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Risks and benefits of mitigating low marine survival in wild salmon using smolt-to-adult captive-reared supplementation

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Foreword

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ABSTRACT

Most salmon supplementation programs capture and spawn wild adults and release large numbers of their captive-reared juveniles. A rarely adopted alternative is smolt-to-adult supplementation (SAS), wherein migrating smolts are captured, captive-reared until maturation and subsequently released in freshwater. Where marine return rates are low, SAS could potentially offer advantages over juvenile supplementation towards mitigating population declines by:

(i)   providing a predictable input to adult population size;

(ii) avoiding well-documented genetic risks to captive-rearing at early life stages experiencing high mortality; and,

(iii) maintaining free mate choice in the wild.

Nevertheless, uncertainties exist concerning the potential genetic and ecological risks of SAS to wild populations, and whether the benefits of SAS are fully realized in the wild. In particular, the extent to which SAS reduces marine adaptation (or adaptation to freshwater-marine linkages) through unintentional or relaxed selection, or causes negative carry-over effects on fitness, is unknown. If such changes are as strong as with juvenile supplementation, SAS may not provide any additional demographic benefits to wild populations, according to life stage elasticities/sensitivities. There is an urgent need to quantify and compare the lifetime fitness of SAS progeny versus wild progeny, and their second generation progeny under natural conditions, but such controlled experiments require a decade to complete in salmon. To minimize risk in the interim, any potential adoption of SAS must ensure that:

(i)   deviations from wild phenotypic trait distributions are minimized as much as possible;

(ii) SAS is only used sparingly as a short-term approach to supplementing at-risk wild populations; and that,

(iii) SAS comprises only a small-to-modest proportion of the total number of returning adults, unless a larger proportion is needed to avoid population extirpation.

Risques et avantages de l'atténuation du faible taux de survie en mer du saumon sauvage par l'ensemencement avec des saumons juvéniles/saumoneaux élevés en captivité jusqu'à l'âge adulte

RÉSUMÉ

La plupart des programmes d'ensemencement avec du saumon capturent et font se reproduire des adultes sauvages et remettent en liberté un grand nombre de juvéniles élevés en captivité. Une autre solution rarement utilisée est l'ensemencement avec des saumons juvéniles/saumoneaux élevés en captivité jusqu'à l'âge adulte (ESA), c'est-à-dire que des saumoneaux en migration sont capturés, élevés en captivité jusqu'à leur maturation, puis remis en liberté en eau douce. Lorsque les taux de montaison en milieux marins sont faibles, l'ESA serait plus avantageux que l'ensemencement avec des juvéniles pour atténuer les déclins des populations :

(i)   en augmentant de manière prévisible la taille de la population d'adultes,

(ii)   en éliminant les risques génétiques bien connus liés à l'élevage de poissons à leurs premiers stades biologiques et qui connaissent une mortalité élevée, et

(iii) en permettant aux poissons de frayer librement à l'état sauvage.

Néanmoins, il existe des incertitudes entourant les risques génétiques et écologiques potentiels de l'ESA sur les populations sauvages, et à savoir si les avantages de l'ESA se manifesteront pleinement en milieu naturel. Plus particulièrement, on ignore dans quelle mesure l'ESA réduit l'adaptation marine (ou l'adaptation au passage entre eau douce et eau marine) par une sélection involontaire ou assouplie ou entraîne des effets négatifs sur la valeur adaptative. Si de tels changements sont marqués à la suite de l'ensemencement avec des juvéniles, l'ESA pourrait ne procurer aucun avantage démographique supplémentaire aux populations sauvages, d'après les élasticités/sensibilités des stades biologiques. Il est urgent de quantifier et de comparer la valeur adaptative globale de la descendance associée à l'ESA par rapport à la descendance des saumons sauvages, ainsi que de la descendance de seconde génération dans des conditions naturelles, mais de tels essais contrôlés prendraient dix ans à réaliser dans le cas du saumon. Entre-temps, afin de réduire les risques, toute adoption potentielle de l'ESA devra garantir que :

(i)   les écarts dans la distribution des caractéristiques phénotypiques des poissons sauvages sont réduits au minimum;

(ii)   l'ESA n'est utilisé qu'à court terme pour ensemencer les populations sauvages en péril; et

(iii) l'ESA ne représente qu'une proportion de faible à modeste du nombre total d'adultes en montaison, à moins qu'une grande proportion soit nécessaire pour éviter la disparition de la population.

INTRODUCTION

In the face of growing environmental changes from human activities, captive-rearing or supplementation programs are increasingly adopted to salvage endangered species from extinction or to prevent populations from experiencing further decline (IUCN 2013; Seddon et al. 2007; Frankham 2008). That such programs are not without ecological and genetic risks has long been discussed, and perhaps nowhere have such risks been better studied than in salmonid fishes, one of the northern hemisphere's most socioeconomically important group of fish species (see reviews by Fleming and Peterson 2001; Jonsson and Jonsson 2006; Araki et al. 2008; Fraser 2008; Kostow 2009). Nevertheless, the science of conducting effective captive-rearing, that is, determining how to achieve its desired demographic benefits whilst minimizing its potential genetic or other ecological risks, is still in need of further development. Many uncertainties remain with respect to best captive-rearing practices (Seddon et al. 2007; Fraser 2008). Moreover, aside from the rigorous assessment of Bowlby and Gibson (2011), there remain few attempts of quantitative modelling of demographic-genetic trade-offs to facilitate management decision-making for supplementation programs.

Previous reviews and empirical works on the genetic risks and demographic benefits of captive-rearing, including on salmonids, have routinely recommended that the risks can be substantially reduced by, among other things:

- using local populations for captive-breeding/supplementation (Araki et al. 2008; Fraser 2008);

- reducing the duration of captivity (Frankham 2008),

- minimizing environmental differences between wild and captive environments (Braithwaite and Salvanes 2005; O'Reilly and Doyle 2007; Wilke et al. 2015),

- restricting captive breeding to life history stages where natural mortality is not as severe in the wild (O'Reilly and Doyle 2007; Clarke et al. 2016), and

- allowing free mate choice (Fleming 1994; Pitcher and Neff 2007; Consuegra and Garcia de Leaniz 2008; Neff et al. 2011).

Given the general recommendations for reducing the risks posed by captive rearing (Frankham 2008; Fraser 2008; Kostow 2009), it is an attractive idea in circumstances of low marine return rates of wild anadromous salmonids to capture wild smolts, rear these in captivity until the adult stage, and subsequently release the adult captive-reared fish back into the river of origin to complete the life cycle. Indeed, such smolt-to-adult supplementation (hereafter abbreviated SAS) would use local fish and avoids captive rearing at early life stages that generally experience the most mortality in salmonids. SAS could also conceivably minimize some environmental differences between captive and wild environments if conducted in marine sea-pens. Furthermore, SAS would still allow adults to choose mates in the wild. Moreover, and very importantly, SAS could provide a predictable input to adult population size and prevent the complete collapse of individual age cohorts (Stark et al. 2014), whether the goal of the SAS program was to increase the number of fish for harvesting or to increase population viability. In the extreme case where marine survival rates are essentially zero, and alternative (non-anadromous) life histories cannot demographically rescue a declining anadromous population (e.g. see Fraser 2014), SAS is arguably the only way to demographically maintain or boost a wild, anadromous salmonid population whilst maintaining genetic diversity and sufficiently minimizing risks associated with captive-rearing. Such a situation is exemplified by recently emerging SAS programs for endangered Atlantic salmon (*Salmo salar*) populations from the Inner and Outer Bay of Fundy, Canada (Clarke et al. 2016; Jones et al. 2014) and Maine, USA

(Stark et al. 2014). SAS has also been adopted in certain historical instances of perilous population declines in Pacific salmon (Thomas 1996; Berejikian et al. 2005; Kline and Flagg 2014; Stark et al. 2014), but as yet in only one case for supplementing wild population size where declines had not reached precipitous levels (Dempson et al. 1999).

