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Gulf Region

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Science Advisory Report 2016/017

RISKS AND BENEFITS OF JUVENILE TO ADULT CAPTIVE-REARED SUPPLEMENTATION ACTIVITIES TO FITNESS OF WILD ATLANTIC SALMON (*SALMO SALAR*)

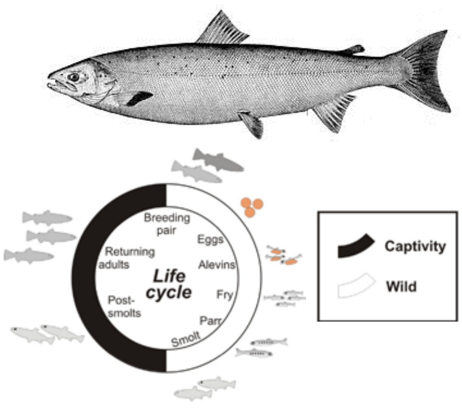

Figure courtesy P. O'Reilly (DFO)

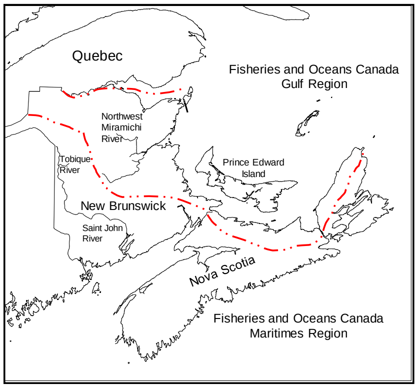

Figure 1. Location of rivers mentioned in text and of Fisheries and Oceans Canada Gulf Region in the Maritime Provinces.

Context:

In response to particularly low returns of Atlantic salmon to the Northwest Miramichi River (New Brunswick, Canada; Fig. 1) in 2012 to 2014, a group of non-government organizations in New Brunswick proposed a stock supplementation program consisting of the capture of wild Atlantic salmon smolts, rearing these in captivity in freshwater to the adult stage, and subsequently releasing the adult captive-reared fish back to the river (Appendix 1). This activity is intended to circumvent the low marine smolt to adult return rates of Atlantic salmon and to increase spawning escapement. Rearing of wild captured Atlantic salmon juveniles to adult stages in captivity, and release of captive reared adults to targeted rivers to spawn, has been undertaken by DFO Maritimes Region as one of the recovery actions for endangered populations of salmon in the Inner Bay of Fundy and in the Saint John River (NB; Fig. 1) however it has not been done for salmon populations in Gulf Region that are not considered at risk of extinction.

As a precedent setting activity for supplementation of Atlantic salmon populations in DFO Gulf Region, a science peer review was recommended to provide advice to DFO Fisheries and Aquaculture Management, the sector responsible for issuing the permits for such an activity. The advice provided will be relevant in the context of the proposed captive-reared adult supplementation activity for the Northwest Miramichi River and could be used to address similar requests in other watersheds should these arise. The science review does not consider the risks of juvenile (fry, parr, or smolt) supplementation programs which currently occur in several DFO Gulf Region rivers.

This Science Advisory Report is from the regional science peer review meeting of December 14 to 16, 2015 to review the risks and benefits of adult captive-reared supplementation activities to fitness of wild Atlantic salmon. Participants at the review included DFO Ecosystems and Oceans Science (Gulf, Maritimes, Newfoundland and Labrador, Pacific, and National Capital regions), DFO Ecosystems and Fisheries Management (Gulf), invited national and international experts, participants from the proponent NGO groups, provincial governments of the Maritime provinces, and aboriginal organizations.

April 2016

SUMMARY

- This review was challenging due to the paucity of information available to assess the benefits and risks of juvenile/smolt to adult supplementation (SAS).
- SAS consists of the capture of juvenile salmon at freshwater stages, rearing them in a captive environment to maturity, and releasing the adults back to the rivers of origin to spawn. The anticipated benefits to salmon populations are by circumventing the marine phase of the life cycle thereby resulting in a demographic boost in abundance of salmon populations subjected to low marine survival.
- Currently, SAS is being used in areas where salmon populations are at high risk of extinction and in cases where very low numbers of adult salmon are putting the population at risk of loss of genetic diversity which could affect long-term population viability.
- SAS reduces some of the known risks associated with traditional supplementation of juvenile stages but introduces risks at other points in the anadromous life cycle that are not well understood.
- Adaptive genetic changes associated with captivity through unintentional selection, domestic selection, and relaxation of natural selection can occur rapidly, even within one generation.
- An immediate benefit resulting from an increased abundance of salmon as a result of the increase breeding/spawning of SAS fish may be offset by the expectation that mean fitness of the captive-reared progeny will be reduced relative to wild fish. The reduced fitness may be the result of phenotypic differences (body size, growth rates, maturation rates) and in reduced survival at sea of progeny inherited from the parents. Some of these effects may manifest themselves in the first generation and for several generations following release of adults.
- Genetic mixing by interbreeding of released captive-reared SAS fish with wild fish is expected to occur. As long as there is some risk that SAS will cause phenotypic and genetic changes that reduce fitness of progeny in the wild, there is a risk that genetically mixed progeny may have reduced fitness in the wild. The risks to wild population abundance and characteristics will in general be greater when:
    - (i) SAS generates reductions to fitness of progeny relative to wild fish,
    - (ii) SAS is continuously practiced over successive generations, and
    - (iii) SAS releases represent an increasing proportion of the total number of adults in the population at spawning time.
- River populations in which there is sub-basin structuring with local adaptation at the tributary level are more likely to be negatively impacted by SAS conducted on a basin wide scale, unless collection and release of adults is conducted on a tributary basis.
- Within limits, as the scale of the SAS activity increases, the extent of potential benefits will increase, monitoring capacity and the power of assessment due to larger numbers of animals will increase, but the risks overall to the wild populations of salmon will also increase. The scale dimensions are spatial (size of the basin), demographic (number of animals being monitored) and temporal (seasons and years) and these characteristics should be considered in any decisions on proposed SAS activities.
- Due to the large uncertainties on the benefits and risks of SAS activities to wild Atlantic salmon fitness, if a SAS activity is conducted, it should be at a geographic and demographic

scale that allows and includes an adequate monitoring and assessment capability to address the vast knowledge gaps on benefits and risks to wild salmon population persistence and productivity.

- The monitoring and assessment capabilities using genomic tools are improving rapidly. The development of new genetic markers and high throughput technologies will augment the capacity to evaluate parentage of progeny and to assess relative fitness and contributions to future generations of wild, SAS, and wild/SAS interbred salmon.

INTRODUCTION

The objective of most Atlantic salmon supplementation programs historically has been to increase adult abundance to support fisheries or to mitigate freshwater anthropogenic impacts. These programs frequently involved the capture of returning adult salmon, artificial spawning in captivity, and release of juveniles at various stages into native river habitat (Fig. 2). The choice of life stage to release in order to increase juvenile production and ultimately adult returns can depend upon the life history stage that is constraining adult abundance:

- If spawning success, survival of eggs in the redd or even early stage survivals in freshwater are low, then artificial spawning and use of incubation boxes or stocking as unfed fry or at first feeding fry stages, is a reasonable measure to boost juvenile production and adult returns.
- If density dependence in freshwater occurs early, for example between the egg to fry stage, then artificial supplementation with post-fry stages when abundance at older ages is seemingly density independent, may increase total smolt production and adult returns.
- If the freshwater rearing environment is at carrying capacity or there are important anthropogenic mortality factors during the downstream smolt migration, artificial supplementation at the smolt stage could be considered to increase adult returns.
- Translocation of wild adults from other tributaries within the same river or from neighbouring rivers has also been used to initiate juvenile production in rehabilitated habitat or when previously inaccessible habitat has been opened up for production. Provided the removal of adults from the donor river is of minimal concern, this would be preferable to using adults reared in captivity for all or a portion of their life cycle.

The bulk of the scientific studies and literature regarding effects of captive-rearing and supplementation of Atlantic salmon have addressed the impacts of spawning in hatcheries and supplementation of various juvenile stages from eyed eggs to the smolt stage though some research has been carried out on Pacific salmonids (Fraser 2008). Previous reviews and empirical works on the genetic risks and demographic benefits of captive-rearing have routinely recommended that the risks to wild populations can be substantially reduced by, among other things:

- reducing the duration of time spent in captivity of single generations,
- reducing the number of generations spent in captivity,
- minimizing environmental differences between wild and captive environments with the objective of minimizing phenotypic differences between captive and wild salmon,
- restricting captive breeding to life history stages for which natural mortality and hence selection pressures in the wild are lowest, and

- allowing free mate choice when risk of inbreeding is low.

More recently, an alternative intervention, juvenile/smolt-to-adult supplementation (SAS) has gained favour in some circles, wherein juveniles or migrating smolts are captured, captive-reared until maturation, and subsequently released back to the river, usually directly in freshwater, to spawn (Fig. 2). Due to its recent development, much less empirical data are available to adequately describe the risks and benefits of SAS programs to wild populations of Atlantic salmon.

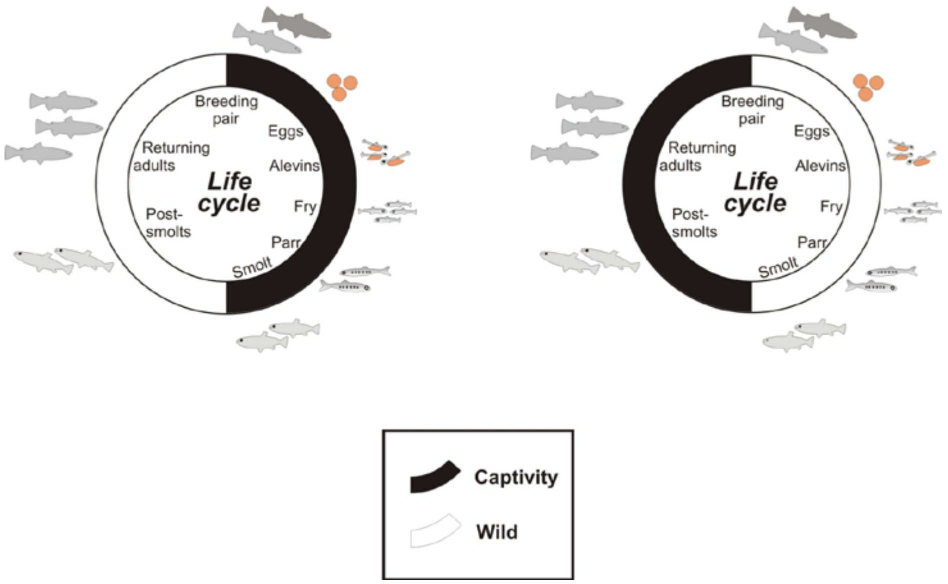

Figure 2. Contrasts between juvenile supplementation programs (left panel) and juvenile/smolt to adult supplementation (SAS) programs (right panel) in terms of life stages and processes which are impacted by captive rearing and those which occur in the wild (figure courtesy of P. O'Reilly, DFO).

