SOUTH COAST OF NEWFOUNDLAND)

The south coast of Newfoundland is deeply incised with fjords and sits within the Maritime Barrens ecoregion of Newfoundland; an area characterized by relatively cool summers and mild winters (Department of Natural Resources 2012). Autumn is a period of increased winds and precipitation, though the relatively warm marine environment results in a warmer season than other areas of the province (Memorial University of Newfoundland 2012).

The climate of the south coast makes it the only area of Newfoundland thought to be suitable for commercial finfish aquaculture (G. Perry, DFO pers. comm.) as it is usually free from the damaging effects of sea ice and has relatively warm water that extends the growing season (Figure 1).

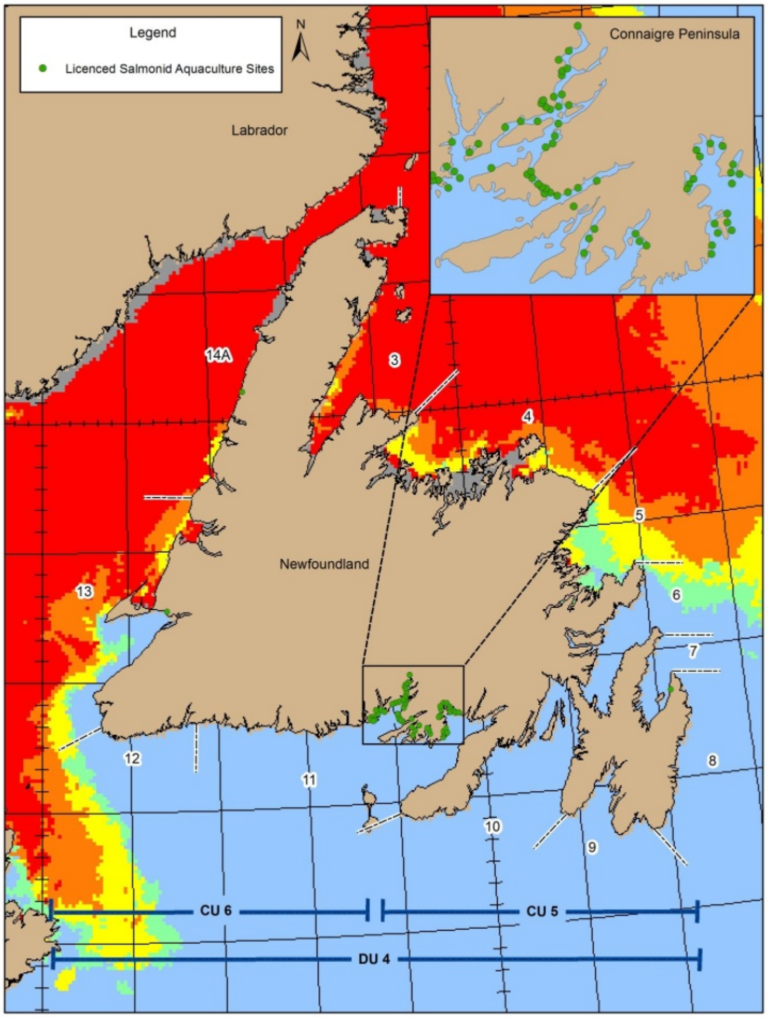

Figure 1. Licensed salmonid aquaculture sites in Newfoundland (green circles) (Department of Fisheries and Aquaculture 2011). Superimposed is the maximum ice coverage for East Coast of Canada 1981-2010 (areas outside of yellow and red have <10% chance of ice coverage; Environment Canada 2012), Fisheries and Oceans Canada salmon fishing areas (3 – 14A), south coast Conservation Units (CU 5 and CU 6), and the extent of COSEWIC's South Coast of Newfoundland Designatable Unit for Atlantic salmon (DU 4). Inset shows a magnification of the region of highest finfish aquaculture intensity.

The lakes and rivers of the south coast are also influenced by the warmer climate as spring freshets occur earlier and winter flows are maintained relative to other parts of the island due to rain events. In some watersheds, reservoirs associated with hydro-development further dampen the seasonality of flows (Memorial University of Newfoundland 2012). In comparison to Norway where farmed European-origin Atlantic salmon broodstock originate, Newfoundland's salmon rivers are of more moderate gradient and their flows are less dominated by snowmelt. Like Norway, however, waters of the south coast are vulnerable to acidification (pH 5–6; Environment Canada 2004) and this potential stressor is considered a burden if not a threat to aquatic animals including salmon in this area (COSEWIC 2011).

Salmonid aquaculture (Atlantic salmon and steelhead) activities in Newfoundland are restricted to the Bay d'Espoir, Fortune Bay and the Connaigre Peninsula along the south coast (Figure 1; Department of Fisheries and Aquaculture 2011), although the inner Bay d'Espoir is used exclusively for Steelhead culture due to its brackish water. Spread across 81 commercial licenses (2,056 ha), the industry on the south coast produced over 14,000 tonnes of fish worth $112 million in 2011 (Department of Fisheries and Aquaculture 2011). While production is low relative to other areas of Canada, it is increasing (Figure 2) as in other areas of the world (Thorstad *et al.* 2008). Production cycles in Newfoundland are typically between 18 and 24 months in duration after which there is a one year fallow period. In any single year, only approximately 40 farms are in production (G. Perry, DFO, pers. comm.), to which smolts can be introduced to the marine environment in either the spring or the fall. Generally, farms within an area are spatially separated (G. Perry, DFO, pers. comm.) but some have been spaced within 2.5 km of each other.

Reported escapes of Atlantic salmon from aquaculture in Newfoundland exceeded 140,000 individuals in 1996 (Figure 2) but the numbers of reported escapes in Newfoundland have declined dramatically despite significantly increased Atlantic salmon production. It is difficult to assess the accuracy of reports for this region; however, as there is little monitoring data available with which to assess the prevalence of escapees in south coast rivers.