Like all forms of supplementation involving some captive-rearing, however, SAS is not without risks. It has major differences that distinguish it from the more traditional supplementation approach of collecting wild adults, spawning them in a hatchery and stocking juveniles at various life stages. The purpose of this advisory paper is therefore to consider five key issues associated with SAS, with a particular emphasis on wild Atlantic salmon:

- the genetic risks of SAS to short- and long-term fitness;

- the ecological risks of SAS;

- criteria and metrics for assessing risk of SAS;

- conditions under which SAS could be considered a negligible risk to wild fitness; and

- a specific assessment of risk of SAS activity to wild salmon of the Miramichi River, Canada, as a case study.

GENETIC RISKS OF SAS TO SHORT-TERM AND LONG-TERM FITNESS

GENETIC ADAPTATION TO CAPTIVITY, DOMESTICATION SELECTION, NON-GENETIC CHANGES AND CARRY-OVER EFFECTS THAT AFFECT WILD FITNESS

It is well known that environmental conditions and selective pressures invariably differ between captive and natural environments (Fleming 1994; Fleming and Peterson 2001; Frankham 2008, Araki et al. 2008; Fraser 2008; Christie et al. 2012). It is also well known that, owing to such environmental differences, the captive environment causes plastic and genetic changes to phenotypes associated with fitness in natural environments, often resulting in reduced fitness in captive-reared individuals when they are released back into nature as part of species restoration programs (Waples 1999; Frankham 2008; Christie et al. 2012; Evans et al. 2014, 2015). These plastic and genetic changes can occur in all aspects of phenotypes, such as morphology, life history, behaviour, physiology and disease resistance, and they affect all life stages (Fleming and Peterson 2001; Consuegra and Garcia de Leaniz 2008; Fraser 2008; Normandeau et al. 2009; Houde et al. 2010; Christie et al. 2012; Evans et al. 2014, 2015). Moreover, adaptive genetic changes to captivity can occur rapidly, even in one or two generations (for good examples in salmonids, see Araki et al. 2007b; Christie et al. 2012; Milot et al. 2013; Evans et al. 2014). Whether such fitness reductions are irreversible in the longer-term, and how long it might take for wild populations to recover from these changes once supplementation is arrested, are largely open questions. Captive-wild hybridized populations often persist after supplementation at what are considered 'normal' densities (Halbisen and Wilson 2009; Hansen et al. 2009), and this suggests that natural selection removes maladaptive alleles following hybridization, returning wild fitness to previous levels (Harbicht et al. 2014). For instance, in wild populations of brook trout (*Salvelinus fontinalis*) that hybridized with captive-reared fish, there is some evidence of reversion to original wild fitness levels 6-11 generations after supplementation was arrested (Harbicht et al. 2014). Furthermore, indirectly, the establishment of feral populations of salmonids from domesticated hatchery strains suggests that maladaptive genetic changes to captive exposure can be overcome in some situations.

Maladaptive genetic changes in captivity (collectively referred to as domestication selection; Waples 1999) are brought about via two chief mechanisms: either

(i)   through a relaxation of natural selection, or

(ii) through unintentional selection.

Unintentional selection in the captive-rearing process appears to be the more frequent mechanism, at least for juvenile supplementation programs (Theriault et al. 2011; Christie et al. 2012), but both mechanisms can result in maladaptation to the wild environment. Captive-rearing can also generate carry-over effects on fitness in the wild (Araki et al. 2009; Evans et al. 2014; Clarke et al. 2016). For example, in salmonids, maternal provisioning in offspring is heavily influenced by the environmental conditions that a female experiences (Heath et al. 2003; Rollinson and Hutchings 2013; Haring et al. 2016). These maternal effects can also have a genetic component in salmonids, including in Atlantic salmon (Debes et al. 2013), and can affect juvenile offspring growth and survival (Einum and Fleming 1999, 2000). It is thus also important to consider how maternal effects might be influenced by captive-rearing and thus affect fitness in subsequent life stages in nature, whether or not they are environmentally-induced strictly speaking.

Genetic adaptation to captivity and domestication selection involving SAS

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 salmonids. 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; preferably, the lifetime success of the offspring would then be compared between the two groups of fish to rule out the influence of different parental environments (see Araki et al. 2007a vs. Araki et al. 2007b and discussion on experimentation in Fraser 2008 for examples in the juvenile supplementation literature).

Based on what is known of genetic risks of captive-rearing, however, it is expected that SAS will elicit plastic and genetic changes to phenotypes that affect wild Atlantic salmon fitness (Fleming 1994; Fleming and Peterson 2001; Araki et al. 2007a, 2007b, 2008, 2009; Consuegra and Garcia de Leaniz 2008; Frankham 2008; Fraser 2008; Neff et al. 2011; Christie et al. 2012; Milot et al. 2013; Evans et al. 2014, 2015; Clarke et al. 2016). Indeed, changes to adult body size, maturation age, aggression, maternal provisioning, egg quality and/or spawning time have been documented in SAS programs for Atlantic and Chinook salmon (Dempson et al. 1999; Stark et al. 2014). The degree to which average short-term (immediate generation) and long-term fitness (successive generations) in a population are affected will depend on a number of different 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 (Tables 1, 2, 3).

More specifically, it is important to consider that although demographically-speaking, SAS avoids captive-rearing at the early life stages which experience the highest mortality (96.8-99.8%), smolt-to-adult mortality is still very substantial in wild salmonids. For example, in Atlantic salmon, it commonly ranges between 82.5% and 98.5% (92.6% average for 1SW; Hutchings and Jones 1998) and is especially high in candidate wild populations where SAS is being considered or has been recently initiated (e.g. Clarke et al. 2016). Because smolt-to-adult mortality will be much lower using SAS (Dempson et al. 1999), relaxation of natural selective pressures is a likely possibility. Based on empirical evidence from related studies, particularly likely is a relaxation of natural selective pressures associated with predation in the marine phase (Fritts et al. 2007; Houde et al. 2010) and with marine parasite/pathogen resistance if rearing is conducted in freshwater (Dick et al. 1987; Valtonen and Koskivaara 1994; Mangel and

Stamps 2001). Wild populations undergoing SAS may also experience relaxed selection for traits associated with migratory vigor and activity levels (Fleming et al. 1994; Jonsson and Jonsson 2006; Pulcini et al. 2013), perhaps particularly in populations with longer-distance migrations.

Furthermore, unintentional selection in SAS facilities (tanks in freshwater facilities or marine cages) will arise if any non-random die-offs occur during captive-rearing, or through carry-over effects. Importantly, significant mortality has been observed when wild smolts were brought into the captive environment and transitioned onto artificial aquaculture feed (Strademeyer 1991, 1994; Dempson et al. 1999; Kline and Flagg 2014; Clarke et al. 2016). Under SAS rearing, 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, whether fish are reared in marine or freshwater, and these changes may affect subsequent reproductive success and/or offspring survival in the wild (e.g. Fleming et al. 1996, 1997; Sheehan et al. 2005; Jonsson and Jonsson 2006; Lawlor et al. 2009). Again, changes in body size, maturation, aggression, maternal provisioning and egg quality have been documented in SAS programs involving Atlantic and Chinook salmon (Dempson et al. 1999; Stark et al. 2014).