SAS activities may be of benefit when the transition from smolt migration to adult returns is affected by sufficiently excessive levels of mortality that adult returns are reduced to the point where freshwater juvenile production declines substantially below carrying capacity. In that situation, adult captive reared supplementation, which circumvents the marine phase, may maintain adult escapement and naturally increase juvenile production levels to avoid the population entering an extinction vortex.

Given the general considerations above regarding juvenile supplementation activities, and in circumstances of low marine survival of the anadromous salmonid strategy, the interception of wild smolts, rearing them in captivity until the adult stage, and subsequently releasing the adult captive-reared fish back into the river of origin to complete the life cycle is attractive. Such a program would respect a number of the considerations for reducing risks to wild populations described above because:

- SAS would use local fish,
- SAS would avoid captive rearing at early life stages that experience high and generally density dependent mortality,
- SAS could conceivably minimize some environmental differences between captive and wild environments if the rearing conditions mimicked those encountered by anadromous salmon,

- SAS would allow for possible intra-male competition and female mate choice in the wild, and potential benefits of associated sexual selection for reproductive traits, and
- SAS could provide a measurable and predictable input to adult population size where nature has already had a role in the selection process throughout the first several years of freshwater life.

In the extreme case where marine survival rates are essentially zero, and alternative (non-anadromous) life histories cannot demographically rescue a declining anadromous population, recourse to live gene banking intervention, rather than natural mating processes that would be provided by SAS, may be the only effective means of maintaining genetic diversity (DFO 2008).

Like all forms of supplementation involving some captive-rearing, however, SAS is not without risks. This advisory report, and supporting documents, consider five key issues associated with SAS of Atlantic salmon:

1. the genetic risks of SAS to short and long-term fitness;
2. the ecological risks of SAS;
3. criteria and metrics for assessing risk of SAS;
4. conditions under which SAS could be considered a negligible risk to wild Atlantic salmon fitness; and
5. a specific assessment of risk to wild salmon of a proposed SAS activity of the Miramichi River, New Brunswick, Canada.

ASSESSMENT

The majority of SAS programs to date were initiated in areas where salmon populations were at high risk of extinction due to demographically very low numbers of adult salmon putting the population at risk of negative genetic consequences. Only the experiment at Conne River, Newfoundland (Dempson et al. 1999) was attempted to compensate for continued low abundance of salmon for a population not considered at risk of extinction. The increased use of SAS in the recovery actions for endangered Atlantic salmon populations of the Inner Bay of Fundy and the Outer Bay of Fundy and the associated monitoring programs are providing empirical data with which to assess the benefits of such recovery actions as well as information on unintended risks to fitness of wild Atlantic salmon populations (DFO 2008; Jones et al. 2014).

Review of risks of supplementation activities to fitness of wild Atlantic salmon

For purposes of this assessment, fitness is defined as the capacity of individuals within a population to survive and reproduce successfully. Fitness depends on the environment in which the organism lives. Fitness is most often referred to in relative terms of how many surviving offspring are produced by particular groups of individuals, such as wild versus SAS origin parents.

The degree to which average short-term (first generation) and long-term fitness (successive generations) in a population are affected will depend on a number of factors, including whether SAS is practiced continuously or intermittently, the proportion of individuals in the population that experience SAS, the environmental conditions under which SAS salmon are reared, and specifically how much these conditions differ from those to which a wild population is normally exposed (Fraser 2016).

The extent to which fitness reductions are irreversible in the longer-term is a largely open question, however, indirectly, the establishment of feral populations of salmonids from domesticated hatchery strains suggests that maladaptive genetic changes due to exposure to captive rearing can be overcome in some situations.

Adaptive Genetic Changes

Adaptive genetic changes to captivity can occur rapidly, even in one generation. Owing to environmental conditions and selective pressures that invariably differ between captive and natural environments, the captive environment may cause plastic and genetic changes to phenotypes resulting in reduced fitness of captive-reared individuals when they are released into the wild. These environmental and selective pressure driven changes can occur in all aspects of phenotypes including morphology, life history, behaviour, physiology, and disease resistance.

Dempson et al. (1999) in an experiment involving the rearing in sea cages of wild Atlantic salmon smolts from Conne River (Newfoundland), reported that 1SW caged-reared salmon of the same smolt class as wild sea run 1SW Atlantic salmon returning to Conne River were significantly smaller at length (~46 cm vs 51.8 cm) and weight (~1.2 kg vs 1.54 kg).

In the Saint John River (New Brunswick), captive reared female salmon after one year in freshwater captive rearing were consistently shorter than all sea run female anadromous salmon. After two years in freshwater rearing, they were approximately the same length as wild 1SW maiden sea run fish and after three years in freshwater rearing they were at a size intermediate between wild 1SW and wild MSW (predominantly 2SW) anadromous salmon with exception of a few years when they were as long as wild MSW salmon (Fig. 3). The differences in size are mostly due to the exclusion of the marine phase rather than having spent any part of its life cycle in the hatchery because the anadromous strategy produced returning adults of identical size at maiden sea age for both wild origin smolts and smolts originating from hatchery supplementation at juvenile stages.

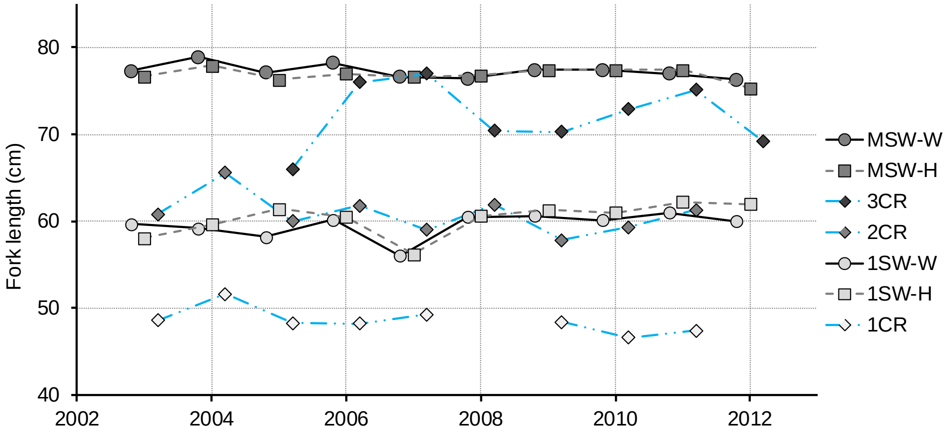

Figure 3. Fork length (cm; mean) of female Atlantic salmon from the captive reared freshwater program (CR) by year in the hatchery (1CR, 2CR, 3CR) and sea run anadromous salmon by sea year which were of wild origin (1SW-W, MSW-W) or hatchery origin (1SW-H, MSW-H) from the Saint John River (NB), 2003 to 2012 (Jones et al.2014). Points are offset from the year for clarity.

Genetic adaptation to captivity can affect fitness

Maladaptive genetic changes in captivity (collectively referred to as domestication selection; Waples 1999) can occur via two chief mechanisms: (i) through unintentional selection, or (ii) through relaxation of natural selection (Fraser 2016). Unintentional selection might occur at the earliest stage of SAS during the collection of smolts if these collections do not represent the full spectrum of smolt migration timing, body size, or other characteristics. It will arise if any non-random die-offs occur during captive-rearing, or through carry-over effects.

In the sea-cage rearing experiment at Conne River, (NL), Dempson et al. (1999) reported that mortalities increased post-transfer and peaked in July with the smolts that died being smaller than the average size of wild smolts that emigrated from the river. The dead smolts sampled in July had lost a substantial amount of weight and had seemingly not taken to feeding, exhibiting characteristics of failed smolt syndrome (Dempson et al. 1999).

There are important differences in the proportion female within the SAS captive reared age groups and compared to the anadromous salmon life histories from the Saint John River (Jones et al. 2014). The anadromous life history produces distinct and temporally consistent differences in the sex ratio at sea age of return, with females generally less than 10% in the 1SW maiden group and generally greater than 80% in the MSW salmon group (Fig. 4). For the captive-reared salmon, females comprised no less than approximately 40% of mature adults after one year in captivity, increasing to 60% to 90% or more after two and three years in captivity (Fig. 4). The juveniles that contributed to the captive-reared programs in those years were from fall pre-smolt and parr collections and spring smolt collections (Jones et al. 2014). Sampling of juvenile collections indicated that pre-smolts were predominately female (80%) while the parr were predominately precocious males. This may be sufficient to explain the high proportion females in the captive reared adults. The differences in the sex ratio of captive-reared adults compared to anadromous adults is an example of unintentional selection.