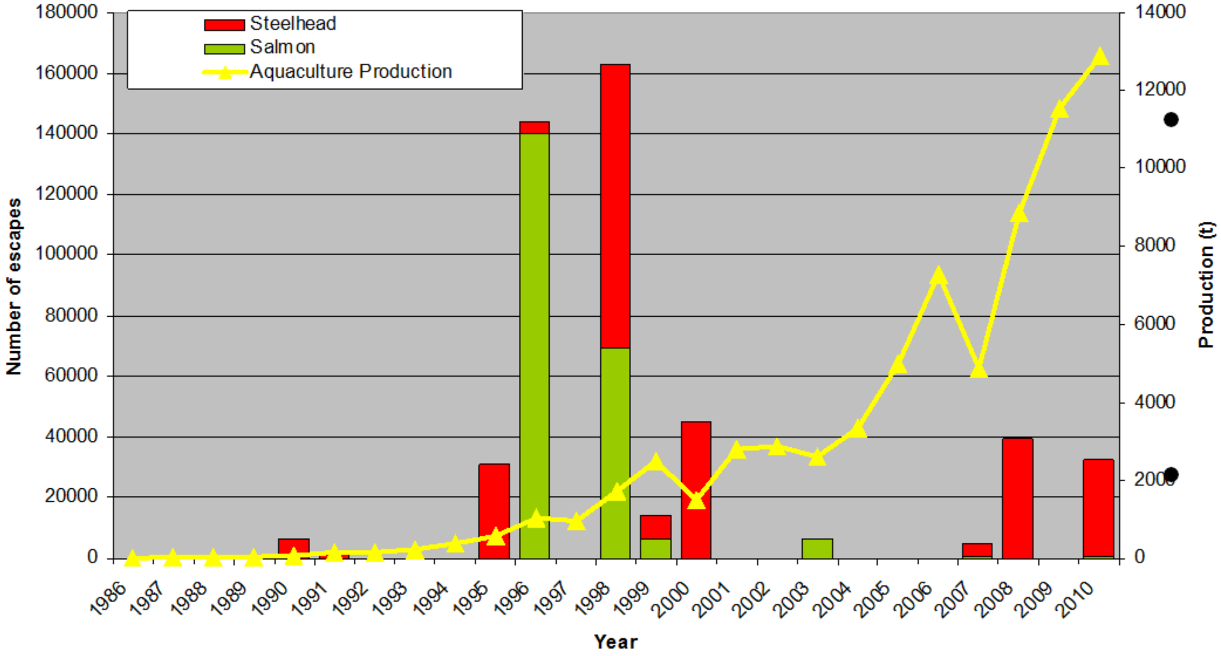

Figure 2. Atlantic salmon and steelhead trout reported escapes and salmonid aquaculture production for Newfoundland, 1986-2010 (figure provided by G. Perry, DFO, unpublished data).

Atlantic salmon populations from the south coast of Newfoundland are considered a discrete and evolutionarily significant unit (DU) by the Committee for the Status of Endangered Wildlife in Canada (COSEWIC). These populations are located in 104 rivers within Salmon Fishing Areas (SFAs) 9–12 (Figure 1; COSEWIC 2011). Most rivers along the south coast have small populations of less than 500 spawning adults (Dempson *et al.* 2006). Atlantic salmon from the south coast of Newfoundland (DU 4) are estimated to have declined in abundance by 42% over the past three generations (Figure 3; DFO 2012) and have been listed as Threatened by COSEWIC (2011). Abundance trends in this area are over-represented by the populations found in the rivers in the eastern portion of the south coast (within SFAs 9-11), due to the size and/or accessibility of the rivers. Specifically, the particularly steep population declines of Conne River (in SFA 11) overshadow what is occurring in smaller rivers or areas where population abundance data are unavailable. Nonetheless, the Conne River population is proximal to the key area of finfish aquaculture production along the south coast. Freshwater resident populations of Atlantic salmon (ouananiche) are also found along the south coast but relatively little is known about their status.

Impacts from North American-origin (St. John River strain) farmed–wild Atlantic salmon interactions are not well understood for the south coast of Newfoundland. In previous years, marine escapes have occurred and farmed adults have been detected at low abundance in Conne River (<2% of the run; DFO 1999) and in other rivers along the south coast (Verspoor *et al.* 2015). However, only a fraction of Atlantic salmon sampled in these rivers undergo detailed analysis (e.g., morphometric measurements, fin condition assessments, scale analysis) to identify whether they are of farmed origin. Furthermore, sampling periods at southern Newfoundland counting fences are not well matched to the run-timing of escapees seen in other parts of Atlantic Canada. Therefore, it is possible that many escaped farmed-origin Atlantic salmon go undetected in rivers on the south coast of Newfoundland.

