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Risks and benefits to wild Atlantic salmon populations from hatchery and stocking activities with particular emphasis on smolt to adult captive-reared supplementation

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Risks and benefits to wild Atlantic salmon populations from hatchery and stocking activities with particular emphasis on smolt to adult captive-reared supplementation

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This paper briefly outlines what is known of the risks and benefits to smolt-to-adult supplementation (SAS) in wild Atlantic salmon. Literature on the hatchery and stocking of wild Atlantic salmon populations is dominated by programs that capture and spawn wild adults and release large numbers of hatchery-reared juveniles. Much less is known of SAS, wherein migrating smolts are captured, captive-reared until maturation and subsequently released in freshwater. The marine environment for Atlantic salmon is changing rapidly in many regions, particularly at the southern part of the species range. With these changes has been a dramatic decline in smolt-to-adult survival. Where this occurs, SAS has potential advantages over juvenile supplementation towards mitigating population declines. First, it provides a predictable input to adult population size. Second, it avoids well-documented genetic risks to captive-rearing at early life stages experiencing high mortality. Third, SAS maintains free mate choice in the wild. However, SAS is not without risks or uncertainties. SAS may reduce marine adaptation (or adaptation to freshwater-marine linkages) through unintentional or relaxed selection. SAS may also cause negative carry-over effects on wild fitness. Several SAS programs have been initiated on endangered salmon populations in North America but the full results of these long-term experimental studies are awaiting final results. Possible maladaptation generated from SAS in the form of changes to wild phenotypic trait distributions should be minimized as much as possible. A balancing act also occurs between the number of wild smolts required for SAS to be effective, the proportion of SAS adults released relative to wild adults, and maintaining at-risk wild populations.

Background

Hatchery stocking programs are increasingly adopted to salvage endangered populations of salmon or to prevent populations from experiencing further decline. The ecological and genetic risks of these activities have long been discussed. Yet the science of conducting effective hatchery-rearing is still in need of further development, specifically to determine how to achieve its desired demographic benefits whilst minimizing its potential genetic or other ecological risks. Previous works on the risks and benefits of captive-rearing, including on salmonids, have recommended that the risks can be substantially reduced by using local populations for captive-breeding/supplementation, reducing the duration of captivity, minimizing environmental differences between wild and captive environments, restricting captive breeding to life history stages where natural mortality is not as severe in the wild, and allowing free mate choice (O'Reilly & Doyle 2007; Pitcher and Neff 2007; Fraser 2008).

Given these general recommendations, SAS is an attractive tool for stocking salmon populations where marine return rates are low. SAS would use local fish, it avoids captive rearing at early life stages that generally experience the most mortality in salmonids, it conceivably minimizes some environmental differences between captive and wild environments if conducted in marine sea-pens, it would still allow adults to choose mates in the wild, and it could provide a predictable input to adult population size and prevent the complete collapse of individual age cohorts. SAS programs have recently emerged for endangered Atlantic salmon populations from southern Canada (Clarke et al. 2016) and Maine, USA (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). However, SAS is not without risks like juvenile-oriented supplementation.

Genetic risks of SAS

Environmental conditions and selective pressures invariably differ between the hatchery (captive) and natural environments. Owing to such environmental differences, the hatchery environment causes plastic and genetic changes to phenotypes associated with fitness in natural environments, often resulting in reduced fitness in hatchery-reared fish when they are released back into nature (Araki et al. 2008; Fraser 2008; Christie et al. 2012). These plastic and genetic changes can occur in all aspects of phenotypes, and they affect all life stages; adaptive genetic changes to captivity can occur in only one or two generations. It is largely unknown 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.

Maladaptive genetic changes in captivity are manifested through a relaxation of natural selection or unintentional selection. Unintentional selection in the captive-rearing process appears to be the most common mechanism, but both mechanisms can result in wild maladaptation. Captive-rearing can also generate carry-over effects on fitness in the wild. For example, in salmon, maternal provisioning in offspring is heavily influenced by the environmental conditions that a female experiences. These maternal effects can also be genetically-based in Atlantic salmon and affect juvenile offspring growth and survival (Araki et al. 2008; Fraser 2008).

The genetic risks of SAS have not been rigorously assessed empirically and reported in peer-reviewed literature on Atlantic salmon. This 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; 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 (Fraser 2016). Based on known genetic risks of hatchery-rearing, however, SAS is expected to elicit plastic and genetic changes to phenotypes that affect wild Atlantic salmon fitness. 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 whether SAS is practiced continuously or intermittently, the proportion of individuals in the population that experience SAS, SAS environmental conditions, and specifically how much these conditions differ from those to which a wild population is normally exposed (Fraser 2016).

SAS avoids captive-rearing at the early life stages which experience the highest mortality (96.8-99.8%), but smolt-to-adult mortality is still very substantial in wild salmon (82.5-98.5%, 92.6% average for 1SW; Hutchings and Jones 1998). As smolt-to-adult mortality will be much lower using SAS, relaxation of natural selective pressures is a likely possibility, especially associated with predation in the marine phase and with marine parasite/pathogen resistance if rearing is conducted in freshwater. Wild populations undergoing SAS may also experience relaxed selection for traits associated with migratory vigor and activity levels.