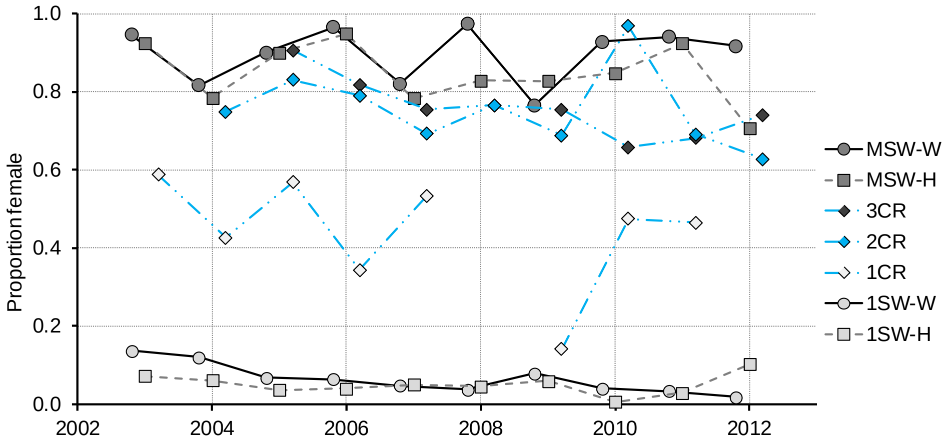

Figure 4. Proportion female of Atlantic salmon from captive reared freshwater program (CR) by year in the hatchery (1CR, 2CR, 3CR) and sea run anadromous salmon by sea year which were of wild origin (1SW-W, MSW-W) or hatchery origin (1SW-H, MSW-H) from the Saint John River (NB), 2003 to 2012 (Jones et al.2014). Points are offset from the year for clarity.

The consequences of this are apparent when comparing the proportion of a smolt class that return as females, over all anadromous or captive reared age groups (Fig. 5). The captive-reared program has produced mostly (> 60%) females for each smolt class collected whereas the anadromous strategy, wild or hatchery origin, has produced more males (55% to 85% male) per smolt class (Fig. 5).

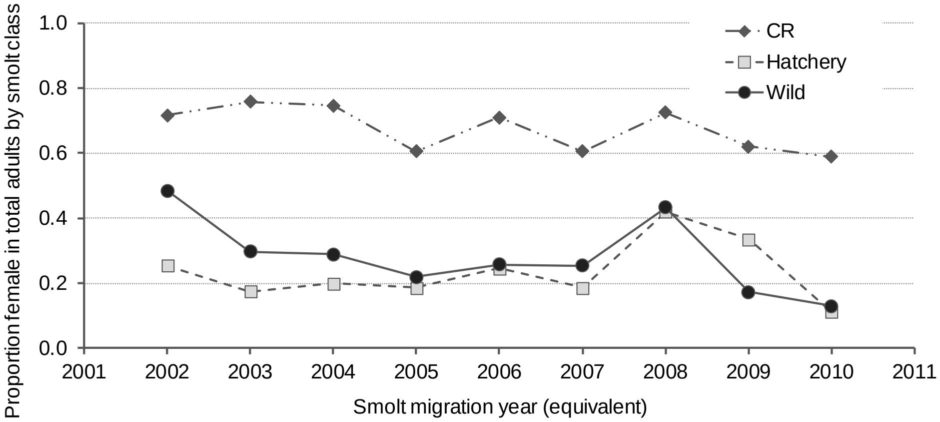

Figure 5. The proportion female in the total adults produced from the captive reared freshwater program (CR), and by the anadromous strategy for wild (W) and hatchery origin (H) Atlantic salmon by smolt class from the Saint John River (NB). Data are based on published total returns of wild and hatchery origin salmon (Jones et al. 2014; Table 3) combined with the life history characteristics by origin and age groups (Jones et al. 2014; Tables 7a, 7b, 7c). For the captive-reared program, smolt migration year refers to the year in which the juveniles collected would have become smolts.

Relaxation of natural selection

Marine mortality is considered to be the most important threat to recovery of salmon populations at risk of extinction and in some of these situations, SAS and other interventions (such as live gene banking) are being used to prevent extirpation, minimize loss of genetic diversity, and maintain Atlantic salmon populations until conditions, primarily marine, become favorable (DFO 2008).

Although demographically-speaking, SAS avoids captive-rearing of the early life stages which experience high mortality in freshwater in the wild (cumulative mortality from egg to smolt of 96.8-99.8%), smolt-to-adult mortality is still very substantial in wild Atlantic salmon, commonly attaining 98.5% or higher in recent years.

Because smolt-to-adult mortality will be much lower using SAS than what is realized in the wild, relaxation of natural selective pressures is likely. Based on empirical evidence from related studies, the relaxation of natural selective pressures would be associated with factors such as predation in the marine phase, marine parasite/pathogen resistance if rearing is conducted in freshwater ponds or land-based seawater ponds and/or marine net pen enclosures since all these environments will be highly divergent from the marine conditions experienced by anadromous migrants. Wild populations undergoing SAS may also experience relaxed selection for traits associated with social interactions (rearing in high densities, schooling, aggression), migratory vigor (from being contained in rearing environments), activity levels (swimming, orientation, feeding), and homing, particularly in populations with longer-distance migrations.

Atlantic salmon populations exhibit a considerable degree of local adaptation in freshwater at different geographic scales. Although little is known of local adaptation in the marine phase of anadromous salmonid life cycles, adaptation to different marine areas would be expected. Studies of Atlantic salmon and Pacific salmon report lower return rates of hatchery smolts to common rivers originating from distant stocks compared to those of local stocks. More importantly, local adaptations in freshwater are intimately linked to the marine phase in anadromous salmonids (Fraser et al. 2011). It is not unreasonable to hypothesize that, all else being equal, the more locally adapted a wild Atlantic salmon population is to the marine phase of the life cycle, or to the freshwater-to-marine transitional phase, the more likely SAS will result in maladaptive phenotypic and genetic changes that affect wild fitness.

For example, it is likely that individual growth, maturation, and morphological shape trajectories, any correlated behavioural traits (e.g. boldness, aggression), female reproductive allotment (egg size, fecundity), behavioural traits associated with living at higher densities (stress responses) and pathogen resistance will change under SAS captive-rearing, whether reared in marine or freshwater, and these changes may affect subsequent reproductive success and/or offspring survival in the wild (Fleming et al. 1997; Jonsson and Jonsson 2006; Lawlor et al. 2009).

Interbreeding between SAS and wild salmon

An additional genetic risk of SAS is the inter-breeding of released captive-reared SAS fish with wild fish. As long as there is some chance that SAS will cause phenotypic and genetic changes via domestication selection that reduce fitness of progeny in the wild, there is a chance that SAS-wild interbred progeny will have reduced fitness in the wild (Fraser 2016). The extent to which inter-breeding will occur and generate maladaptation will depend on a host of factors including if genetic and ‘plastic’ risks from captive-rearing are minimized and whether the proportion of SAS fish relative to the total adult abundance (SAS + wild) is small (Hutchings and Fraser 2008). It is unlikely that SAS fish could be reared to be so different from their wild counterparts that captive-wild interbreeding does not occur, although if this was possible, such a strategy could provide fishing opportunities without necessarily impacting the genetic integrity of the wild population.

Non-genetic changes and carry-over effects

Captive-rearing can also generate carry-over effects on fitness in the wild. In salmonids, maternal provisioning in offspring is heavily influenced by the environmental conditions that a female experiences (temperature, density, nutrition) and these maternal effects can also have a genetic component that affects juvenile offspring growth and survival.

Captive rearing environments have also been hypothesized to generate heritable epigenetic changes that may also affect the fitness of offspring of hatchery salmon in the wild (O’Reilly and Doyle 2007; Araki et al. 2008). This is not a well-studied phenomenon in salmonids and the effects when examined are not always manifest. Some recent studies have found a relationship between epigenetic variation and life history divergence suggesting that such epigenetic changes might arise if captive rearing elicits life history change.

Ecological considerations of wild versus cultured fish interactions including disease, competition, predation, compensatory mortality

SAS might affect the breeding fitness of released adults (Fraser 2016). Captive-reared males are generally inferior to wild males in courting, in competing for females and in spawning. Captive reared females may also be more likely to retain eggs and less likely to construct or cover nests. Depending upon the program and despite their reduced individual breeding fitness, captive-reared adults can substantially outnumber wild adults and produce a considerable number of juvenile offspring (Jones et al. 2014). Particularly through density dependent mechanisms and when captive-reared fish differ strongly in characteristics from wild fish (e.g. body size, behaviour, aggression), captive-reared fish may displace wild fish to some extent, and contribute to the depletion of wild populations through competition for space and disruption of breeding opportunities (Jonsson and Jonsson 2006).

Because captive-reared fish are reared at higher densities than in the wild, they are commonly susceptible to increased pathogen or parasite exposure and may experience genetic changes associated with differing pathogen/parasite regimes or loading. Hence, captive-reared fish could potentially act as a vector of disease to wild fish and may also contribute to the depletion of wild populations.

In some situations, the state of maturity of SAS fish can only be determined late in the year (fall) and depending upon the date and point of release, SAS fish may not have access to the areas which they originated as juveniles. If SAS fish undertake earlier spawning, offspring may emerge earlier. This may provide a short-term growth/survival advantage in occupying the best feeding territories at early life stages before offspring of later spawning wild fish arrive. Alternatively, early emergence may result in higher mortality if exogenous feeding does not commence before exhaustion of yolk sac nutrients. Later spawning by captive-reared adults has the risk of disturbing wild fish redds and ultimately decreasing survival of wild fish.

Atlantic salmon populations are regulated primarily by density-dependent mortality at juvenile life stages in freshwater (Chaput et al. 2016). If the freshwater juvenile recruitment dynamics are strongly compensatory, the expected gain in smolt production and subsequent adult returns by supplementing the spawning escapement with captive-reared adult spawners will depend upon the abundance of juveniles in the river before supplementation. In addition, due to strong density dependent survival, the addition of a large number of captive-reared adult progeny to the river could result in increased density-dependent mortality of progeny of wild spawners. Although numerically, the abundance of the juveniles may appear to have benefited overall, any reduced fitness of the captive-reared progeny resulting from phenotypic differences (body size, growth rates, maturation rates) and in reduced fitness of survival at sea of wild / SAS interbred progeny inherited from the parents will result in reduced abundance of wild Atlantic salmon.