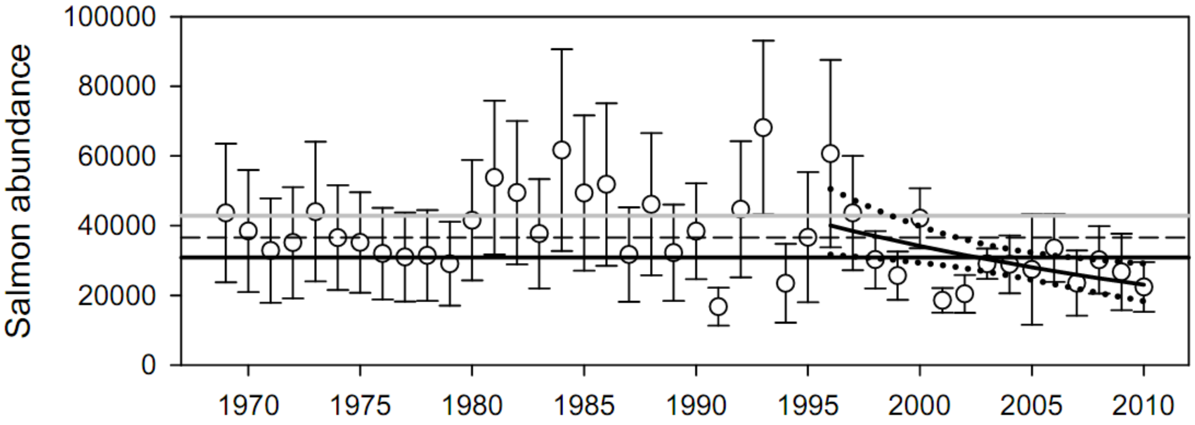

Figure 3. Wild Atlantic salmon returns (mean ± 2SE) to DU 4 (SFA 9-12) rivers (1969-2010) estimated from angling catch data. Superimposed is the general linear model (± 2 SE prediction intervals) used to determine trends in abundance over the past three generations (1996-2010). The three horizontal lines represent the estimated conservation spawner requirement (solid black line), long-term mean (dashed black line), and abundance three generations prior to 1996 (1981-1995) (solid grey line). Figure modified from DFO (2012).

A semi-quantitative assessment of stressors and threats to Atlantic salmon along the south coast of Newfoundland was conducted by Fisheries and Oceans Canada (DFO) and Ministère des Ressources naturelles (MNRF, Québec) (DFO and MNRF 2009) (Table 2). Stressors included low impacts from wastewater, industrial effluent, water extraction, urbanization, and dredging. While moderate impacts in some areas were presumed to occur from hydroelectric facilities and dams, transportation infrastructure (connectivity), forestry/mining, and air pollutants (acid rain); freshwater habitat was not considered a limiting factor to population recovery along the south coast, as supported by existing smolt production (Figure 4). Survival in the marine environment, however, is thought to be the primary driver for observed population declines along the south coast of Newfoundland (Figure 5). Illegal fisheries, mixed stock marine fisheries and by-catch, ecological and genetic interactions with escaped and domestic Atlantic salmon, along with changes in marine ecosystems have been identified as sources of higher marine mortality (DFO 2012). The lack of a clear explanation as to why populations along the south coast are in decline while other DUs of Newfoundland remain healthy underscores the need for a better understanding of the marine ecology of wild Atlantic salmon in this area.

Table 2. Summary assessment of habitat alteration threats to Atlantic salmon (in terms of salmon affected; spawners lost) for the two areas of the South Newfoundland DU as described in DFO and MRNF (2009).

Atlantic Salmon Conservation Unit	Salmon Affected: Spawners Lost												
	Regulated Habitat Alterations										Other		
	Municipal waste water	Industrial effluents	Hydroelectric & dams	Water extraction	Urbanization (hydrology)	Transportation Infrasctructure	Aquaculture siting	Aquaculture forestry mining	Dredging	**Cumulative**	Shipping transport	Air pollutants/ acid rain	Ecosystem change
5. SE Coast	L:L	L:L	L:L	L:L	L:L	M:M	L:L	M:M	L:L	**U:U**	U:U	MU:MU	LU:LU
6. South Coast	L:L	-:L	M:M	L:L	L:L	L:L	M:M	L:L	L:L	**U:U**	-:-	MU:MU	LU:LU

Where “salmon affected” symbol “L” is < 5% of salmon affected; “M” is 5-30% are affected, and “U” is uncertain; “salmon lost” symbol “L” is < 5% of salmon spawners are lost; “M” is 5-30% are lost, and “U” is uncertain; N/A = Not Applicable and “-“ = Not Assessed.

CHARACTERISTICS OF WILD ATLANTIC SALMON ON THE SOUTH COAST OF NEWFOUNDLAND

Genetic data suggest that Atlantic salmon populations along the south coast exhibit reduced gene flow among local rivers and other regions of the Island (Adams 2007; Palstra *et al.* 2007; Verspoor *et al.* 2015). Reduced gene flow has been associated with increased resistance to local pathogens (Dionne *et al.* 2007, de Eyto *et al.* 2007, Dionne *et al.* 2009), though such adaptations have not been confirmed for salmon along the south coast of Newfoundland. Behaviour and life history of Atlantic salmon on the south coast vary considerably and show no clear geographic pattern (Chaput *et al.* 2006). There is a mix of early and late spawning runs, variable smolt age, and variable proportions of female grilse along the south coast. However, only one multi-sea-winter population is known to occur along the south coast (Chaput *et al.* 2006). The widespread early maturity of south coast populations is a primary factor in making them ill-suited for use as commercial broodstock (B. Glebe, DFO, pers. comm.). In contrast to most other places in Atlantic Canada, repeat spawners form a relatively large proportion of returns, such that over 70% of large Atlantic salmon are repeat spawning grilse (DFO and MNRF 2009). Atlantic salmon production on the south coast of Newfoundland is derived from riverine and lacustrine habitats, in contrast to other areas such as Norway, where use of lacustrine habitat is rare.