Unintentional selection might also occur upon the earliest stage of SAS during the collection of smolts before they migrate out to sea. If smolt runs are non-randomly sampled, smolt collections may not represent the full spectrum of smolt migration timing or body size. Survival rates of smolts in captivity might also depend on the timing of their physiological transformation for moving into seawater. Furthermore, many river systems harbour multiple, genetically-distinct and locally adapted populations (Dillane et al. 2008). Hence, efforts to collect smolts may also run the risk of obtaining mixtures of populations beyond a focal population of interest. Depending on their release point, this may affect SAS adult survivorship, and facilitate an unnatural homogenization effect (e.g. Eldridge and Naish 2007).

In summary, at the initiation of SAS or during SAS rearing, the risks associated with trait changes (in terms of potential fitness reductions) would be expected to increase as trait deviations from the wild environment increase.

Other genetic risks of SAS: potential loss or reduction of marine local adaptation in salmon

The best available empirical research on Atlantic salmon and other salmonids suggest that these species exhibit a considerable degree of local adaptation in freshwater at different geographic scales (reviewed in Taylor 1991; Garcia de Leaniz et al. 2007; Fraser et al. 2011; for specific empirical examples in Atlantic salmon, see Dionne et al. 2007; Houde et al. 2011; Bourret et al. 2014; O'Toole et al. 2015). Although little is known of local adaptation in the marine phase of anadromous salmonid life cycles, undoubtedly adaptation exists to different marine areas (Fraser et al. 2011; Bourret et al. 2014; O'Toole et al. 2015). There is evidence from Atlantic salmon (Ritter 1975) and Coho salmon (Reisenbichler 1988) of lower return rates of hatchery smolts stocked in a common river that originated from distant stocks compared to smolts originating from local stocks.

More importantly, local adaptations and genetic polymorphisms in freshwater are intimately linked to the marine phase in anadromous salmonids (Schaffer and Elson 1975; Waples et al. 2004; Fraser and Bernatchez 2005; see Box 2 in Fraser et al. 2011; Gurney et al. 2012; Sloat et al. 2014). Therefore, assessments of risk of SAS must holistically consider how SAS affects the adaptive genetic characteristics of wild salmon during the marine phase and other linked life

stages. It is not unreasonable to hypothesize that, all else being equal, the more locally adapted a wild 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. Maladaptation to the marine phase from SAS is an especially important risk to consider because the marine phase will often be the most limiting factor affecting salmon where SAS is desired. During population declines, salmon may be undergoing a lag period of adaptation to changing marine environmental conditions, so avoiding the marine phase might be very undesirable.

Hybridization between SAS adults and wild adults

An additional genetic risk of SAS that merits consideration is the hybridization of captive-reared SAS fish with remaining wild fish in a population. As long as there is some chance that SAS will cause phenotypic and genetic changes that affect wild fitness via domestication selection (relaxation of selection or unintentional selection), there is some chance SAS-wild hybrids will have reduced fitness in nature. In most situations, it is expected based on previous works in the juvenile supplementation or related literature that SAS-wild hybrids will exhibit intermediate fitness in the wild to that of 'pure' wild and 'pure' captive fish (Fleming et al. 2000; Araki et al. 2007a, 2007b, 2008; Houde et al. 2010). Again, the extent to which such hybridization will occur and generate maladaptation in wild fish (and for how long) will depend on a host of factors; it is expected to be reduced when genetic and 'plastic' risks from captive-rearing are minimized (Frankham 2008) and when the proportion of SAS fish relative to the total adult abundance (SAS + wild) is small (Hutchings and Fraser 2008). Conversely, it is unlikely that SAS fish could be 'engineered' to be so different from their wild counterparts that captive-wild interbreeding does not occur while still generating net demographic benefits to fisheries harvesting (Hutchings and Fraser 2008, box 1; Seamons et al. 2012).

Loss or reduction of standing levels of genetic diversity in wild populations

Although the loss of standing levels of genetic diversity through a reduction in effective population size is a common concern in juvenile supplementation programs (Waples 1999), the degree of risk associated with SAS may depend on the goal of the SAS program. If the goal is to augment harvesting per se, loss of standing genetic diversity is not expected to be a risk under most conditions, provided the ratio of SAS to wild fish is low. This is because a large number of smolts of varying genetic background will be captured for SAS activities and will survive until release as adults. If the goal of SAS is to supplement a very small, depleted population, SAS will probably pose more of a risk to standing levels of genetic diversity in wild salmon populations through multiplicative effects of:

(i)   non-random sampled collections of wild smolts;

(ii)   high selective mortality in captivity; and,

(iii) the release of large numbers of SAS adults relative to wild adults.

Potential effects of epigenetic changes induced by SAS on wild fitness

Manipulations during captive-rearing have been hypothesized to generate chromosomal abnormalities or heritable epigenetic changes, such as DNA methylation, that may affect individual fitness in salmonids (O'Reilly and Doyle 2007; Araki et al. 2008). Research on steelhead (*Oncorhynchus mykiss*) found no evidence that the hatchery rearing environment generates global hyper- or hypo-methylation of the genome or generates differential methylated sites in comparison to the wild environment (Blouin et al. 2010). Nevertheless, this is not a well-studied phenomenon in salmonids, and two other recent studies have found a relationship

between epigenetic variation and life history divergence (Moran et al. 2013; Baerwald et al. 2015), suggesting that such epigenetic changes might arise if captive rearing elicits life history change.

ECOLOGICAL RISKS OF SAS

Homing precision, breeding fitness, mating and offspring competition

SAS can affect the fine-scale homing precision and breeding fitness of adults, which is often reduced in captive-reared fish relative to wild fish (Heggberget et al. 1993; Dempson et al. 1999; Berejikian et al. 2005; Keefer and Caudill 2014). In general, captive-reared males are inferior to wild males in courting, in competing for females and in spawning behaviour (Fleming and Gross 1993; Fleming and Petersson 2001; Jonsson and Jonsson 2006); this has also been documented for SAS reared males by Berejikian et al. (2001a) but not by Venditti et al. (2013). To a lesser extent, adult Atlantic salmon males reared in sea cages can display damage to their kypes and jaw distortion and this too can negatively affect subsequent performance (Jonsson and Jonsson 2006). Captive-reared females, whether originating from juvenile supplementation or SAS rearing, may also be more likely to retain eggs and less likely to construct or cover nests in the wild (Berejikian et al. 2001b; Weir and Grant 2005; Jonsson and Jonsson 2006). Collectively, it is very possible that the benefits of retaining free mate choice through the adoption of SAS may not be fully realized after captive rearing, the extent to which has received very limited empirical attention to date.

Despite their often reduced breeding fitness, captive-reared adults can substantially outnumber wild adults and produce a considerable number of juvenile offspring (Kostow et al. 2003; Berejikian et al. 2008; Stark 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), captive-reared fish may displace wild fish to some extent, and contribute to the depletion of wild populations through competition for space and breeding opportunities (Jonsson and Jonsson 2006). For example, variation in growth rate, adult size, age at maturity, egg size, and fecundity induced by captive-rearing can influence competitive ability, spawning behaviour, reproductive success, and fitness, with effects on biomass and production of fish in nature (Berejikian et al. 1996, 2001a, 2001b, 2008; Fleming and Gross 1993, Fleming et al. 1997, 2000; Fleming and Petersson 2001; Wertheimer et al. 2004).