Criteria and metrics for assessing risk of captive-reared adult supplementation program

The criteria and metrics for assessing the genetic and ecological risks from conducting SAS are based on two contexts: (i) how much captive-reared fish might deviate from wild phenotypes (and/or underlying genotypes), and (ii) the proportion of SAS fish relative to the total population size of a supplemented wild population (Fraser 2016) The first context accounts for how much maladaptation SAS might be generated in a species whose general biology is founded in the local adaptation of phenotypic traits (Appendix 2). The second context accounts for how the magnitude of the effects of maladaptation from SAS might affect wild salmon population productivity and persistence (Appendix 3). The criteria, metrics, genetic and ecological considerations, weight of evidence and the assessed risk to long term fitness are summarized in Appendices 2 and 3.

Conditions under which captive-reared adult supplementation programs would be considered negligible risk to fitness of wild Atlantic salmon populations

For purposes of this analysis, negligible risk is defined as an impact on the productivity of the wild population which can be mitigated by the wild population within one generation once the impact ceases. Generation time for Atlantic salmon is relatively short, in the range of 5 to 6 years for most populations.

A number of factors need to be considered in assessing risk to fitness: heritability of traits that affect fitness (growth rates, age at maturity, run-timing, disease and pathogen resistance), the extent of fitness loss associated with captivity as well as for hybrids, and the proportions which captive reared spawners represent of all spawners (Fraser 2016). Because SAS supplementation is a recent activity, there is less empirical evidence available to quantify risks to long-term fitness of wild populations and under what circumstances SAS supplementation may be considered negligible risk.

In salmonid fishes, phenological traits and some morphological traits that could be affected by SAS strategy have high heritability, but many physiological traits associated with migration have not been thoroughly studied in salmonids. Values of generational fitness loss in captivity of 30-60% per generation are frequently reported in literature (Fraser 2016). Carry-over effects of captive rearing per se (e.g. how maternal effects can modify subsequent offspring performance) and how these might affect fitness must also be considered. Finally, the effect of captive-wild interbreeding on successive generational losses to fitness must also be considered because SAS fish might represent a large proportion of spawning adults, especially within a small, supplemented population.

With respect to population productivity, short-term, intermittently conducted SAS will pose less risk to wild Atlantic salmon. The risks to wild population productivity increase, and likely cannot be mitigated by the wild population within one generation once ceased, when SAS:

1. generates greater reductions to wild fitness,
2. is continuously practiced over successive generations, and
3. represents a greater proportion of the total number of adults (or of either sex) in the population.

Risk assessment of captive-reared adult supplementation activity to wild Atlantic salmon of the Miramichi River

Atlantic salmon population of the Miramichi

The Atlantic salmon population of the Miramichi is characterized by complex phenotypic diversity (Chaput et al. 2016). Juvenile salmon rear in freshwater for two to five years, with most migrating to sea after two and three years. The population has important one-sea-winter (1SW) and multi-sea-winter (MSW) maiden spawner components and diverse spawning history strategies including important conributions of repeat spawners. In any given year, there are six year classes of immature fish in the combined freshwater and marine ecosystem. There are increasing numbers of repeat spawners and recently, up to nine year classes of salmon are present in the spawning run (exclusive of precocious male parr). There are important and consistent differences in size at spawning history (Fig. 6) and reproductive contributions of female salmon are enhanced by increased body size with sea age, increased egg size and fecundity with increasing body size and diverse spawning habitat utilization.

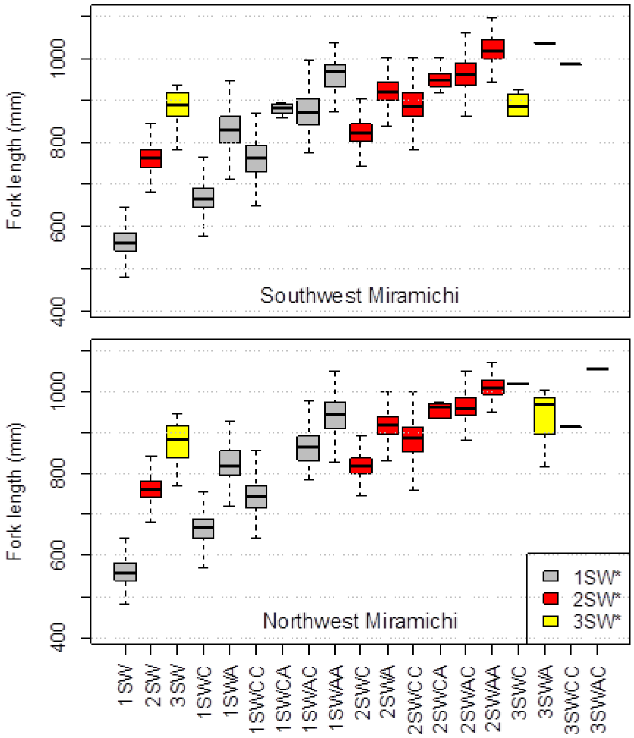

Figure 6. Boxplots of fork length (mm) distributions of wild Atlantic salmon from the Southwest Miramichi system (top panel) and the Northwest Miramichi system (bottom panel) by spawning history type from 1992 to 2013 (Chaput et al. 2016). The 1SW, 2SW and 3SW labels are maiden first time spawners. The other categories are repeat spawners according to sea age at first spawning followed by a sequence of repeat spawner types, with C representing consecutive spawning life history and A representing alternate spawning life history. Single letters (C, A) are categories of fish on a second spawning. CC, CA, AC, and AA represent categories of fish with three or more spawning events with the first two repeat spawning histories indicated by the letter codes.

Several phenotype characteristics of Atlantic salmon are consistent with sub-basin population structuring in the Miramichi:

- Annual run-timing to the rivers is characterized by a bimodal seasonal distribution with the first mode occurring in the summer (prior to August 31) and the second in the fall (after August 31) (Fig. 7). Early and late run contributions have changed over the past decade to a dominant summer mode, consistent for both large salmon (>= 63 cm fork length) and small salmon (< 63 cm fork length) and on both major branches of the Miramichi River (Douglas et al. 2015; Fig. 7).
- Salmon in headwater areas of the river at higher elevations are predominantly fish from the early run and the proportions of late run salmon increase at lower elevation sites in the river.

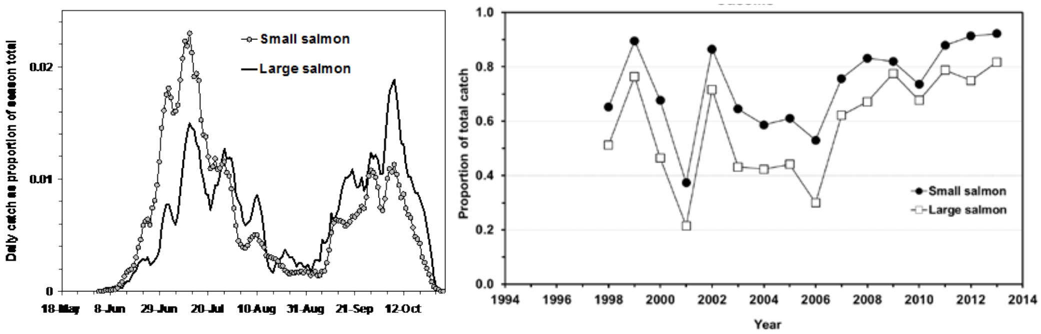

Figure 7. Seasonal timing of catches of small salmon and large salmon at estuarine trapnets in the Northwest Miramichi (left panel) and the proportion of the total annual catch at the estuary trapnets in the Northwest Miramichi which were taken prior to September 1 during 1998 to 2013 (right panel).

There are important sex ratio biases between the maiden sea age groups with males more abundant in 1SW salmon and females more abundant in 2SW salmon. There are important sex ratio differences within 1SW salmon with higher proportions of females in the early runs compared to the late runs (Fig. 8). This is not the case for 2SW salmon. There are higher proportions of female in 1SW salmon from Northwest Miramichi compared to Southwest Miramichi.

Atlantic salmon from the Miramichi undergo long oceanic migrations and were historically harvested in marine commercial fisheries of Gulf of St. Lawrence, Newfoundland, Labrador, and presently are harvested in the mixed stock fisheries at St. Pierre and Miquelon, and Greenland. Both smolts and alternate repeat spawners undertake the long distance migrations to Greenland. Some salmon are also found in the vicinity of Faroes (northeast Atlantic) in second winter at sea and can return to the Miramichi within five months.

Estimated adult abundance of all sea age groups to the Miramichi River overall varied from 17,745 to 74,940 fish during 1998 to 2014 (DFO 2015). Annual returns of all anadromous sea age groups to the Northwest Miramichi system, representing about one third of the salmon rearing habitat of the Miramichi, varied from 2,500 to 23,000 fish over the same period. Returns of small salmon and large salmon in 2014 were lowest of the time series for the Northwest Miramichi beginning in 1992. Indices of returns of small salmon in 2015 indicate improved abundance compared to 2012 to 2014 with indices of large salmon in 2015 similarly improved from 2012 to 2014.

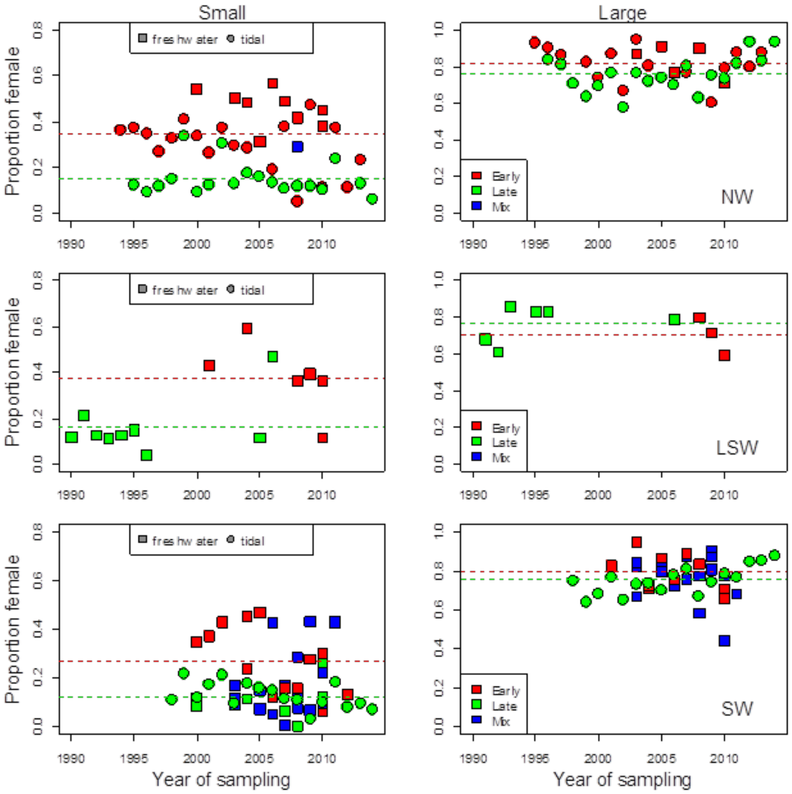

Figure 8. Proportion female in small salmon (left column), large salmon (right column) by season of return group (early, late, mixed) from samples in the Northwest Miramichi system (top row), the Little Southwest Miramichi River (middle row), and the Southwest Miramichi system (bottom row) (Chaput et al. 2016). Square symbols represent samples obtained at freshwater locations (counting fences, seining) whereas circles are samples from estuary trapnets. Horizontal dashed lines and corresponding colours are the means of the samples in each panel.