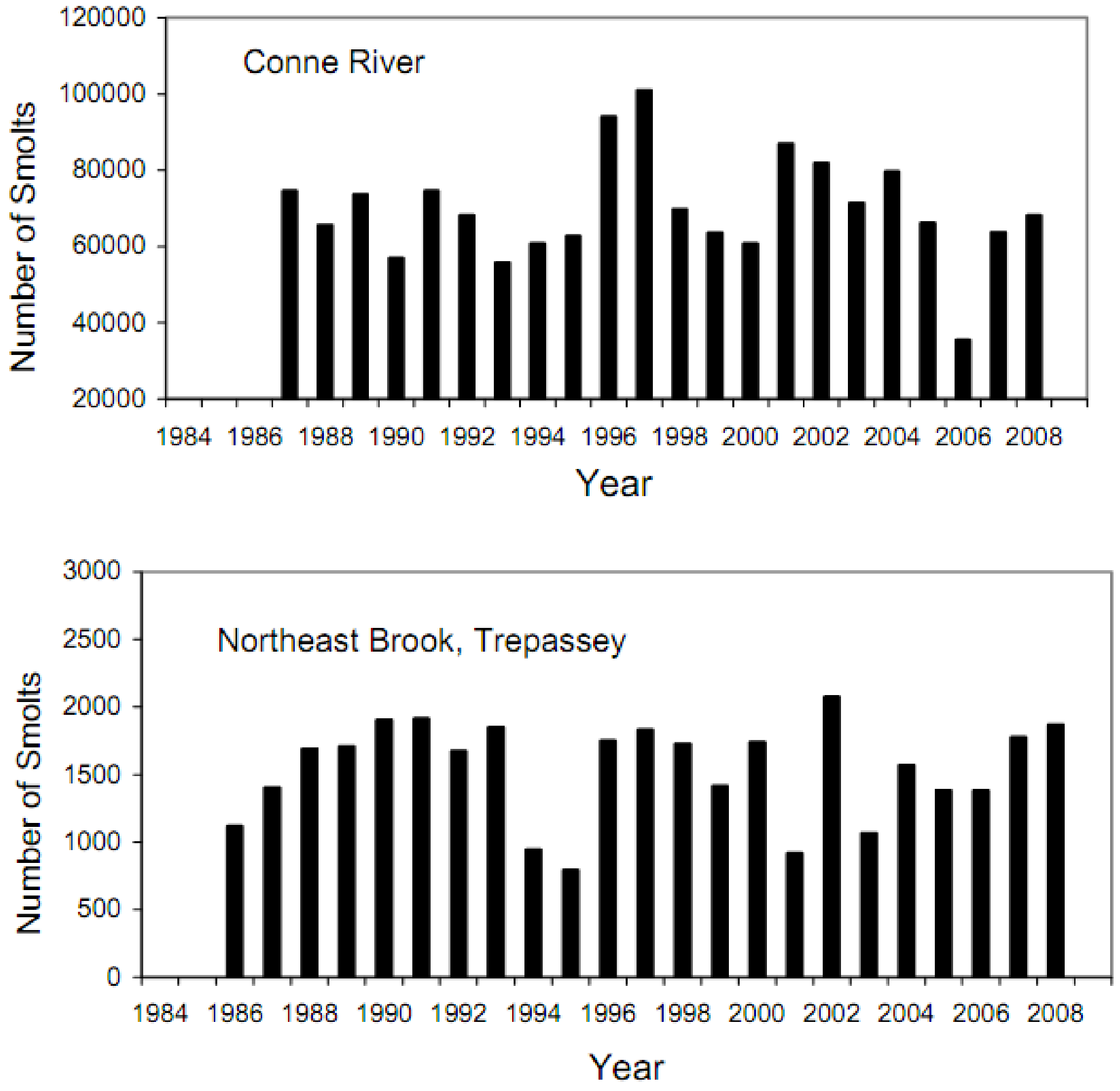

Figure 4. Trends in smolt production from Conne River and Northeast Brook, Trepassey, Newfoundland (COSEWIC DU 4) (COSEWIC 2011).