Spread of pathogens or parasites to wild fish

Because captive-reared fish are reared at higher densities than in the wild, they are commonly susceptible to increased pathogen or parasite exposure (e.g. Krkosek et al. 2005, 2007) and may experience genetic changes associated with differing pathogen/parasite regimes or loading (Mangel and Stamps 2001; Lawlor et al. 2009). Hence, captive-reared fish can act as a vector of disease to wild fish and may also contribute to the depletion of wild populations (Krkosek et al. 205; 2007; Jonsson and Jonsson 2006). To some extent, SAS rearing could avoid some of these risks if conducted in freshwater tank facilities where certain pathogens can be controlled. However, the full spectrum of pathogens is unlikely to be completely avoided, and freshwater instead of marine rearing poses additional risks, including relaxed selection for marine pathogen/parasite tolerance.

Ecological consequences of changes to phenology traits in SAS salmon

SAS rearing can also affect timing of upstream migration and spawning. For example, captive-reared Pacific and Atlantic salmon are known to enter rivers to spawn earlier or later in the season, move around more, and/or stay within the river for a shorter duration than wild fish

(Jonsson et al. 1990; Økland et al. 1995; Berejikian et al. 1996; Dempson et al. 1999; Stark et al. 2014). The ecological consequence of earlier spawning by captive-reared fish is that offspring 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, but captive-reared fish may ultimately have poor survival to adult stages (Berejikian et al. 1996; Huntingford and Garcia de Leaniz 1997). Alternatively, later spawning by captive-reared adults has the risk of disturbing wild fish redds and ultimately decreasing hatching success (Kostow and Zhou 2006; Kostow 2009).

Caveats: breeding fitness and competition of captive fish in relation to assessing SAS risk

Despite the different ecological risks of captive-rearing discussed above relating to homing precision, breeding fitness and competition with wild fish, it is important to emphasize that a substantial amount of the aforementioned research in this section 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. The possible impacts to wild population breeding fitness and competition with SAS fish are more uncertain. However, the more the genetic and plastic changes associated with captive rearing are minimized, the more any negative ecological effects are expected to be minimized (Fleming et al. 1994; Frankham 2008; De Mestral et al. 2013; Wilke et al. 2015; Clarke et al. 2016). Indeed, more recent works on developing SAS programs suggest that, at the very least, spawning habitat selection and courting behaviour can be similar between SAS and wild adults (Stark et al. 2014; but see Berejikian et al. 2001a).

Density-dependence, population productivity and SAS

There is substantial empirical evidence that Atlantic salmon populations are regulated primarily by density-dependent mortality at early life stages and by density-independent factors at reproductive stages (Einum and Nislow 2005; Einum et al. 2006). Therefore, in Atlantic salmon, returning SAS fish are not expected to generate density-dependent mortality in adults under many circumstances. Exceptions might be in very small populations or when SAS fish represent a large proportion of returning adults (SAS and wild combined). However, the progeny of SAS adults could elicit density-dependent mortality in the next generation and this would be a concern if SAS elicits phenotypic and genetic changes that negatively impact wild fitness (see section above entitled Genetic risks of SAS to short-term and long-term fitness). Furthermore, although the effects of large-scale releases of SAS salmonids on other competing wild species and other ecosystem components (e.g. nutrient deposition, foodweb restructuring) have not been well-studied (but see Höjsjö et al. 2005; Kostow 2009), the effects of SAS per se are expected to be reduced relative to situations of captive-rearing involving a greater degree of domestication.

Releases of captive-reared alevins, parr, and smolts are intended to increase the productivity of habitats, but such supplementation may only sometimes result in the desired effects and instead either decrease the productivity of wild populations (Chilcote 2003; Nickelson 2003) or result in no productivity change (Hayes et al. 2004; Waples et al. 2007; Scheuerell et al. 2015). Releases of SAS fish are also intended to increase wild population productivity, but whether such releases increase, decrease or have no effect on wild population productivity has not been fully experimentally assessed in the wild. It seems less likely that under many circumstances SAS releases will result in an overexploitation of available food resources or overwintering space where receiving wild populations are well below carrying capacity when SAS is adopted. Nevertheless, of note here is that in cases where juvenile releases caused a decrease rather

than an increase in total population size, maladaptation induced by adaptation to captivity was regularly invoked as a cause (Araki et al. 2007a,b; Waples et al. 2007).

Compensatory vs. additive mortality in wild populations experiencing SAS

A last ecological risk relates to how potential harvesting derived from SAS might affect compensatory vs. additive mortality in wild Atlantic salmon, a consideration that has received no direct empirical research attention in salmonids. Harvesting involving SAS releases would be considered compensatory if the fish harvested would have died anyways from natural occurrences (e.g. weather, predation), and hence harvesting would not affect the wild population (Nichols et al. 1984). SAS harvesting would conversely be considered an additive mortality risk to a wild population, if the stocking of SAS fish or how changes to harvesting add to the number of deaths of wild fish that would have occurred naturally.

At the collection stage for SAS, removal of wild smolts from a population might effectively represent additive mortality by reducing wild adult abundance if the wild population is small and if there is a non-negligible risk that a catastrophe during SAS rearing results in a large loss of captive-reared smolts. In such a case, the removal of wild smolts would likely add to the mortality that would have been experienced naturally.

At the adult release stage of SAS, most SAS adult fish would be similar to wild fish in being expected to die after spawning and to not contribute to the population in subsequent years. In many candidate populations for SAS, the wild population is likely below carrying capacity, and so presumably there would not be much mortality in the absence of harvesting, meaning that harvesting mortality would be additive. The extent to which harvesting mortality could shift from additive to compensatory mortality with SAS supplementation might increase as the carrying capacity is approached, but it is unlikely that the SAS would be used under such circumstances.

SAS harvesting appears more likely to pose an additive mortality risk to a wild population. For instance, wild fish survival can be decreased when the presence of large numbers of captive-reared fish results in the overharvest of small wild populations by fishers (Flagg et al. 1995; Hilborn and Eggers 2000). Moreover, additive mortality is more likely to occur via competition or stress in years where environmental conditions in rivers are poor for salmon survival, spawning and/or recruitment (e.g. very high water temperatures and below seasonal flows) (see Levin et al. 2001). Additive mortality might also increase in wild salmon if the SAS process facilitates the spread of pathogens and parasites to remaining wild fish existing in the population (e.g. Krkosek et al. 2005).

If it is a management concern, a simple tagging system (e.g. adipose fin clip) could be used on SAS fish to facilitate the prevention of harvesting of pure wild fish; if this is not possible, real-time parentage assignment using molecular genetics could be employed (see Dann et al. 2013 for an example).

CRITERIA AND METRICS FOR ASSESSING RISK OF SAS ACTIVITIES

Like juvenile supplementation, the severity of genetic and ecological risks from conducting SAS depends largely on:

(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 (Tables 1, 2, 3).

Therefore, it is recommended that criteria and metrics for assessing the risk of SAS be based on each of these two contexts. 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 (Garcia de Leaniz et al. 2007; Fraser et al. 2011). The second context accounts for how the magnitude of the effects of maladaptation from SAS might affect population productivity and persistence (Fraser 2008; Bowlby and Gibson 2011). This latter context is particularly relevant to consider for SAS programs initiated on small, at-risk populations where small reductions in wild fitness have a higher probability of influencing the threshold between population persistence and extirpation.