Juvenile abundances were at low levels until the late 1970s, increased following on targeted fisheries closures in 1984, peaked in the late 1990s and generally declined since. Trends in small parr were similar to those of fry. Trends in large parr abundance indices have increased over the period 1971 to 2014 in both the Northwest and Southwest systems with large parr abundances higher in the Northwest compared to the Southwest (DFO 2015; Chaput et al. 2016).

Stock and recruitment analyses of indices from the Northwest and Southwest Miramichi indicate that the most important density dependent control occurs between the egg and fry stage (Fig. 9). Fry densities, although highly variable annually, remain at moderate levels in all rivers despite the decline in egg depositions since the peaks of the early 1990s (DFO 2014; Douglas et al. 2015; Chaput et al. 2016).

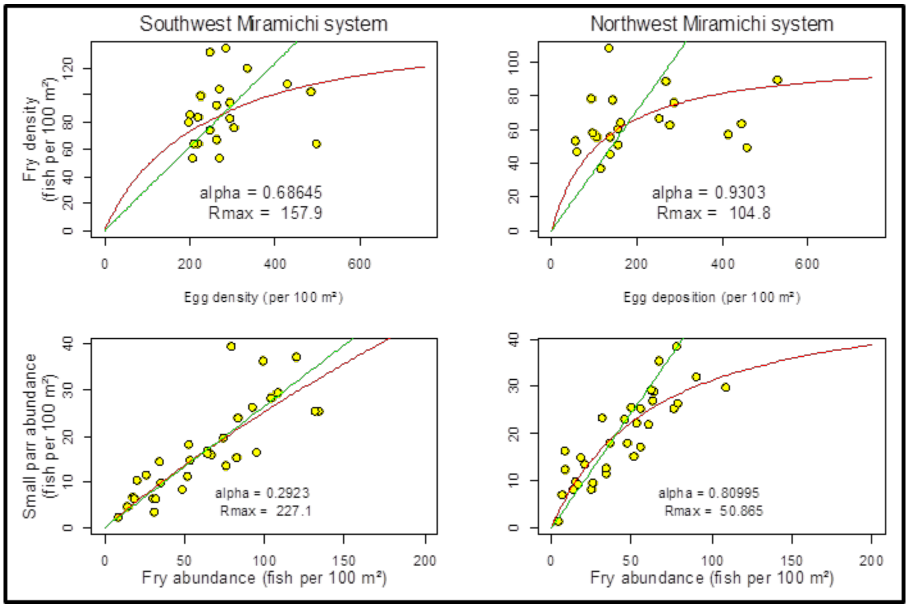

Figure 9. Stock and recruitment analyses of egg deposition rate (eggs per 100 m²) in year i to index of fry abundance (fry per 100 m²) in year i+1 (upper row; 1992 to 2013 spawning years with available data) and of fry abundance index in year i to index of small parr abundance in year i+1 (lower row; 1971 to 2013 spawning years with available data) for the Southwest Miramichi system (left column) and the Northwest Miramichi system (right column). The red line in the upper row panels is the median Beverton-Holt stock and recruitment curve whereas the green line is the median proportional linear fit (with multiplicative error) of the same data.

Risk assessment of captive-reared supplementation to Miramichi

The smolt to adult supplementation proposal provided to DFO in May 2015 (Appendix 1) consisted of an initial capture of 1,500 Atlantic salmon smolts from the Northwest Miramichi in 2015, for rearing in freshwater facilities, and release back to the Northwest Miramichi River to spawn. Although not specified in the project description in Appendix 1, but based on subsequent discussions, it was indicated that the mature adults from this program would be released in tidal waters to allow the fish to migrate to their river of origin and that the program would be expanded in the future with the objective of achieving egg depositions by wild and captive-reared adults corresponding to the conservation requirements for the Northwest Miramichi.

The proposed collection of 1,500 Atlantic salmon smolts from the Northwest Miramichi system in 2015 itself was considered to be negligible risk to the wild Atlantic salmon population of the Northwest Miramichi because it represented a very small proportion (< 1%) of the expected total smolt production, which had been in the range of 150,000 to as high as 750,000 when estimated during 1999 to 2011 (Chaput et al. 2016). This removal from the smolt run of 2015 represented a very small number of potential wild salmon returns of all maiden sea age groups in 2016 and 2017 based on recent estimated return rates of 1.6% to 7.2% (24 to 108 wild adult salmon, respectively).

If the survival rates of smolt to SAS adults are similar to values for the Tobique River captive reared program in DFO Maritimes Region (29% to 81%; 11 years of data; R. Jones DFO unpublished data), the SAS adults potentially released to the Northwest Miramichi system (450 to 1,200 adults) could represent an important proportion (10% to 25%) of total adult spawners, particularly if wild adult returns remain at the average of the 2012-2014 levels of less than 5,000 wild spawners. These proportions of SAS adults in the proportion of adult returns would increase if the number of smolts reared for supplementation purposes is increased and/or if wild adult returns in the Miramichi continue to decline.

There are four specific concerns with the proposed SAS activity in the Northwest Miramichi (Fraser 2016):

- The proposed activity aims to conduct smolt-to-adult rearing in freshwater. Although undoubtedly employed for practical reasons, freshwater SAS rearing means that many characteristics associated with salmon survival in the marine realm (e.g. physiological transitioning to seawater and then back to freshwater, homing precision, marine pathogen/parasite resistance) may be affected. If SAS releases interbreed with wild salmon, and differences are passed onto offspring via one or more possible mechanisms, there could be a long term impact on the fitness of the population.
- There is a high degree of multi-sea winter (MSW) maturation in Miramichi salmon. Populations with large MSW components are more likely to be impacted by SAS rearing than primarily 1SW populations, because genetic and plastic changes associated with captive-rearing increase with increased time in captivity. Accelerating maturation timing to reduce captive-rearing time in MSW populations would likely exacerbate these changes.
- The Miramichi system harbours a complex of genetically-distinct populations of salmon that have local adaptations. Mixing of these populations may therefore not be easily avoided when conducting SAS, and effective monitoring of SAS versus wild progeny with sufficient statistical power may be very difficult within such a large and complex river system.
- There is evidence from juvenile monitoring in the Miramichi that the egg to fry stock and recruitment relationship is strongly compensatory, that abundance of fry peaked in the late 1990s at values estimated to be near theoretical carrying capacity of the sampled habitat, and that fry abundance indices have since declined as estimated egg depositions declined. Increased average fry densities from the lower values of recent years should be realized with increased egg depositions (from SAS or otherwise) but with a concomitant increased density dependent compensatory mortality on juveniles of all parental origins. This is particularly concerning if progeny of SAS parents and SAS / wild interbred progeny have reduced fitness, particularly in sea survival, relative to progeny of wild parents, resulting in either no increase or a further decrease in wild anadromous adult Atlantic salmon population size.

Monitoring and assessment of SAS programs

Almost all the information available to date on SAS programs for Atlantic salmon have been limited to descriptions of migrations, observations on spawning behaviour, and whether offspring are produced (Dempson et al. 1999; Carr et al. 2004; O’Reilly et al. 2010; Stark et al. 2014).

The assessment of risks to fitness of wild Atlantic salmon resultant from SAS activities requires analyses of the relative contributions of each parent type (SAS, wild, SAS/wild interbreeding) to subsequent generations. This assessment is best achieved using parentage analysis approaches based on genetic markers wherein sampled progeny can be attributed to specific parents and therefore parent type (Flanagan et al. 2006; Jones et al. 2010; Pavey 2016). Any variable genetic marker that is stably transmitted from parents to offspring can be used for parentage analysis (Jones et al. 2010). In brief, since Atlantic salmon progeny get half their genome from each parent, if a potential parent shares neither of its alleles with an offspring, it can be excluded as a possible parent. If all potential parents of interest have been sampled and genotyped, for example SAS adults, then it is possible to exclude SAS adults as parents of sampled progeny, and conversely to include them as parents of progeny if the latter share the combination of SAS parental alleles. With these techniques, the number of surviving progeny from SAS adults, SAS/wild interbred, can be compared to the number of surviving progeny from wild parents.

Genetic parentage assignment has been undertaken using two types of molecular markers. The most frequently used marker is microsatellites, which consist of tandemly repeated arrays of 2-6 base pair segments of DNA. The more informative microsatellites available in Atlantic salmon species may exhibit 10’s of different alleles in a given population, and are very powerful in excluding non-true parents. The second type of marker is single nucleotide polymorphisms (SNPs); these can have as many as four alleles per locus although typically have only two allele differences per locus but with technological advances in sequencing, a large number of SNP loci, into the thousands, can be analyzed. New technologies and laboratory techniques have resulted in high throughput techniques for genotyping at both microsatellites and SNPs.

A large amount of data can be generated in these analyses and the assignment of progeny to parents relies upon advanced statistical techniques; fortunately much of the analytical work has been coded and tested in several computer analysis packages (Pavey 2016). Each of the packages has strengths and weaknesses, different assumptions and analytical approaches, and data exploration with several packages is warranted; it is likely that two or more will converge on similar results.