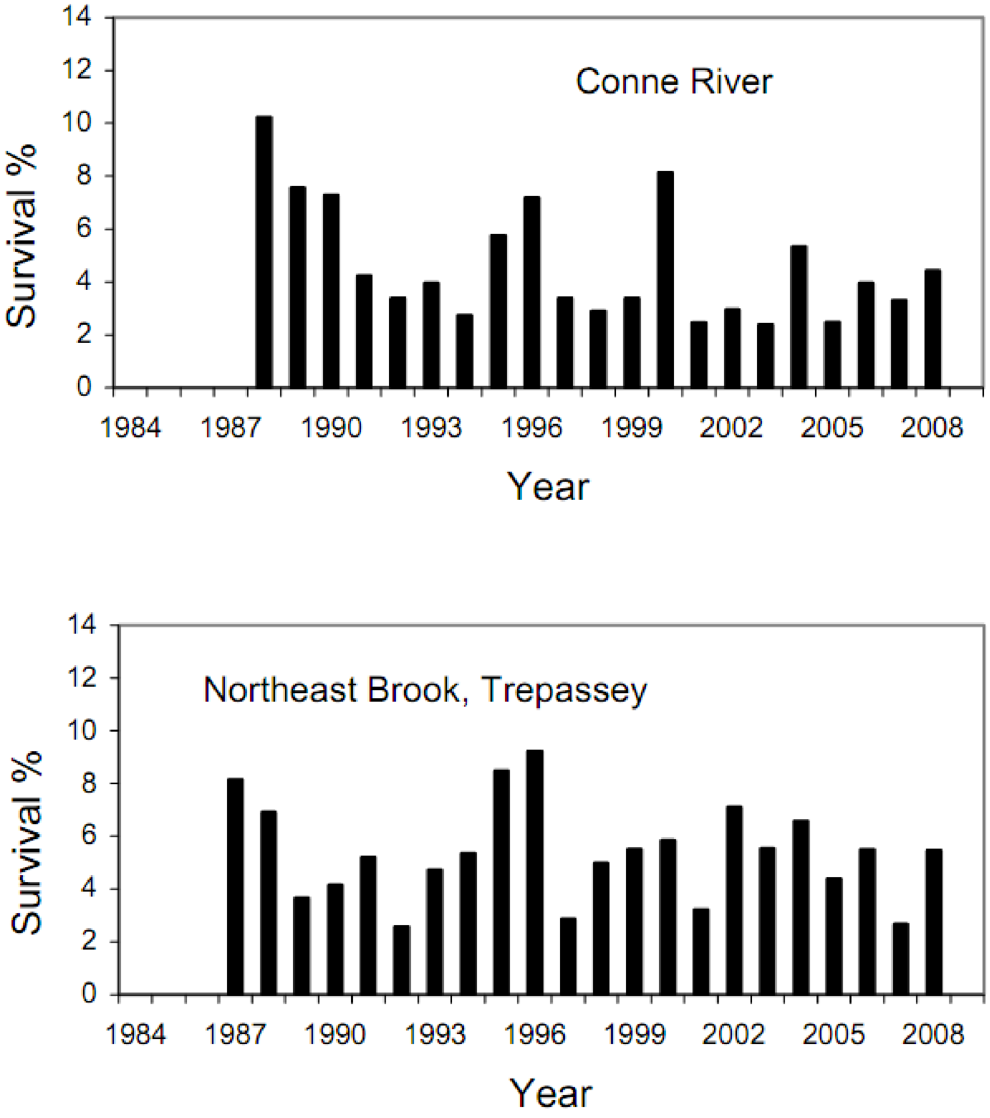

Figure 5. Sea survival of Atlantic salmon from Conne River and Northeast Brook, Trepassey, Newfoundland (COSEWIC DU 4) (COSEWIC 2011).

PREDICTED IMPACTS OF FARMED EUROPEAN-ORIGIN ATLANTIC SALMON

Predicted impacts of escaped farmed European-origin Atlantic salmon are considered in terms of the pathways of escapee impact as defined by Leggatt *et al.* (2010). These include fish health, predation, marine phase competition, freshwater juvenile competition, reproductive interference, and ecological effects of hybridization. Based on expectations outlined above, it is assumed that farmed European-origin Atlantic salmon will exhibit faster growth, larger size at each life history stage, and later maturity, based on intentional selection of these traits during domestication (Ferguson *et al.* 2007). It is also expected that genetic divergence will be even greater between farmed European-origin Atlantic salmon strains and south coast Newfoundland wild stocks than was the case for previous studies of escapee impacts (Bourret *et al.* 2012). These expectations are summarized in Table 3.

Table 3. Comparison of expected differences between European-origin and native-origin farmed Atlantic salmon related to likelihood of escape, hybridization, predation on conspecifics, intra-specific competition, and pathogen transmission. The geographic relevance of the documented impacts of native origin farmed salmon is also provided. Prediction of farmed European-origin Atlantic salmon impacts are based on their expected characteristics resulting from extended exposure to intentional (e.g., growth) and unintentional (e.g., reproductive behaviour) selection.

		Evidence for North American-origin farmed salmon				Expected severity relative to North American strains[a,b]
		Laboratory	Field			
			All regions	Atlantic Canada	South coast of NF	
Likelihood of escapes			High	High	High	Similar
Hybridization	Evidence of population-wide genetic change		Yes	Yes	NR[c]	Greater
	Expectation of maladaptive change	Yes	Yes	Not studied	NS[c]	Greater
Predation on conspecifics			NS[c]	NS[c]	NS[c]	Similar
Competition	Marine	No	Limited	Limited	NS[c]	Similar
	Freshwater-juvenile	Yes	Yes	Yes	NS[c]	Greater
	Reproductive interference	Yes	Yes[d]	Yes[d]	NS[c]	Less to Greater[e]
Pathogen transmission	Evidence of transmission		Yes	Yes	NS[c]	Less[f]
	Severe population effects		Yes	No	NS[c]	Less

[a] Native strains of farmed salmon are believed to have differing degrees of negative implications on wild salmon populations for each of these of these ecological interactions, with the possible exception of marine competition (see "Current knowledge of ecological impacts related to farmed-wild salmon interactions" for additional detail).

[b] The basis of predictions of farmed European-origin Atlantic salmon characteristics are provided in "Predicted Impacts of farmed European-origin Atlantic salmon"

[c] NR – not reported; NS – not studied

[d] Evidence of hybridization indicates that at least competition for gametes has occurred.

[e] Lower competitive ability of adults could be offset by increased likelihood of destroying redds if spawning occurs after wild populations. Also, increased growth of EOS parr could result in improved competitive ability of precocious males.

[f] Transmission in this context relates to comparisons of European and North American strains that are already infected.

FISH HEALTH

Genomes of Atlantic salmon populations are river specific and show adaptation to local conditions (Garcia de Leaniz *et al.* 2007). Disease resistance, in particular, has been noted as a locally-adapted trait (Dionne *et al.* 2007; de Eyto *et al.* 2007; Dionne *et al.* 2009) as pathogen communities vary geographically (Dionne *et al.* 2007; Raynard *et al.* 2007; Homarus 2012). This is supported by the observations in Norwegian waters of the spread of *Gyrodactylus* to wild fish (Raynard *et al.* 2007) following introduction of cultured fish outside their native range. While farmed European-origin Atlantic salmon are expected to be from certified disease-free sources, some pathogens may be poorly characterized and, therefore, there remains some risk of introducing novel pathogens from farmed European-origin Atlantic salmon source environments. Even if imported farmed European-origin Atlantic salmon are truly disease free, they and their hybrids would be expected to have lower disease resistance to locally-occurring pathogens relative to fish of North American origin due to lack of local adaptation. For example, lower disease resistance to local strains of Infectious Salmon Anemia virus (ISAv) has been observed in Norwegian salmon outside their native range (B. Glebe, DFO, pers. comm.). Furthermore, the reduced genetic diversity associated with broodstock under extended domestication may also limit the capacity of farmed European-origin Atlantic salmon hybrids to respond to new pathogen environments (types, strains, and/or distribution) caused by changing environmental conditions (e.g., climate change) (National Research Council 2003; de Eyto *et al.* 2007; Harris *et al.* 2007; Raynard *et al.* 2007). Increased size and growth have also been linked to increased disease vulnerability in salmonids in some circumstances (Saksida *et al.* 2011; Karlsson Drangsholt *et al.* 2012), though these studies were unable to identify growth/size as the causal mechanism. While reductions in disease resistance might increase the potential for farmed European-origin Atlantic salmon to contract disease and act as reservoirs, poor survival could also limit the potential of individuals to carry disease to wild populations. Introgression and resulting poor survival of farmed x native Atlantic salmon hybrids vulnerable to naturally occurring diseases would have direct consequences on wild populations. Furthermore, surviving hybrids could also serve as reservoirs for disease, increasing exposure of wild fish. In addition to concerns of introgression-related reductions in disease resistance of wild salmon, farmed European-origin Atlantic salmon could potentially alter the virulence of native diseases through a change in the selective environment of native pathogens (i.e., availability of new hosts, altered host/pathogen distribution, increased pathogen abundance). As farmed strain comparisons related to disease have not been conducted in controlled conditions (B. Glebe, DFO, pers. comm.), the extent of any impact on native Atlantic salmon and pathogens remains uncertain.