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 (Fraser 2016). Under SAS rearing, individual growth, maturation and morphological shape trajectories, any correlated behavioural traits, female reproductive allotment, behavioural traits associated with living at higher densities and pathogen resistance will likely change, whether fish are reared in

marine or freshwater; these changes may affect subsequent reproductive success and/or offspring survival in nature. Unintentional selection might also occur upon the earliest stage of SAS during the collection of smolts before they migrate out to sea. Smolt collections may not represent the full spectrum of smolt migration timing or body size if non-randomly sampled (Fraser 2016). Survival rates of smolts in captivity might also depend on the timing of their physiological transformation for moving into seawater. Efforts to collect smolts may also run the risk of obtaining mixtures of populations beyond a focal population of interest, especially in larger river systems.

Atlantic salmon exhibit a considerable degree of local adaptation in freshwater at different geographic scales (Garcia de Leaniz et al. 2007). Little is known of local adaptation in the marine phase, but undoubtedly adaptation exists to different marine areas (Fraser et al. 2011; O'Toole et al. 2015). Local adaptations and genetic polymorphisms in freshwater are also intimately linked to the marine phase in salmon. Management must consider how SAS affects the adaptive genetic characteristics of wild salmon during the marine phase and other linked life stages. Marine maladaptation from SAS is critical to consider because the marine phase is often 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 (Fraser 2016).

An additional genetic risk of SAS is the hybridization of hatchery-reared SAS fish with remaining wild fish in a population. SAS-wild hybrids are expected to have exhibit intermediate fitness in the wild relative to 'pure' wild and 'pure' captive fish; the extent to which such hybridization will occur and generate maladaptation in wild fish will depend on a host of factors.

Manipulations during SAS-rearing might also generate chromosomal abnormalities or heritable epigenetic changes, such as DNA methylation, that may affect individual fitness in salmonids. This is not a well-studied phenomenon in salmonids, and recent studies have offered mixed evidence that epigenetic changes induced by the hatchery affect life history change that may influence fitness (Blouin et al. 2010; Baerwald et al. 2015).

Ecological risks of SAS

SAS might affect the fine-scale homing precision and breeding fitness of adults, which is often reduced in captive-reared fish relative to wild fish (Dempson et al. 1999; Berejikian et al. 2005). In general, captive-reared males are inferior to wild males in courting, in competing for females and in spawning behaviour (Jonsson and Jonsson 2006). Adult Atlantic salmon males reared in sea cages can also 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 (Jonsson and Jonsson 2006). Overall, it has not been evaluated empirically whether the benefits of retaining free mate choice through adopting SAS are fully realized after captive rearing.

Despite their often reduced breeding fitness, captive-reared adults can substantially outnumber wild adults and produce a considerable number of juvenile offspring (Kostow 2009; Stark et al. 2014). 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 hatchery-rearing can influence competitive ability, spawning behaviour, reproductive success, and fitness, with effects on production of fish in nature (Berejikian et al. 2005; Fleming et al. 1997).

As hatchery-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. Hatchery-reared fish can act as a vector of disease to wild fish and may contribute to wild population depletion (Jonsson and Jonsson 2006). SAS rearing could avoid some of these risks if conducted in freshwater tank facilities where certain pathogens can be controlled. However, freshwater instead of marine rearing poses other risks, including relaxed selection for marine pathogen/parasite tolerance.

SAS rearing may also affect timing of upstream migration and spawning given that hatchery-reared 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 (Dempson et al. 1999; Stark et al. 2014). Earlier spawning by captive-reared fish results in their offspring emerging earlier, which 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. Later spawning by captive-reared adults conversely may disturb wild fish redds and decreasing hatching success (Kostow 2009).

Criteria and metrics for assessing SAS risks

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 (Fraser 2016). Criteria and metrics for assessing the risk of SAS should be based on each of these two contexts. The first context accounts for how much maladaptation SAS generates in a species whose general biology is founded in the local adaptation of phenotypic traits. The second context accounts for how the magnitude of the effects of maladaptation from SAS might affect population productivity and persistence.

Wild fitness reductions would be expected to increase as trait deviations from the wild environment increase in the hatchery. Thus, 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 (Fraser 2016). 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 population (Fraser 2016).

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 hatchery-reared and wild fishes (Araki et al. 2008; Fraser 2008). Ecological risk from SAS is also expected to increase 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 (Kostow 2009). However, due to a lack of empirical data, there is considerable uncertainty in providing simple quantitative criteria or metrics for assessing these specific risks with SAS.

Other risk metrics could monitor and quantify fitness in SAS fish and their progeny relative to wild fish, throughout the course of a SAS program. This 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’. Such research typically requires more than a decade to complete based on the generation time of wild Atlantic salmon.

When do SAS programs pose the least harm to fitness of wild Atlantic salmon?

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.

General recommendations on the application of SAS

A series of management recommendations have been recently put forth with respect to improved research, evaluation, and implementation of SAS in wild Atlantic salmon (from Fraser 2016):

- Conduct experimentation to effectively quantify and compare the lifetime fitness of SAS versus wild progeny and second generation progeny under natural conditions.
- 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 beyond those currently assayed.
- Conduct population viability analyses or analogous modelling exercises to explore under what combinations of variables generate positive and negative demographic effects through SAS relative to traditional juvenile supplementation.
- Use SAS only as a short-term approach to supplementing severely dwindled wild populations and avoid the use of SAS over successive generations
- Keep a low-to-modest ratio of SAS adults relative to wild adults in the population

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