A number of sampling and analytical considerations are relevant in the context of assessment of SAS programs.

Errors can be introduced at multiple stages of the process:

- Tissue samples for genetic analysis must be collected from potential parents and progeny. There are large number of points in this process which can result in mismatched tissue samples and corresponding sampling information.
- Errors in determination of the sex of the spawners can occur, particularly in anadromous and SAS Atlantic salmon sampled early in the spawning season. Mis-assignment of sex can result in incompatible parentage assignments of progeny, for example when the assigned parents are both identified as female.
- Errors in the attribution of progeny to a yearclass resulting from difficulties or misinterpretation of ages from scales can misalign progeny with potential parents.
- Genotyping errors or mutations can result in incompatibilities between offspring and true parents. Genotyping errors occur when a given locus is misread, fails to amplify, or spuriously produces a misleading result (Jones et al. 2010) whereas mutations result in the allele inherited by the offspring being changed from the allele present in the parent. Some analytical models can at least in part accommodate these types of errors.

To facilitate the assessment of parental contributions, a number of sampling and analytical details should be considered (Pavey 2016):

- All SAS potential spawners should be tissue sampled and important phenotypic characteristics including sex, length, weight, river age, and release date recorded before release.

- Where possible, at least equal numbers of wild potential to SAS potential parents should be sampled and genotyped. This balanced design will facilitate direct comparisons of attribution of progeny to supplemented and wild individuals, and in estimation of relative fitness.
- As the interest is in assessing relative fitness of different life stages among parental types, the progeny should be sampled at a stage and at a point in the river where an unbiased mixture sample of parental origin progeny can be obtained. This is most likely realizable at the smolt migration stage and at the returning adult stage sampled near the estuary or the head of tide.
- Sample size requirements should be simulated to determine the power of the monitoring program to detect differences in fitness and other life history characteristics between parental types. The number of potential wild parents (sampled and unsampled), the number of SAS released parents, the expected number of progeny to be produced from each parental type at each life stage, the proportion of the total progeny from each yearclass which can be sampled, and the capacity of the genotype data to resolve parentage, are all factors which need to be taken into account.
- It is critical that the error rate of the genetic markers be empirically estimated and that the number of all potential parents be estimated. These variables are explicitly included in the parentage models, and are extremely important for confident assignments (Jones et al. 2010). Note that these numbers may be very different between male and female, due to the presence of precocious male parr.
- Specifically for the Miramichi, SNP and microsatellite profiles must be characterized to allow a final panel of sufficiently polymorphic unlinked loci to be defined. Simulations with existing software can be conducted with the chosen panel of markers, an assumed error rate, and unsampled parent proportions to assess performance of these markers for the specific project under consideration.

Sources of Uncertainty

Because SAS is a recent activity, there is less empirical evidence available to quantify risks to long-term fitness of wild populations and under what circumstances SAS activities may be considered negligible risk although it is considered an important intervention for a number of Atlantic salmon populations that are considered to be at high risk of extinction.

Whether or not captive-rearing technologies can be used to effectively increase the abundance of anadromous adult salmon in future generations while minimizing genetic and ecological risks is highly uncertain and unproven. Many uncertainties remain with respect to best captive-rearing practices and there have been few attempts to rigorously assess through quantitative modelling the demographic-genetic trade-offs to inform management decision-making for supplementation programs. In addition, in the absence of improved marine survival conditions from those that contributed to low abundance of anadromous salmon, the objective of increasing abundance of adult anadromous salmon in subsequent generations will be difficult to realize.

To date, the genetic risks of SAS per se have not been rigorously assessed empirically and reported in peer-reviewed literature in Atlantic salmon or any other salmonid. To do so would require, at a minimum, comparing the survival, reproductive success and offspring survival of a sample of SAS adults vs. wild adults originating from the same population, in the natural environment. Assessment of relative fitness would require quantifying the lifetime success of the offspring through the next generation between the two groups of fish to rule out the influence of different parental environments.

The possible impacts to wild population breeding fitness and competition with SAS fish as proposed are uncertain. Most of the research on risks to wild salmon of interactions with captive-reared fish was conducted using captive-reared fish with a high degree of domestication, through several, continual generations in captivity and/or through intentional selection for aquaculture purposes. However, the greater the genetic and plastic changes associated with captive rearing, the greater the risk of negative ecological effects.

Whether releases of SAS fish increase, decrease or have no effect on wild population productivity has not been assessed to date. An assessment of first generation adult spawners from SAS programs would require samples of returning adults four to seven or more years in the future, depending upon the smolt age and maiden sea age at maturities for the population under study. Such experiments require a long term investment in resources.

In-depth research, evaluation and modelling of existing or proposed SAS activities are required. The compilation of these additional assessment results would facilitate proper-decision making on when, where, and how SAS might provide desired, net-demographic benefits to wild salmon populations.

CONCLUSIONS AND ADVICE

Juvenile/smolt-to-adult supplementation (SAS) consisting of the interception of wild salmon at juvenile life stages, rearing them in captivity until the adult stage, and subsequently releasing the adult captive-reared fish back into the river of origin to complete the life cycle is considered to be an important recovery action for the endangered Outer Bay of Fundy population and for the endangered and listed Inner Bay of Fundy population of Atlantic salmon. Since marine mortality is considered to be the most important threat to recovery of salmon populations at risk of extinction, SAS and other interventions (such as live gene banking) are being used to circumvent the marine phase and maintain adult numbers with the goal of preventing extirpation, minimizing loss of genetic diversity, and maintaining Atlantic salmon populations until conditions, primarily marine survival, become favorable (DFO 2008).

SAS reduces some of the known risks associated with traditional programs consisting of wild captured broodstock spawned in the hatchery and stocking of juvenile stages but it introduces risks at other points in the anadromous life cycle whose effects are uncertain, particularly those associated with selection during the marine phase (Fraser 2016). Due to its recent development, much less empirical data is available to adequately describe the risks and benefits of SAS programs to wild populations of Atlantic salmon.

It is clear that juvenile Atlantic salmon can be reared in captivity, in either freshwater or marine conditions, to the adult stage, and that once released SAS adults can at least to some extent behave like their wild counterparts, successfully spawn and produce offspring in the wild, and that some of the offspring can complete the anadromous life cycle and return as adults to spawn to their river of origin. What is uncertain is whether the progeny of SAS adults are less fit than the progeny of their exclusively wild counterparts.

Owing to environmental conditions and selective pressures that invariably differ between captive and natural environments, the captive environment may cause plastic and genetic changes to phenotypes resulting in reduced fitness of captive-reared individuals relative to wild fish when the former are released into the wild. These environmental and selective pressure driven changes can occur in all aspects of phenotypes including morphology, life history, behaviour, physiology, and disease resistance.

Maladaptive genetic changes in captivity (collectively referred to as domestication selection) can occur via two principal mechanisms: (i) through unintentional selection, or (ii) through relaxation of natural selection. Unintentional selection might occur at the earliest stage of SAS during the collection of juveniles if these collections do not represent the full spectrum of smolt migration timing or body size, by non-random die-offs during captive-rearing, or through carry-over effects. There are examples of unintentional selection in SAS activities that have been documented in eastern Canada.

In salmonids, maternal provisioning or allocation of nutrients to eggs, which may be affected by environmental conditions (temperature, density, nutrition) can impact the growth and survival of early-stage offspring in the wild. Additionally, the rearing environment may also bring about epigenetic changes (e.g., via either DNA methylation or histone modification) that can effect levels of gene transcription and, ultimately, an individual’s phenotype. Recent research in other taxa including fishes indicates that environmentally induced epigenetic changes such as these may also be passed from parents (maternal and paternal) to offspring (carryover effects), and represent another way the parental rearing environment can be expected to impact the fitness of SAS offspring (and SAS/wild offspring) in the wild.

An additional genetic risk of SAS is the interbreeding of captive-reared SAS fish with wild fish in a population. As long as there is some chance that SAS will cause phenotypic and genetic changes that reduce fitness of progeny in the wild via domestication selection, there is a chance that SAS-wild interbred progeny will have reduced fitness in the wild.

Considering the above, the progeny of SAS adults in the wild are expected to have reduced fitness relative to wild progeny and progeny of interbred SAS and wild parents would be expected to have intermediate levels of fitness to pure SAS progeny and pure wild progeny (Fraser 2016).

The degree to which average short-term (first generation) and long-term fitness (successive generations) in a population are affected by SAS activities will depend on a number of factors, including whether SAS is applied continuously or intermittently, over successive generations of salmon, the proportion of the population that originate from SAS, and the extent to which environmental conditions of SAS rearing differ from those to which a wild population is normally exposed. The extent of the deviance of the traits of SAS adults and their progeny from those of wild fish is expected to be related to fitness differences of progeny of these parental types.

High marine mortality is considered to be the most important constraint to recovery of salmon populations. SAS programs circumvent that stage and smolt-to-adult survival is expected to be much higher using SAS than what would be realized in the wild. This is likely to result in relaxation of natural selective pressures associated with all aspects of marine ecology of Atlantic salmon including predation, migration, homing, parasite/pathogen resistance, social interactions, migratory vigor, and activity levels particularly in populations with long distance marine migrations.

Considering the presently high marine mortality rates of Atlantic salmon in eastern Canada, the anadromous salmon that are returning are likely those which have the best combination of fitness traits for the current environment. Any dilution of these traits via SAS activities and particularly via SAS/wild interbred progeny may delay the recovery in abundance of the wild anadromous phenotype which is presently subjected to strong natural selection at sea. Or worse, it may increase the risk of further declines in abundance of the anadromous phenotype due to an increased proportion of progeny which are maladapted to surviving the current marine conditions.

Although little is known of local adaptation in the marine phase of anadromous salmonid life cycles, adaptation to different marine areas would be expected. More importantly, local adaptations in freshwater are intimately linked to the marine phase in anadromous salmonids and it is not unreasonable to hypothesize that, all else being equal, the more locally adapted a wild Atlantic salmon population is to the marine phase of the life cycle, or to the freshwater-to-marine transitional phase, the more likely SAS will result in maladaptive phenotypic and genetic changes that affect wild fitness.