PREDATION

There is a poor understanding of the impacts of predation by farmed Atlantic salmon, particularly in Atlantic Canada (Leggatt *et al.* 2010). Domesticated salmon forage on similar prey to wild fish in freshwater and marine phases (Thorstad *et al.* 2008) and farmed (Pacific) salmonids (genus *Oncorhynchus*) have shown the capacity to prey on wild under-yearlings, albeit at low levels typically (Naman and Sharpe 2012). The larger size of farmed European-origin Atlantic salmon might enable them to prey on larger organisms (Sogard 1997) but the absence of information precludes evaluating this potential pathway with certainty. Certainly, the abundance of escaped Atlantic salmon, whether native or farmed European-origin, would be expected to influence the degree of impact on prey communities.

MARINE PHASE COMPETITION

There are few documented cases of farmed salmonids impacting wild counterparts through competition pathways in the marine environment (but see Holt *et al.* 2008 and Ruggerone *et al.* 2012 for Pacific salmon). For Atlantic salmon in their native range, evidence for density-dependent effects in the marine environment appears to be restricted to the Gulf of St. Lawrence where post-smolts show density-dependent growth for 1-2 months following entry to the marine environment (Friedland *et al.* 2009). Farmed-wild salmon interactions are not well understood in the marine environment but the weight of evidence suggests an absence of density-dependent effects on survival of salmon in the marine environment (e.g., Jonsson and

Jonsson 2004). Coupled with evidence of poor survival of farmed salmon and hybrids (Skaala *et al.* 2012), it is believed that relative to freshwater environments, competition impacts in the marine phase should be relatively small. Existing evidence does not suggest farmed European-origin Atlantic salmon would exceed farmed North American-origin Atlantic salmon in terms of ability to escape captivity, forage on wild prey types, or reach foraging grounds. Therefore, farmed European-origin Atlantic salmon would not be expected to have significant competitive effects on wild salmon in the marine environment.

FRESHWATER JUVENILE PHASE COMPETITION

Farmed, wild, and hybrid juveniles have similar habitat use and diet and therefore are likely to compete when occupying similar habitat (Thorstad *et al.* 2008). Outcomes of competitive interactions are context-dependent but can result in displacement of wild fish and lower production (McGinnity *et al.* 1997; Fleming *et al.* 2000; McGinnity *et al.* 2003; Leggatt *et al.* 2010). Farmed European-origin Atlantic salmon (e.g., Skaala *et al.* 2005), with more years under intentional (faster growth; Ferguson *et al.* 2007) and unintentional selection (earlier hatching; Berg and Moen 1999) and elevated aggressive tendencies (Leggatt *et al.* 2010), might be expected to have elevated competitive advantage over wild parr in freshwater environments relative to farmed North American-origin Atlantic salmon. Size and prior residency play an important role in dominance and could have population level effects when numbers are high enough that density-dependent impacts on productivity occur. Freshwater impacts would require that escapes occurred in the juvenile phase or that adult escapees were successful in producing offspring. Adult farmed European-origin Atlantic salmon may have lower performance (i.e., poorer reproductive success) than farmed North American-origin Atlantic salmon due to extended history of domestication, although this hasn't been confirmed. If so, the impact of farmed European-origin Atlantic salmon progeny could be mitigated by reduced numbers to some extent, but will vary with the magnitude of escapes and the health of the wild populations.

REPRODUCTIVE INTERFERENCE

Life-stage of escape and genetic factors play important roles in the reproductive ability of farmed Atlantic salmon (Thorstad *et al.* 2008). While size plays an important role in fecundity and the availability of opportunities to mate in the wild, semi-natural experiments indicate escaped adults typically have very inferior reproductive performance (reviewed in Thorstad *et al.* 2008). For males, reproductive performance can be 1–24% of wild conspecifics, while females have been documented to have <40% of the reproductive success of wild counterparts (Fleming *et al.* 1996, 2000). In contrast, precocious male parr of farmed-origin and farmed hybrids showed improved competitive ability relative to wild fish (Garant *et al.* 2003; Weir *et al.* 2005). Adult farmed salmon have been detected in rivers of the south coast, though not in great numbers where limited monitoring has occurred. Reproductive interference is contingent on farmed European-origin Atlantic salmon maturing and finding spawning grounds. It remains uncertain whether differences in origin or domestication history will impact the ability of adult farmed European-origin Atlantic salmon to reach spawning grounds and once there, interfere with wild salmon reproduction. However, based on the existing semi-natural trials listed above, it is unlikely that farmed European-origin Atlantic salmon would exceed the impacts of escaped farmed North American-origin Atlantic salmon. The exception being for male parr, whose increased size might be an advantage. While there is a poor understanding of reproductive interference under natural conditions (Thorstad *et al.* 2008), the observations of introgression on both sides of the Atlantic are evidence that it occurs.