DEVIATIONS FROM WILD PHENOTYPES IN SAS FISH

With respect to maladaptive phenotypes in captive-reared fish, potential fitness reductions would be expected to increase as trait deviations from the wild environment increase (Frankham 2008). Therefore, for any phenotypic trait potentially linked to fitness, a deviation in mean and variance between SAS and wild fish would represent a simple, readily quantifiable metric by which to assess SAS risk; a statistically significant deviation would indicate specifically that there is a risk. A sufficient sample size would be required to control for Type II error (conclusion that there is no deviation when in fact there is one). Reduction of both the mean and variance of this trait differential could be considered as a 'balanced' strategy to minimizing risk, to account for the specific distribution of phenotypes within the focal wild Atlantic salmon population. In theory, phenotypic deviations could be partially overcome at the time of release in the wild by matching wild phenotypic distributions with selected SAS fish. A list of phenotypic traits meriting consideration for the assessment of risk is summarized in Table 2 (see also Table 3).

RATIO OF SAS TO WILD FISH

With respect to the ratio of SAS fish to wild fish, risk is expected to increase with increasing phenotypic trait deviations as above but also as this ratio increases in the population, based on what is known of long-term interactions between captive-reared and wild fishes (Hindar et al. 2006; Frankham 2008; Fraser 2008). Risk from SAS is also expected to increase in a purely ecological sense as the supplemented population more closely approaches its carrying capacity and when environmental conditions for salmon spawning and recruitment are poorer, primarily through density dependence and competition with wild fish (Levin et al. 2001; Kostow 2009). However, as discussed in the section Ecological risks of SAS, there is considerable uncertainty in providing simple quantitative criteria or metrics for assessing these specific risks with SAS because of a lack of empirical data. More discussion on population demographic-genetic monitoring is found below and in the next section. Overall, such risks must be balanced with the benefits in a given situation; for example, if the demographic benefits of implementing SAS prevent population extirpation.

REDUCED FITNESS IN SAS FISH RELATIVE TO WILD FISH

Other risk metrics could include the monitoring and quantification of fitness in SAS fish and their progeny relative to wild fish, throughout the course of a SAS program. This would demand significant time and resource investment but represents the only quantitative measure of:

(i)   risk to wild fitness and wild population productivity posed by a specific SAS program; or conversely,

(ii) supplementation 'success'.

Specifically, it would require 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, and then tracking and comparing the lifetime success of the offspring produced by the two groups of fish (and/or their hybrids) to rule out the influence of different environments experienced by the parents. Such research would typically require more than a decade to complete based on the generation time of wild Atlantic (or Pacific) salmon.

POPULATION VIABILITY ANALYSIS

A final approach to assessing risk from SAS would involve conducting formal population viability analyses (PVA) or analogous modelling exercises (e.g. Kareiva et al. 2000; Wilson 2003; Robertson 2005; Scheuerell et al. 2015). These could explore what combination of wild fitness reductions from SAS, and proportions of SAS adults relative to wild adults, generate positive and negative (or zero) demographic effects, relative to traditional juvenile supplementation. Hence PVA could be used to assess genetic-demographic trade-offs with either supplementation activity, even before a supplementation program is undertaken.

An elasticity value indicates how much a proportional change in survival at a particular life stage would result in a change to population growth rate (λ); higher survival elasticities translate into greater changes to λ (Crowder et al. 1994). Available research on different life stages in Atlantic salmon suggests that the survival elasticity of the juvenile marine stage (smolt-to-1SW) is as high or slightly higher than early juvenile stages (parr) (Robertson 2005). Additionally, considered from a habitat perspective, survival elasticity associated with freshwater stages may only be modestly higher than marine habitat/stage elasticity (Robertson 2005). These points suggest that the proportional sensitivity of population growth rate (λ) to changes in annual stage-specific survival probability might actually be very similar between marine and freshwater phases in Atlantic salmon.

Moreover, in wild populations with adult return rates of only a few percent, rates of mortality between early (egg-to-smolt) and later life stages (smolt-1SW) can be very similar (see Hutchings and Jones 1998). In other words, it cannot be ruled out that there is an equal potential for different, natural selective pressures to affect mortality in marine and freshwater life stages. Hence, the rationale for using SAS in dwindling populations to avoid well-documented genetic risks of traditional juvenile supplementation is an uncertain one. Furthermore, these considerations suggest that if SAS elicits as strong a reduction in wild fitness as documented for juvenile supplementation, SAS might not generate net demographic benefits (e.g. a greater contribution to λ) beyond those of juvenile supplementation.

Any such PVA or other modelling exercises would also have to consider whether, in situations of declining wild populations, comparable wild fitness reductions induced by supplementation activities at different life stages are in fact equal to one another. For example, in a population where marine survival is the biggest limiting factor, a captive-reared juvenile that survives release to maturation could be argued to have gone through more of the 'lifetime selection gauntlet' than a SAS adult that had only experienced natural selection at juvenile stages, and hence be proportionally more important to population persistence.

UNDER WHAT CONDITIONS ARE SAS PROGRAMS A NEGLIGIBLE RISK TO FITNESS OF WILD ATLANTIC SALMON?

For the purposes of addressing this question, the following working definition of 'negligible risk' is used: an impact on the productivity of the wild population which can be mitigated by the wild population within one generation once the impact ceases.

There have been very few formal attempts to develop quantitative modelling for assessing how reductions to wild fitness from captive rearing affect the productivity of wild populations, and

none specifically on SAS. Bowlby and Gibson (2011) used existing data to demographically model how adaptation to captivity in endangered Atlantic salmon might affect population size trajectories and extinction risk when supplementing wild populations with captive individuals, relative to a scenario where no such genetic effects were present. The modeling was based on two alternative heritability values (0.1, 0.3), three alternative values of generational fitness loss in captivity (15%, 30%, and 45%), and two different proportions of the population reared in captivity ('lower' vs. 'higher').

The values of heritability simulated by Bowlby and Gibson (2011) were realistic for many salmonid fishes that might be affected by SAS. Nevertheless, some phenology traits and some morphological traits can have higher heritability (e.g. adult run timing is commonly 0.3-0.5), and many physiological traits associated with migration have not been studied thoroughly in salmonids (reviewed in Carlson and Seamons 2008; see Atlantic salmon examples in Table 4).

The values of generational fitness loss in captivity simulated by Bowlby and Gibson (2011) were realistic based on empirical estimates from salmonid captive-rearing/supplementation programs involving local-derived captive fish but are not entirely applicable to SAS for several reasons. For example, empirical studies commonly report fitness reductions closer to the upper two values employed by Bowlby and Gibson (2011) (e.g. 30-60% per generation: Araki et al. 2007b; Araki et al. 2009; Christie et al. 2012; Milot et al. 2013; Evans et al. 2014). Furthermore, the modelling of Bowlby and Gibson (2011) was based on juvenile supplementation programs, not SAS, and it did not account for carry-over effects of captive rearing per se (e.g. how maternal effects affect subsequent offspring performance) and how these might affect fitness. Finally, the modelling did not consider the effect of captive-wild interbreeding on successive generational losses to fitness. This is an important caveat for SAS risk assessment, because SAS fish might represent a large proportion of spawning adults, especially within a small, supplemented population.