Atlantic salmon population abundances are regulated primarily by density-dependent mortality at juvenile life stages in freshwater. If the freshwater juvenile recruitment dynamics are strongly compensatory, there may be very little gain to be realized in smolt production and subsequent adult returns by supplementing the spawning escapement with large numbers of captive-reared adult spawners, in the case where freshwater habitat is being utilized at or approaching carrying capacity. In that case, the addition of a large number of captive-reared adult progeny to the river could result in increased density-dependent mortality of progeny of wild anadromous spawners.

The criteria and metrics for assessing the genetic and ecological risks from conducting SAS are based on two contexts: (i) how much captive-reared fish might deviate from wild phenotypes (and/or underlying genotypes), and (ii) the proportion of SAS fish relative to the total population size of a supplemented wild population. It is possible to monitor the phenotypic traits which may be expected to deviate from that of the wild population as a result of the SAS activities. The specific choice of SAS activity may result in different levels of probability of producing traits of SAS fish that deviate from the wild condition.

A number of factors need to be considered in assessing risk to fitness: heritability of traits that affect fitness (growth rates, age at maturity, run-timing, disease and pathogen resistance), the extent of fitness loss of offspring of SAS adults associated with captive rearing as well as for interbred progeny, and the relative proportion of SAS to all wild (adult and precocious mature males) spawners. The effect of captive-wild interbreeding on successive generational losses to fitness must also be considered because SAS fish might represent a large proportion of spawning adults, especially within a small, supplemented population. The risks to wild population productivity increase, and likely cannot be mitigated by the wild population within one generation once ceased, when SAS:

- generates reductions in fitness of progeny relative to wild fish,
- is continuously practiced over successive generations, and
- represents a greater proportion of the total number of adults (or of either sex) in the population.

Benefits and risks also depend upon the scale of the SAS activity. As the scale increases, in terms of the number of the SAS spawners and the geographic size of the basin in which SAS spawners are introduced, the potential benefits in terms of future production may also increase, particularly if there is substantial underutilized freshwater productive capacity. As the proportion of the SAS spawners to total spawners increases, the power of assessment to quantify fitness consequences will also increase. However, in both cases, the risks overall to the wild populations of salmon will also increase; in the former case because of non-random unintentional selection that may occur during SAS activities if there is complex sub-basin population structuring, in the latter case because SAS progeny will invariably over-represent proportions of the sub-basin population components of the wild population. These characteristics should be considered in any decisions on proposed SAS activities.

There are four specific concerns with the proposed SAS activity for the Northwest Miramichi. First, the proposed freshwater SAS rearing means that many characteristics associated with salmon survival in the marine environment and selection for the best set of anadromous characteristics will be relaxed. Second, populations with important multi-sea-winter anadromous life histories such as those of the Northwest Miramichi are more likely to be impacted by SAS rearing than primarily one-sea-winter populations, because many juveniles from MSW populations will be late maturing and require several years in captivity to reach maturity. Genetic and plastic changes associated with captive-rearing increase with increased time the individuals are held in captivity. Third, the Miramichi River system is expected to have a complex of genetically-distinct locally adapted populations of salmon. Mixing of these populations may not be easily avoided when conducting SAS collections and unintentional selection for components may occur to the detriment of others. As well, effective monitoring of the SAS activity with sufficient statistical power may be very difficult within such a large and complex river system. Finally, there is evidence from juvenile monitoring in the Miramichi that the egg to fry stock and recruitment relationship is strongly compensatory. Increased average fry densities from the values of recent years should be realized with increased egg depositions (from SAS or otherwise) but with a concomitant increased density dependent compensatory mortality on juveniles of all parental origins. This is particularly concerning if progeny of SAS parents and SAS / wild interbred progeny have reduced fitness, particularly in sea survival, relative to progeny of wild parents, resulting in either no increase or a further decrease in wild anadromous adult Atlantic salmon population size.

As there are a large number of uncertainties associated with quantifying the benefits and risks of SAS to wild fitness, any SAS activity that is undertaken should have a monitoring and evaluation component included. This evaluation component should be designed to provide empirical data to reduce the uncertainty with the assessment of risks and benefits of SAS interventions on long-term fitness of wild populations. The most important question to address is the generational contribution of SAS adults relative to wild adults. This question can be examined using genomic techniques that allow for assignment of progeny to their parental origin (wild-wild, wild-SAS interbred fish, SAS-SAS) and consequently estimates of short-term (first generation) and long-term (successive generation) fitness.

OTHER CONSIDERATIONS

Depending on the duration of the Atlantic salmon SAS activity in a single river or river system/watershed, short-term or long-term addition to the harvestable component of the river will occur. If the initial intent of SAS is to mitigate the freshwater anthropogenic impacts on the salmon population, a clear harvesting management objective/strategy on wild and SAS salmon would be required prior to the implementation of any SAS activity. This would be especially important to protect the wild population from exploitation, if the SAS activity is conducted in a river or an area with existing harvesting activities, such as Aboriginal Food, Social and Ceremonial fisheries and recreational fisheries (of any type, retention or catch and release only).

SOURCES OF INFORMATION

This Science Advisory Report is from the December 14 to 16, 2015 regional science peer review meeting on the Review of risks and benefits of adult captive-reared supplementation activities to fitness of wild Atlantic Salmon. Additional publications from this meeting will be posted on the Fisheries and Oceans Canada (DFO) Science Advisory Schedule as they become available.

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APPENDICES

Appendix 1. Proposal for a smolt to adult supplementation program for the Northwest Miramichi submitted by proponents, version May 20, 2015

There is grave concern over the plight of the Atlantic salmon in the Maritimes following the poor returns of adult salmon from 2012 to 2014 and one of the hardest hit areas in the Gulf of St. Lawrence is the NW Miramichi River, where only 22% of the number of adults for spawning requirements entered the river in 2014. This amounts to a little over 1,200 grilse and 1,200 large salmon and doesn't take into consideration any removals/losses that might have occurred upstream of the DFO counting facilities in the tidal portion of the river. As the Ministerial Advisory Committee meets to prepare a number of recommendations to the federal government on an action plan to restore salmon runs, many groups in the private sector are also planning projects to reverse this decline.

The Miramichi Salmon Association operates the former DFO salmon hatchery in South Esk and has been stocking the Miramichi River with juveniles since DFO turned over the facility in 1997. With salmon numbers in dire straits, there is an increased call for more stocking to take place. With this in mind, a group of vital stakeholders in the Miramichi Watershed including JD Irving Ltd., Cooke Aquaculture, Atlantic Salmon Federation, Rocky Brook Camp, the University of New Brunswick and the Miramichi Salmon Association met to discuss the issues facing the Atlantic salmon and what could be done to improve the survival of the species. A report was prepared and submitted to the Ministerial Advisory Committee to address some of the broader issues and then a detailed discussion took place on immediate action that could take place locally, including stock supplementation.

The advantages and disadvantages of different stocking strategies were discussed and the option chosen that has the potential to cause the least amount of harm and the most benefit is to capture wild smolts from the NW Miramichi and rear them to the adult stage and then release the mature salmon to swim up to their natal area to spawn. This will occur in a land-based freshwater recirculation facility at the Miramichi Salmon Conservation Centre (MSCC) in South Esk and will involve major upgrades to the facility. The benefit of this strategy is the wild smolts have spent 2, 3 or 4 years in freshwater and have been exposed to the process of survival of the fittest. Since the major identified problem with salmon survival is in the marine environment where only 2% to 3% survive to return, then this is the area where the greatest gains can be made. Releasing the mature salmon and letting them go back to their natal area to select a mate and spawn, also has the benefits of some natural selection. Starting in 2016, adult broodstock collections will be reduced in the NW Miramichi from 50 pairs to 25 pairs as this program begins to provide additional adults in the river.

This smolt to adult rearing strategy has been used by DFO in the gene banking program in the Bay of Fundy as an emergency measure and since the stocks were very low when this program began, the gene pool was limited to choose from. The NW Miramichi River still has an adequate genetic bank so members of the same family are less-likely to mate with each other and a research team will be assembled to fully assess the benefits of this program.

The Details of the Program

It is proposed to collect wild smolts in the spring of 2015 from the Northwest Miramichi to start the program. The initial plan would be to collect 200 smolts from the NW Miramichi smolt wheel, 200 smolts from the Sevogle smolt wheel and 1,100 smolts from an additional smolt wheel that will be installed at Upper Oxbow on the LSW Miramichi for a total of 1,500 smolts. The smolts will be brought to the Miramichi Salmon Conservation Centre in South Esk and held in separate tanks. Once the collection is complete, a team will pit-tag the smolts, take a piece of fin tissue for genetic work, measure and weigh the fish and vaccinate them for furunculosis. The fish will be fed freeze dried krill for the first few days and then be weaned onto commercial pellets. The fish will spend the summer in the Small Greenhouse at the MSCC while renovations are done on the Large Greenhouse to upgrade the facility to operate on recirculation technology.

Genetic mapping of the wild salmon in the various branches of the Northwest Miramichi will be conducted by a team from UNB during the summer of 2015 and the plan is to monitor the captive adult salmon once released in the wild by placing radio tags on the fish and observing where they spawn. Salmon fry from the immediate area will be sampled for genetic material and tracked during their time in freshwater to compare survival of the “enhanced” offspring to “wild” offspring through to the smolt stage.

The program will be expanded to a larger number of smolts in subsequent years, once construction is complete, but will only be done as a short term strategy until the success of the program can be determined.

Appendix 2. Summary of risks associated with specific components of an Atlantic salmon SAS program that may lead to deviations from wild characteristics.

Table A2. The evidence column indicates the source of information that supports the scoring when provided of the probability (low, medium, high) of the extent of deviation. Evidence is grouped as: direct evidence based on SAS empirical research on Atlantic salmon (AS) or Pacific salmon (PS), indirect evidence from juvenile supplementation programs (AS or PS) or indirect other (other species, modelling or theoretical studies). Literature references for each are provided in Fraser (2016).