Reproductive interference could also occur without direct interactions with wild fish. Spawning along the south coast typically occurs in late October to early November (B. Dempson, pers. comm.), while farmed European-origin Atlantic salmon are derived from stocks that spawn in November (Thorstad *et al.* 2008). Should farmed European-origin Atlantic salmon arrive at spawning areas after wild salmon (Ferguson *et al.* 2007; Thorstad *et al.* 2008), there remains potential to damage existing redds of wild salmon during spawning activities.

Overall, it is likely that the most severe reproductive interference will stem from fish that have lived in the wild since younger life stages (juvenile escapes or wild-born offspring), though high abundances of adult escapes could have large impacts. The potential for farmed European-origin Atlantic salmon to reproductively interfere with wild populations beyond the effects known for farmed North American-origin salmon remains unknown.

HYBRIDIZATION

Effects of hybridization are amongst the greatest concerns related to farmed European-origin Atlantic salmon (Naylor *et al.* 2005; O'Reilly *et al.* 2006). The extent of genetic consequences of hybridization are discussed more thoroughly in Verspoor *et al.* (2015), but an examination of the ecological implications of farmed European-origin Atlantic salmon is explored here. There is strong evidence indicating that greater genetic divergence associated with European-origin Atlantic salmon is expected to increase maladaptive traits due to out-breeding depression (Bourret *et al.* 2011; Homarus 2012). Outbreeding depression will affect ecological traits of disease resistance (discussed above), life history characteristics, physiology, and behaviour. The expected improvements to growth of farmed European-origin Atlantic salmon will have life history implications on wild salmon populations if introgression occurs. For instance, increased size is linked to a reduced probability of repeat breeding; an important loss, given the enhanced survival of repeat spawners in Atlantic Canada in recent years (COSEWIC 2011). Increased growth has also been linked to the prevalence of maturation in parr (Naylor *et al.* 2005; Ferguson *et al.* 2007), though selection for late maturity could in fact lower the occurrence of male parr (Ferguson *et al.* 2007). Timing of spawning (Thorstad *et al.* 2008) and egg incubation time (Berg and Moen 1999) also have a genetic component in Atlantic salmon, where natural selection is thought to optimize hatching and feeding times to local conditions. In Norway, farmed salmon maintained spawning timing consistent with their area of origin, despite variable run timing of native wild salmon in the various rivers to which they had dispersed (Thorstad *et al.* 2008). Therefore, spawning characteristics of native stocks could change with introgression of farmed European-origin Atlantic salmon.

Hybridization would also affect the survival of salmon through altered trait expression. Hybrids in the lab are less risk averse (Einum and Fleming 1997; Houde *et al.* 2010b), making predation-related mortality more likely. Additionally, changes to growth could have either positive (Sogard 1997) or negative (Cote *et al.* 2008) repercussions via selective foraging by predators.

Population level impacts are expected to be controlled by the frequency of hybridization and the abundance and health of the wild population (Ferguson *et al.* 2007). Paradoxically, the genetic divergence of farmed European-origin Atlantic salmon make it likely that the impacts of introgression, should they occur, will be relatively large (outbreeding depression), but this non-adaptive divergence also makes it less likely that introgression will occur due to the poor survival and performance of these fish in the wild. Therefore, impacts are only likely to occur if the exposure of wild fish to farmed European-origin Atlantic salmon is of relatively large magnitude or over extended temporal scales (e.g., Houde *et al.* 2010a). This is an important consideration, given that other risk elements like disease will be to a large extent affected by hybridization.

ENVIRONMENTAL FACTORS

The influence of the receiving environment on the persistence of European-origin salmon and its role in mediating impacts on native salmon is difficult to predict. While European-origin salmon will lack the local adaptation of native stocks, the extent of their ability to persist and thrive in the ocean and rivers of the south coast is difficult to forecast due to the complexity of interactions between fish and environment (e.g., adaptation, plasticity, acclimation, etc.) and the lack of experimental data (e.g., common garden experiments).

However, the environment of the south coast of Newfoundland has several features that could influence the severity of impacts of farmed European-origin Atlantic salmon. Perhaps most important, are the declining numbers of wild salmon in this area (COSEWIC 2011). Populations at low abundance are thought to be most vulnerable to introgression from farmed salmon. Low numbers of wild salmon would negate some of the reproductive deficiencies of farmed salmon (e.g., mate competition) and enhance their opportunities to spawn and hybridize. Furthermore, low numbers of wild salmon can speed introgression and increase the time for natural selection to remove maladaptive traits from a population in the unlikely event that pressure from farmed escapees ceases. Recent modeling of south coast rivers (DFO 2012) indicates that under current conditions there is a greater likelihood that salmon populations will continue to decline, further adding to their vulnerability. While farmed salmon can disperse great distances, escapees near maturity often enter nearby rivers (Thorstad *et al.* 2008). In freshwater, low juvenile abundance may limit the negative effects of competition, provided that farmed-origin salmon are also at low levels.

The south coast also harbors many genetically distinct landlocked populations. While some populations can occur sympatrically with anadromous conspecifics, many are isolated by barriers in a terrain characterized by high topological relief. These isolated populations will remain resistant to introgression from farmed salmon provided hatchery escapes do not occur above these barriers.

The south coast of Newfoundland is also characterized by the presence of fjords, whose sheltered waters are valued by the aquaculture industry for farming. The natural boundaries of these areas in concert with the retentive gyre-like nature of their currents (Bradbury *et al.* 2000), means that interactions among aquaculture sites and between wild and farmed salmon are more likely (Finstad *et al.* 2007). As suitable aquaculture locations in Atlantic Canada are not widespread, aquaculture sites occur in relatively high densities (Finstad *et al.* 2007). This increases the potential for transmitting mobile life stages of pathogens among sites and altering the pathogen environment experienced by wild post-smolts (Finstad *et al.* 2007; Krkosek *et al.* 2013), who are known to reside in fjords for several weeks before migrating out to sea (Dempson *et al.* 2011). Extended co-occurrence of wild and escaped fish in fjords could increase marine competition for smolts (e.g., Friedland *et al.* 2009). Furthermore, fjords likely focus farmed salmon impacts on local rivers (but see contrary evidence in Norway from Solem *et al.* (2012)). For example, fjord systems of the south coast of Newfoundland appear to contain the dispersal of escapees, who show a propensity to disperse to the rivers at the head of the fjord (Bridger and Garber 2007).