Under the scenarios of heritability between 0.1-0.3 and high generational fitness loss (45%) in the modelling of Bowlby and Gibson (2011), juvenile supplementation did not increase population size relative to a null model of no genetic/fitness effects from captive rearing. A medium (30%) to high generational fitness loss also had two additional effects: it impeded population growth in a supplemented population, with attainment of recovery targets requiring more time (Bowlby and Gibson 2011). Nevertheless, medium and low (15%) fitness loss scenarios most commonly had a net benefit of increasing population size in the first four to six generations of supplementation (based on a generation time of approx. 3.5 to 3.7 years in Atlantic salmon), after which the fitness loss in captivity overwhelmed these initial benefits and led to population declines (particularly under the 30% and 45% scenarios), presumably because of a decrease in the average individual fitness (Bowlby and Gibson 2011). Whether a higher or lower proportion of the population was reared in captivity each generation did not appear to have an overall large effect on population recovery and extinction risk, but a wider range of values was not explored. For other conditions of interest that were not modelled (captive-wild interbreeding), a greater extent of supplementation is expected to have a greater impact on population recovery (Hindar et al. 2006; Frankham 2008; Fraser 2008).

Generalizing the available modelling results to whether SAS poses a negligible risk to wild Atlantic salmon populations has a considerable degree of uncertainty. Furthermore, analogous modeling exercises emphasize that it can be extremely challenging to determine both the impact of supplementation programs as well as the causal basis for observed outcomes (Scheuerell et al. 2015). However, with respect to population productivity, available modelling suggests that a short-term, intermittently conducted SAS will pose less risk to wild Atlantic salmon. In other words, the risks to wild population productivity increase, and likely cannot be mitigated by the wild population within one generation once ceased, when SAS:

(i)   generates greater reductions to wild fitness;

(ii) is continuously practiced over successive generations; and

(iii) represents a greater proportion of the total number of adults (or of either sex) in the population.

RISK ASSESSMENT OF SAS ACTIVITY TO WILD ATLANTIC SALMON OF THE MIRAMICHI RIVER

In response to low adult returns of Atlantic salmon to the Miramichi River in 2014, particularly in the Northwest Miramichi (DFO 2015), SAS has been proposed to supplement the population. The proposed SAS activity in the Northwest Miramichi River would rear to the adult stage a total of 1,500 wild-caught smolts from three smolt wheels (Northwest Miramichi, n = 200; Sevogle, n =200; Little Southwest Miramichi, n =1,100) (DFO 2016). Rearing is to take place in a land-based, freshwater recirculating facility. Smolt-to-adult survival is estimated to be as low as 1.7% up to greater than 6% in the Miramichi system in recent years, and adult returns were estimated to be as low as 2,475 salmon in the Northwest Miramichi in 2014 (DFO 2015).

With these numbers, the proposed collection represents only a very small number of the probable total smolt production in the Northwest Miramichi River system (see Chaput et al. 2016). The wild adult abundance foregone from the Northwest Miramichi River for supplementation efforts (smolt collections) would also be very small, and hence would represent a low risk activity to population persistence. However, SAS adults derived from wild-caught smolts could comprise a significant proportion of total adult returns if wild adult returns remain at 2012-2014 levels (e.g. approximately 13.5-32.6% assuming an 80% survival rate in captivity). These proportions of total adult returns could increase if the number of smolts reared for supplementation purposes is increased and/or if wild adult returns in the Miramichi continue to decline.

What the aim of the proposed SAS activity in the Miramichi 'should be' is beyond the scope of this review. Nevertheless, if the intent of the proposed SAS activity is primarily to permit increased harvesting in the Northwest Miramichi, it may not pose a major risk to the wild population provided:

(i)   SAS fish are easily demarcated from wild fish for targeted harvesting; and,

(ii) most SAS fish are harvested.

However, if this is not easily achieved (which is very likely), or if the main intent of the proposed SAS activity is to demographically boost the wild population size in the Northwest Miramichi because of concerns over population viability, then the genetic and ecological risks discussed above merit full consideration. Finally, the intent of the proposed activity might be to use the Miramichi system as a model for conducting long-term experimentation on the potential merits of SAS for regional, adaptive management of Atlantic salmon in eastern Canada. In such a case, the genetic and ecological risks must still be considered, as well as logistical trade-offs regarding where best to conduct research to reduce its risks and derive the most adaptive management benefits.

Four specific concerns with the proposed SAS activity in the Miramichi are as follows. First, 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. A second concern is the high degree of multi-sea winter (MSW) maturation in

Miramichi salmon (Chaput et al. 2016). 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. A third concern is that the Miramichi system harbours a complex of genetically-distinct populations of salmon that have local adaptations (Riddell et al. 1981; Stahl et al. 1983; Moore et al. 2014). Mixing of Miramichi populations may therefore not be easily avoided when conducting SAS, and effective monitoring of SAS vs. wild progeny with sufficient statistical power may be very difficult within a large, complex river system. A final concern is that there is some evidence from existing juvenile production data in the Miramichi that the river system is near its carrying capacity (DFO 2015; Chaput et al. 2016). This suggests that a substantial increase in supplementation (SAS or otherwise) may result in increased density dependence on juveniles and not necessarily any increases to adult population size.

GENERAL RECOMMENDATIONS FOR MONITORING SAS RISK AND SAS USE

In-depth research, evaluation and modelling of existing or proposed SAS activities are sorely needed. Additional assessments of this type would facilitate proper-decision making on when, where, and how SAS might provide desired, net-demographic benefits to wild salmon populations. In order to reduce the risks from SAS activities, the following recommendations are proposed for adaptive management of wild Atlantic salmon:

- Conduct experimentation to effectively quantify and compare the lifetime fitness of SAS versus wild progeny and second generation progeny under natural conditions. A particularly effective approach would also include traditional juvenile supplementation in the same experiment, to determine the relative genetic risks to population growth from different supplementation practices. The feasibility of generating sufficient statistical power at different life stages for adaptive management must be considered judiciously before choosing geographical locations to initiate such research.

- Minimize deviations from wild phenotypic trait distributions as much as possible in all SAS programs currently underway (or being considered). Many aspects of phenotype should be considered in risk assessments beyond those commonly assayed in the literature (growth, morphology, life history), such as physiological, behavioural and phenology traits (see Table 2). Wild and SAS phenotypic distributions should be tracked annually to account for possible temporal fluctuations and to ensure that released SAS fish match wild fish.

- Conduct population viability analyses or analogous modelling exercises to explore what combinations of variables generate positive and negative demographic effects through SAS relative to traditional juvenile supplementation. Such analyses should account for a range of values in wild fitness reductions through SAS at different life stages, the proportion of SAS adults relative to wild adults, the duration and frequency (continuous vs. intermittent) of SAS activity, population-specific life history characteristics (e.g. 1SW vs. MSW, egg-to-smolt survival, smolt-to-adult survival etc.), and how SAS is conducted (e.g. freshwater vs. marine rearing) (Table 1). This would also facilitate cost-benefit analyses given it is expected that SAS will require considerable economic resources.

- Use SAS only sparingly as a short-term approach to supplementing severely dwindled or already at-risk wild populations. Avoid the use of SAS over successive generations; SAS should only be used as a long-term approach if the alternative of not adopting SAS is population extirpation.

- Keep a low-to-modest ratio of SAS adults relative to wild adults in the population if SAS is adopted. Exceptions might occur if the goal of SAS is to provide short-term increases to harvesting, but only if SAS and wild fish can be easily differentiated (to avoid overharvesting of wild fish) and if most SAS fish can be harvested.