Activity Specific process	Why components may deviate from wild	Source and how much deviation from wild	Evidence
Juvenile capture			
timing and effectiveness of capture activities	- phenotypic characterisitcs (run timing, freshwater ages, sex ratio, body size, etc.) of the collection of smolt obtained for SAS may not be representative of the entire out-migrating population of wild smolt	unintentional selection - deviation can be higher in large rivers with stock structuring, less in small rivers with less structuring	Direct (AS) Indirect (PS)
Juvenile to adult rearing			
transfer from wild to captive environment	- differential survival from collection to hatchery based on smolt size or condition - smolts not adapted to seawater transfer	unintentional selection - low probability of deviation	Direct (AS)
	- initiation of feeding in captivity - feeding on artificial feed	domestication selection - high probability of deviation from wild (wild smolt diet changes from surface feeding to water column feeding; failed smolt syndrome in captivity)	Direct (AS and PS) Indirect (AS)
rearing at high densities	- natural territorial behaviour of juveniles which are not smolts	domestication selection - low probability of deviation (juvenile salmon studies show transition to schooling behavior of smolts; territoriality is relaxed in smolts and subsequent stages as shown by adult behavior in rivers in pools)	Indirect (AS and PS)
	- aggression, risk taking, competition for food, social behavior	domestication selection - high probability of deviation from wild (from studies on juvenile supplementation, associated with generally small school sizes at sea)	Indirect (AS and PS) Indirect (other)
	- growth rates associated with density effects	domestication selection - high probability of deviation from wild (from supplementation programs to optimize survival and growth; growth rate at sea not likely affected by density)	Indirect (AS and PS) Indirect (other)

Activity Specific process	Why components may deviate from wild	Source and how much deviation from wild	Evidence
rearing at high densities	- maternal provisioning for eggs, male reproductive fitness	domestication selection - high probability of deviation from wild (high density stressful environment may result in lower investment in egg quality and quantity)	Direct (AS and PS) Indirect (other)
	- microbiota interactions, parasite pathogen loading and dynamics	domestication selection - high probability of deviation from wild	Indirect (AS)
artificial diet	- nutrient composition from artificial feed differs from nutrition in the wild	domestication selection - high probability of deviation from wild (diet research from aquaculture that favours growth but low maturation rate; diverse diet of wild fish at sea)	Indirect (AS)
feeding regime	- timing and intensity of feeding (periodic feeding in captivity versus potential for continuous feeding in the wild)	domestication selection - high probability of deviation from the wild	Indirect (other)
	- source of food (surface feeding in captivity versus water column feeding in the wild)	domestication selection - high probability of deviation from the wild	Indirect (other)
abiotic factors associated with rearing (temperature, salinity, photoperiod, water chemistry,…)	- marine temperatures in the high seas differ from temperatures in sea captivity -freshwater temperature cycles differ from marine temperature cycles - association of growth with temperature (metabolic rates) - effects on maturation schedules and initiation of spawning once released	domestication selection - high probability of deviation from wild (diverse evidence from captive rearing activities, supplementation activities, aquaculture)	Direct (PS) Indirect (AS and PS)
	- epigenetic effects (rearing environment may possibly effect methylation or histone packing of genes, which do effect DNA transcription, and which may be passed from parents to offspring)	domestication selection - high probability of deviation from wild	Indirect (other)
rearing in confined environment	- relaxation of risk averse strategies, reduced interspecies interactions	domestication selection - high probability of deviation from wild in landbased systems - low to high probability of deviation in sea cage environment , context dependent (supplementation program studies, behavior of naïve stocked fish, probability of deviation depends upon the rearing practices)	Indirect (AS)
rearing in confined environment	- effects on body form and condition, migratory vigor	domestication selection - low to high probability of deviation (correlated with density of rearing, short length, heavy fish, stub tails, head morphology, rearing practice dependent)	Direct (AS) Indirect (AS and PS)

Activity Specific process	Why components may deviate from wild	Source and how much deviation from wild	Evidence
duration of captivity	- prolonged captive rearing to maturity (diverse sea age at maturity anadromous strategies (1SW, 2SW, 3SW) that vary by sex)	domestication selection - low to high probability of deviation (higher probability of deviation from wild for MSW stocks, particularly reared in freshwater; lower probability of deviation for 1SW stocks raised at sea)	Direct (AS) Indirect (AS and PS) Indirect (other)
use of vaccination, antibiotics, salt baths to treat disease/pathogen incidences	- artificial selection for fish of various pathogen resistance	unintentional selection and domestic selection - high probability of deviation from wild (occurs in captive rearing environments to retain high survival rates of captive fish)	Indirect (AS) Indirect (other)
choice of rearing environment	- differences between freshwater and marine rearing, pathogens, microbiota, gut flora, stress from confinement	domestic selection - high deviation from wild for freshwater rearing - low deviation from wild for marine but varies with local versus distant exposures	Indirect (AS) Indirect (other)
Release of adult fish			
Release location freshwater	- SAS fish released in location(s) that may not match stock origin of juveniles - stray to freshwater rearing location	unintentional selection, domestic selection - low to high probability deviation (dependent upon straying rate of wild fish)	Direct (AS)
Release location tidal or marine	- SAS fish not fully imprinted to source river, increased stray rate to other rivers	unintentional selection - low to high probability of deviation (dependent upon how smolts were transferred to sea cage, imprinting legacy)	Direct (AS)
Timing of release	- suboptimal release timing that does not match run timing of wild stocks (dependent upon identification of maturity state in captivity)	unintentional selection, domestic selection - high probability of deviation in large rivers with run timing structure - low probability of deviation from wild for stocks of smaller rivers	Direct (AS and PS)
Timing of release	- misidentification of maturity state of SAS fish	unintentional selection - immature released fish lost to spawning in year of release - high probability of deviation from wild, since all returning anadromous adults are spawners	Direct (AS)
	- releases are not proportional to wild stock in terms of freshwater age, sex ratio, body size	unintentional selection - high probability of deviation from wild	Direct (AS) Indirect (PS)
	- microbiota communities differ due to rearing practices and treatments	domestication selection - high probability of deviation of wild (anadromous fish will have different microbiota communities than those of captive reared salmon due to rearing practices / treatments and locations, pre-release diagnostic testing)	Indirect (AS)

Appendix 3. Possible interactions and effects of maladaptation from SAS on wild salmon population productivity and persistence.

Table A3. The evidence column indicates the source of information that supports the probability scoring (when available; low, medium, high) of the extent of the effect on fitness. Evidence grouped as: direct evidence based on SAS empirical research on Atlantic salmon (AS) or Pacific salmon (PS), indirect evidence from juvenile supplementation programs (AS or PS) or indirect other (other species, modelling or theoretical studies). Literature references are provided in Fraser (2016).

Interaction	Why components may affect fitness of wild population	Source and probability of extent of effect on fitness	Evidence
Adult SAS release			
competition for mates, disruption of wild spawning	- rearing condition effects on spawning behavior - aggression, disruption of mate choice in wild spawners	domestic selection - increased probability of reduced fitness relative to wild fish with increased deviation of traits of SAS adults from those of wild fish	cumulative, synergistic effects of deviations in multiple characteristics of SAS fish, see Appendix 2
Spawn timing earlier or later than wild fish	- rearing condition effects on maturation rates and timing and choices of timing of release -superimposition of eggs deposited by wild females by potentially later spawning SAS females	domestic selection - probability of reduced fitness to wild fish in large rivers where spawning times extended over a long period due to heterogeneous environmental and stock characteristics	not examined except for unintended released fish - extended spawning in large rivers like Miramichi that are sub-basin specific
Progeny of SAS parents			
SAS progeny compete with wild juveniles	- aggression behavior of SAS parents transferred to progeny - earlier emergence if earlier spawning - territoriality of juveniles - differences in offspring size -potential numerical dominance	- wild population fitness is reduced under density dependent freshwater survival - reduced fitness of wild salmon when there are strong density dependent mortality effects from high juvenile densities	density dependence in freshwater is well established for Atlantic salmon
Fitness of SAS progeny in freshwater	- egg provisioning, other non-genetic maternal and paternal (epigenetic) effects influence fitness of progeny	- wild population fitness affected only through density dependent interactions with SAS and SAS / wild progeny	
Fitness of SAS and wild interbred progeny in freshwater	- loss of local adaptation	- high probability of intermediate fitness of SAS / wild interbred progeny relative to wild	Indirect (AS, PS)

Interaction	Why components may affect fitness of wild population	Source and probability of extent of effect on fitness	Evidence
Loss of marine adaptation	- relaxed marine phase selection of SAS parents could translate into lower mean at sea survival of their offspring as compared to progeny from wild population	- high probability of reduced mean fitness for captive reared progeny associated with relaxed to no marine selection of SAS parents - high probability of intermediate value for SAS/wild progeny	Indirect (AS)
Scope of project			
Increased proportion of SAS fish relative to total wild population size (SAS + wild)	- see fitness consequences above	- increasing probability of reduced fitness of wild population as SAS progeny and hybrids increase as proportion of entire population	Not known how many generations until natural selection restores fitness
Duration of SAS interventions (collection, rearing , stocking) resulting in generations of fish in captivity until objectives are met (competing objectives: rebuild populations to reduce risk of extinction / rebuild to fisheries access)	- cumulative domestic selection and loss of local adaptation	- increasing probability of deviation from wild the longer the activity takes place	Not known how many generations until natural selection restores fitness
Increased use of wild smolts (small populations)	- reduction of the size of the wild population going to sea	- increasing probability as abundance of wild progeny declines	Not known how many generations until natural selection restores fitness
Status of the wild population	- if intrinsic rate of increase is low (e.g. near 1) for wild fish, interactions with SAS progeny may reduce the rate to levels below replacement	- increasing probability of fitness consequences to wild fish if already low reduced intrinsic rate of increase (rate of population replacement) is further reduced due to interactions with SAS progeny	Not known how many generations until natural selection restores fitness
Objectives of the SAS program - supplementation of fisheries - reducing risk of extirpation	- increased fisheries related losses due to fisheries access granted on SAS released fish	- increasing anthropogenic mortality on wild fish which are at low and intrinsic rate of increase (rate of population replacement) is increased due to interactions with SAS progeny	Indirect (PS)

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