A final consideration needs to be made to acknowledge the remote nature of many areas of the south coast. This condition has limited the availability of information with which to assess the state of wild Atlantic salmon stocks along the south coast of Newfoundland (COSEWIC 2011) and has hindered the assessment of the consequences of interactions between wild and farmed Atlantic salmon escapees.

CONCLUSIONS

Escaped farmed Atlantic salmon may interact genetically with wild Atlantic salmon and ecologically with wild salmon and their habitats, but these interactions are strongly context- and location-dependent. There is significant evidence that escape events from aquaculture are inevitable (Naylor *et al.* 2005; Jensen *et al.* 2010) and that wild populations at low abundance will be most vulnerable to negative impacts (Thorstad *et al.* 2008; Leggatt *et al.* 2010; Krkosek *et al.* 2013).

Predicting ecological impacts along the south coast of Newfoundland remains difficult due to sparse information on the state of wild Atlantic salmon populations and the degree they are affected by farmed North American-origin Atlantic salmon. South coast Newfoundland Atlantic salmon populations are listed as “Threatened” (COSEWIC 2011), with subsequent analysis suggesting that, under existing conditions, further declines are likely (DFO 2012). Despite opposing trends of the health of wild stocks and expansion of the aquaculture industry, limited monitoring has provided little local epidemiological, genetic, or ecological evidence that links declines in wild stocks with aquaculture activities beyond the detection of low numbers of farmed salmon in some rivers.

Existing information suggests that farmed European-origin Atlantic salmon will have three primary effects that are mediated to some degree by the ability of these fish to hybridize with wild conspecifics. First, should genetic introgression occur, it is almost certain to change adaptive traits associated with disease resistance, life history, and ability to adapt to change. Such phenotypic changes are expected to be maladaptive (Fleming *et al.* 2000; McGinnity *et al.* 2003; Skaala *et al.* 2005; Darwish and Hutchings 2009; Bourret *et al.* 2011), occur quickly (Grant 2012), and take several generations to dissipate under favourable conditions of natural selection (Lawlor and Hutchings 2004, Hindar *et al.* 2006; Glover *et al.* 2012). Under poor population recovery conditions, such as low numbers of wild fish and/or chronic introgressive pressure, these changes may be more persistent. Second, assuming that freshwater escapes are limited through closed hatchery systems (i.e., no direct connection to freshwater systems), competitive interactions between farmed European-origin Atlantic salmon juveniles and wild Atlantic salmon will occur primarily through the interactions of farmed progeny. Selection during domestication, whether intentional (e.g., growth) or unintentional (e.g., aggression), may impart an advantage to hybrid Atlantic salmon when competing with wild juveniles. This could have greater population level impacts due to increasing hybrid abundance under density-dependent conditions (e.g., Elson 1975). Third, while reproductive interference can occur in the absence of successful mating (e.g., competition for mates or spawning habitat), successful hybridization exacerbates other related types of interference by consuming wild gametes that would otherwise contribute to pure wild genotypes (Homarus 2012).

Assessing the likelihood of hybridization is made difficult by the context-dependent nature of these interactions and the dynamic nature of conditions along the south coast of Newfoundland. Wild stocks along the south coast are in flux and are expected to continue to decline (DFO 2012), increasing their vulnerability to ecological and genetic interactions. Escapement rates (i.e., in terms of proportion of the farmed population) may remain low but still create ecological impact if the scale of the aquaculture industry continues to expand. Furthermore, changing environmental conditions have the potential to alter the fitness of both farmed and wild fish and alter ecological interactions. The inability of scientists to determine the mechanism for declining wild stocks (DFO 2012) only adds to the uncertainty as the potential for cumulative impacts cannot be assessed (Cairns 2001).

Assuming the use of disease-free gametes in south coast hatcheries, the risk potential for fish health-related impacts of farmed European-origin Atlantic salmon on wild salmon populations will be largely limited to pathways associated with genetic introgression (i.e., decreases in pathogen resistance in native populations), changes to native pathogen virulence, and altered prevalence of native pathogens.

There are considerable data gaps that exist regarding possible ecological impacts of farmed European-origin Atlantic salmon. Many aspects of farmed/wild interactions (e.g., reproductive interference) are derived from semi-natural conditions or natural experiments from other regions. In addition to the lack of data to assess the health of wild stocks on the south coast (COSEWIC 2011), the lack of monitoring activities targeted to assessing the current extent of escaped farmed salmon in the region means that the current impacts of farmed salmon interactions are less understood compared to other regions in the world. Inferring impacts to farmed European-origin Atlantic salmon is made even more difficult by the absence of controlled experiments that compare ecological traits (e.g., disease resistance) and performance (lifetime survival) of strains of farmed salmon under conditions reflective of the western Atlantic, let alone the south coast of Newfoundland. Not only does this limit assessments of specific impacts but also the ability to conduct risk (e.g., Pearsons and Busack 2012) and cost-benefit assessments related to introducing foreign strains.

Past decisions regarding the importation of farmed European-origin Atlantic salmon in eastern North America highlighted the lack of certainty regarding the extent and severity of farmed European-origin Atlantic salmon – wild salmon interactions as the primary reason for recommending against importation (DFO 1999; National Research Council 2003; Newfoundland and Labrador Introductions and Transfers Committee 2011). Despite many advances in our understanding of wild-farmed salmon interactions, the uncertainties loom large when paired with the potential magnitude of negative effects on threatened wild stocks and the logistical challenges of adequately monitoring impacts in a remote environment.

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