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TABLES

Table 1. General criteria for assessing risks associated with smolt-to-adult captive-reared supplementation (SAS) in wild Atlantic salmon and other salmonids. Domestication selection = DS; Local adaptation = LA

Criteria	Risk
Increased time in captivity from smolt-to-adult stage	Increased DS; loss of LA
Population with large MSW component	Increased time in captivity = increased DS
Freshwater rearing instead of seawater	Increased DS; more likely loss of LA
Use of non-local population for supplementation	Loss of LA
Deviations in smolt collections from wild phenotypes	Increased DS; loss of genetic variation
Increased deviations from wild phenotypes (see Table 2)	Increased DS; loss of LA
Increase deviations from maturation curves (see Table 2)	Increased DS; loss of LA
Consecutive generations in captivity	Increased DS; loss of LA
Manipulations during captive-rearing	Epigenetic effects on offspring survival
Carry-over effects	Increased DS; loss of LA; reduced survival, reproductive success
Suboptimal release timing	Reduced survival, reproductive success
Reduced homing capacity	Reduced survival, reproductive success
Increased use of wild smolts (small populations)	Demographic reduction in wild adult returns
Increased proportion of SAS fish relative to total wild population size (SAS + wild)	Interbreeding, loss of LA; density-dependent effects (especially next generation); potential additive mortality, increased breeding competition and competitive displacement of wild fish
No monitoring of performance of SAS fish	No feedback for adaptive management

Table 2. Metrics of risk associated with smolt-to-adult captive-reared supplementation (SAS) at different fitness-related phenotypic traits that could be monitored. A deviation in trait expression represents a statistically significant deviation in mean and variance between SAS and wild fish at the same life stage, for a given SAS program (i.e. the trait distribution of the specific wild population). The list of traits is not exhaustive and could be tailored to a specific SAS program. The ease of monitoring risk is approximated based on the time and resources required to do so, and on feasibility.

Life stage	Phenotypic trait class	Phenotypic trait	Risk notes	Ease of monitoring risk
Smolt	General	All	Sample accidentally captures individuals from non-targeted subpopulations in situations where within-river population structure exists	Straightforward-moderate
Smolt	Phenology	Migration-timing	Sample does not capture the wild distribution	Straightforward
Smolt	Life history	Growth, body size	Sample does not capture wild distribution at onset	Straightforward
Smolt-adult	Life history	Growth, body size	Deviation from wild distribution	Moderate
Smolt-adult	Behavioural	Anti-predator	Deviation from wild distribution	Very difficult
Smolt-adult	Behavioural	Aggression/boldness	Deviation from wild distribution	Very difficult
Smolt-adult	General	Diet	Deviation from wild distribution	Unavoidable
Adult	Life history	Growth, body size	Deviation from wild distribution	Moderate
Adult	Life history	Maturation	1SW and MSW components unmatched with wild	Difficult
Adult	Morphological	Body shape	Deviations in body depth, caudal peduncle region	Difficult
Adult	Phenology	Reproductive timing	Deviation from wild distribution	Very difficult
Adult	Physiological	Migratory rigor	Deviation from wild distribution	Very difficult
Adult	Physiological	Activity levels	Deviation from wild distribution	Very difficult
Adult	Life history	Egg size; fecundity	Deviation from wild distribution, carry over effects	Straightforward
Juvenile	All	All	Carry over effects from SAS adults	Very difficult

Table 3. Risks associated with specific components of an Atlantic salmon SAS program that may lead to deviations from wild characteristics. Literature reference examples are included with each risk where possible and are not exhaustive; these reflect direct evidence based on SAS empirical research on Atlantic salmon (AS) or Pacific salmon (PS), or indirect evidence from juvenile supplementation programs (AS or PS), other species, modelling or theoretical studies. N/A = not available (unknown, to the best of my knowledge).

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	collections are not proportional to run timing, freshwater age, sex ratio, body size	-unintentional selection -deviation could be higher in large rivers with stock structuring, less in small rivers with less structuring	Indirect (PS): McLean et al. (2005)
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): Dempson et al. (1999); Clarke et al. (2016)
	failure to initiate feeding on artificial feed initiation of feeding in captivity	-domestication selection - smolt diet changes from surface feeding to water column feeding - failed smolt syndrome documented	Direct (AS): Dempson et al. (1999); Clarke et al. (2016) Direct (PS): Kline and Flagg (2014); Stark et al. (2014) Indirect (AS): Strademeyer (1991,1994)
Rearing at high densities	natural territorial behaviour of juveniles which are not smolts	-domestication selection low probability of deviation - juvenile salmon studies; transition to schooling behavior of smolts - territoriality may be relaxed in smolts and subsequent stages (adult behavior in rivers in pools)	Indirect (AS): Huntingford and Garcia de Leaniz (1997); Jonsson and Jonsson (2006); see also Hansen and Quinn (1998) Indirect (PS) Berejikian et al. (1996)
	Aggression, risk taking, competition for food, social behavior, aggression	-domestication selection high probability of deviation - associated with generally small school sizes at sea	Indirect (AS): Fleming and Petersson (2001); Jonsson and Jonsson (2006); Hutchings and Fraser (2008); Houde et al. (2010) Indirect (PS): Kostow (2009) references therein; Quinn (2005), references therein Indirect: Braithwaite and Salvanes (2005)

Activity Specific process	Why components may deviate from wild	Source and how much deviation from wild	Evidence
Rearing at high densities	growth rates lower due to 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): Jonsson and Jonsson (2006); Fleming and Petersson (2001) Indirect (PS): Araki et al. (2007a,b); Thompson and Blouin (2015) Indirect: Hansen and Quinn (1998)
	maternal provisioning for eggs, male reproductive fitness	-domestication selection high probability of deviation -high density stressful environment may result in lower investment in egg quality and quantity	Direct (PS): Berejikian et al. (2001a,b); Stark et al. (2014) Direct (AS): Tobique SAS, Jones et al. (2014)Indirect: Heath et al. (2003); Rollinson and Hutchings (2013); Debes et al. (2013)
	microbiota interactions parasite pathogen loading and dynamics	- domestication selection high probability of deviation	Indirect (AS): Fleming and Petersson (2001)
Artificial diet	nutrient composition from artificial feed not comparable to nutrition from wild	- domestication selection high probability of deviation - diet research from aquaculture that favours growth but low maturation rate - diverse diet of wild fish at sea	Indirect (AS), Gjerde and Gjedrem (1984); Christiansen et al. (1995) Indirect (AS), Hansen and Quinn (1998)
Feeding regime	timing and intensity of feeding	- domestication selection high probability of deviation	Indirect: Glover et al. (2004)
	source of food (surface feeding in captivity versus water column feeding in the wild)	- domestication selection high probability of deviation	Indirect: Glover et al. (2004)
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, aquaculture)	Indirect (AS): Jonsson and Jonsson (2006) Indirect (PS): Reisenbichler and Rubin (1999) Direct (PS): Berejikian et al. (2005) Stark et al. (2014)

Activity Specific process	Why components may deviate from wild	Source and how much deviation from wild	Evidence
Abiotic factors associated with rearing	epigenetic effects – rearing environment affects genotype passed to offspring	- domestication selection; high probability of deviation from wild	Indirect: Baerwald et al. (2015)
Rearing in confined environment	relaxation of risk averse strategies, reduced interspecies interactions	- domestication selection; high probability of deviation from wild in land-based 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 scenarios	Indirect (AS): see Jonsson and Jonsson (2006) and references therein; Houde et al. (2010)
	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, stubby tails, head morphs - husbandry condition dependent	Direct+Indirect (AS) : Fleming et al. (1994); Fleming and Petersson (2001); Jonsson and Jonsson (2006) Indirect (PS): Pulcini et al. (2013)
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) : Dempson et al. (1999); Jones et al. (2014) - similar maturation schedule for 1SW stock raised at sea; retention in captivity for three years in wild stocks that are 1SW and 2SW maiden Indirect (PS): Araki et al (2007) Indirect (AS): Clarke et al. (2016) Indirect: Frankham et al. (2008); Fraser (2008)
Use of vaccination, antibiotics, salt baths to treat disease/pathogen incidences	artificial selection for fish of various pathogen resistance	-unintentional selection, domestication selection; high probability of deviation from wild - occurs in captive rearing environments to retain high survival rates of captive fish	Indirect (AS): Lawlor et al. (2009) Indirect: Reisenbichler and Rubin (1999); Araki et al. (2008); Fraser (2008)

Activity Specific process	Why components may deviate from wild	Source and how much deviation from wild	Evidence
Choice of rearing environment	differences between freshwater and marine rearing, pathogens, microbiota, gut flora, stress from confinement	- domestication selection; high deviation from wild for freshwater rearing - low deviation from wild for marine but varies with local versus distant exposures - range of diseases observed in captive reared environment - varied disease exposure at sea (e.g. BKD, furunculosis, ISA)	Indirect (AS): Lawlor et al. (2009) Indirect: Araki et al. (2008); Frankham (2008); Fraser (2008)
RELEASE OF ADULT FISH			
Release location freshwater	SAS fish released in location that does not match stock origin of juveniles and stray to freshwater rearing location	- low to high probability deviation dependent upon straying rate of wild fish	Direct (AS): see Carr et al. (2004) for homing to hatchery source
Release location tidal or marine	SAS fish not imprinted to source river, stray to other rivers	-unintentional selection; low to high probability of deviation -dependent upon how smolts were transferred to sea cage (imprinting legacy),	Direct (AS): Dempson et al (1999)
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, domestication selection; high probability of deviation in large rivers with run timing structure - low probability of deviation from wild for 1SW stocks of smaller rivers	Direct (PS): Berejikian et al. (2005) Direct (AS): release of captive reared salmon in headwaters of Tobique and held until spawning, independent of run-timing (Jones et al. 2014) - no differences in returns of early or late releases from Conne River (Dempson et al. 1999)
	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): Inner Bay of Fundy immature fish survived and spawned the following year (P. O'Reilly, DFO Halifax, personal communication)

Activity Specific process	Why components may deviate from wild	Source and how much deviation from wild	Evidence
Timing of release	releases are not proportional to wild stock in terms of freshwater age, sex ratio, body size	-unintentional selection - low probability of deviation from wild	Direct (AS): sex bias in age at maturity and size at maturity in wild fish (Jones et al. 2014) Indirect (PS): McLean et al. (2005)
	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); Lawlor (2009)

Table 4. Examples of heritability (h2) estimates in Atlantic salmon for phenotypic traits that are likely to be affected by smolt-to-adult (SAS) supplementation. Extracted from Carlson and Seamons (2008).

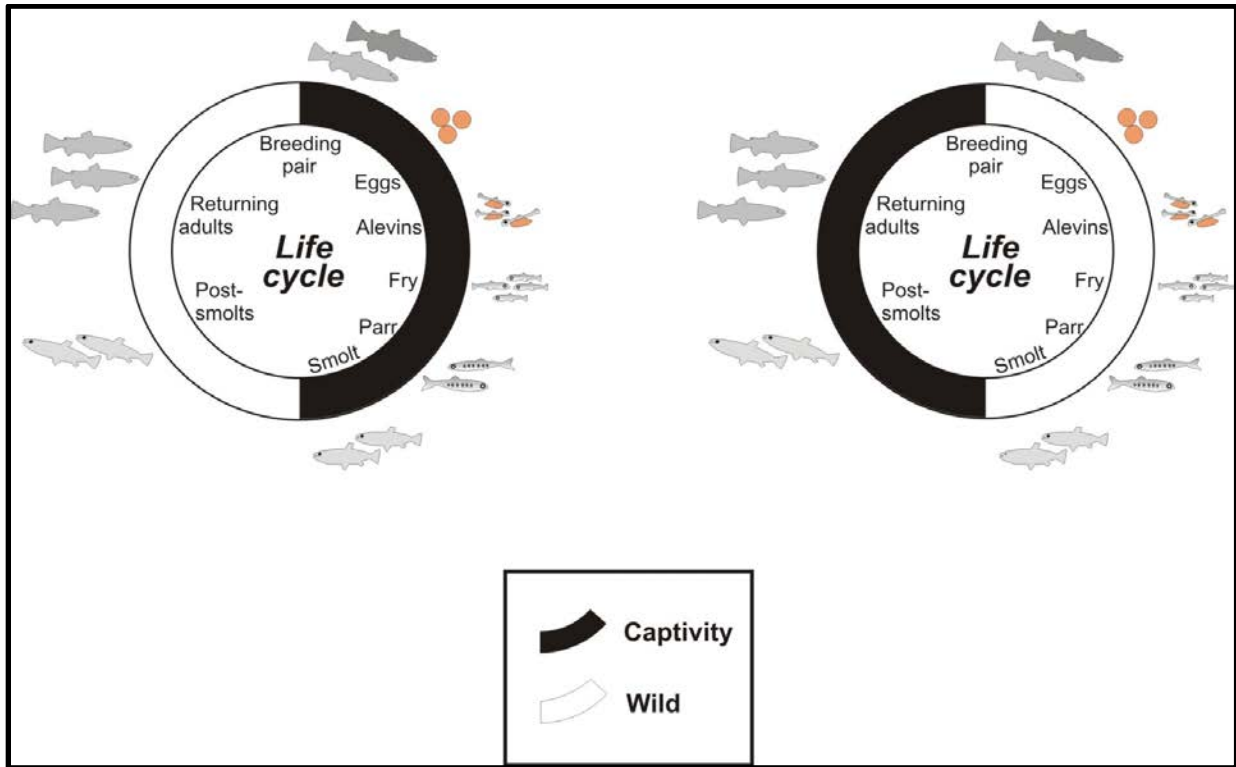| Phenotypic trait	Heritability (h^2)	Reference (s)
Age-at-maturation	0.0-0.49	Gjerde and Gjedrem (1984)
Mass-at-age (immature/mature adults)	0.38-0.55	Gjerde and Gjedrem (1984)
Immune response	0.0-0.1	Fjalstad et al. (1996)
Vertebral deformities (immature adults)	0.0-0.36	Gjerde et al. (2005)
Sea lice tolerance	0.074	Glover et al. (2005)
Adult return rate	0.01-0.24	Jonasson et al. (1997)
Disease response	0.02-0.26	Kolstad et al. (2005)

Figure 1. A comparison between commonly-adopted juvenile supplementation programs (left panel) and less common smolt-to adult-supplementation (SAS) programs (right panel) in the life cycle of Atlantic salmon, in terms of what life stages experience captive and wild environments. Figure produced and provided by P. O'Reilly, Fisheries and Oceans Canada.