



Faster Pace of Life in Wild Atlantic Salmon Following Introgression from Farmed Escapees

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Summary

This paper outlines a talk that was held at NASCO's 2021 Annual Meeting. I argue that the effect of farmed genetic introgression on wild salmon can be better understood in light of pace-of-life theory and provide evidence that such introgression leads to a faster pace of life in the wild. From this theory, we would predict changes in suites of life-history, physiological and behavioural traits. These predictions are supported by current empirical evidence.

Introduction

Farmed Atlantic salmon (*Salmo salar*) escape from captivity and mate with their wild conspecifics, leading to high levels of farmed genetic introgression in many wild salmon populations (e.g. Karlsson *et al.* 2016; Wringe *et al.* 2018). We do know that this introgression is negative for local adaptation and therefore also fitness of wild salmon because:

- 1) it is theoretically improbable that the large genetic changes following selective breeding in captivity is adaptive or neutral in any wild population; and
- 2) we have evidence of reduced survival of genetically farmed salmon and farmed-wild hybrids in the wild environment (Fleming *et al.* 2000; McGinnity *et al.* 2003; Skaala *et al.* 2012; Skaala *et al.* 2019).

Experiments have revealed that farmed genetic introgression also leads to change in a number of other traits including growth and size, development and maturation, behaviour, plastic responses and disease susceptibility (reviewed in Glover *et al.* 2017). However, the effects of introgression have rarely been studied in wild populations (but see Bolstad *et al.* 2017).

To obtain a general understanding of the effects of farmed genetic introgression, I suggest using ecological theory on 'pace of life' and the related concept of 'pace-of-life syndromes' (POLS) (Reale *et al.* 2010). My work builds on previous attempts at getting a more general understanding through the concept of 'behavioural syndromes' (Huntingford 2004). Furthermore, I present new empirical estimates of the effect of farmed genetic introgression across 105 wild salmon populations and interpret these in light of the POLS hypothesis.

The pace-of-life syndrome (POLS) hypothesis and its relation to selective breeding on salmon

It has long been noticed that species differ systematically in their life history, from typically 'slow' (long lived and late maturing) species to 'fast' (short lived and early maturing) species (Stearns 1983; Gaillard *et al.* 1989). Evolution along the fast-slow continuum of life history has important ecological consequences, with fast species typically having higher annual fecundity and mortality and higher annual variation in these demographic rates, and therefore more fluctuating population size, compared to slow species (Sæther and Bakke 2000; Garcia *et al.* 2008; Bjørkvoll *et al.* 2012). The concept of a fast-slow continuum parallels the classic concept of *r*- and *K*-selection (MacArthur and Wilson 1967; Pianka 1970) and focus on life-history traits. The POLS hypothesis extends these concepts by recognising the close link between physiology, behaviour and life-history traits, and states that long-term selection

pressures (e.g. fluctuating density-dependent selection) have integrated whole suites of traits, so that they systematically covary across the fast-slow continuum (Table 1) (Reale *et al.* 2010; Wright *et al.* 2019).

With respect to the selective breeding of salmon in aquaculture in relation to POLS, it is important to note that the main focus of the breeding programmes have been on increased growth rate (Gjedrem and Baranski 2010). From POLS theory we would then expect that genetically farmed salmon has a faster pace of life compared to wild salmon, with correlated changes in several life-history, behavioural and physiological traits (Table 1). Several other traits, such as age at maturity and disease resistance, have also been under selection (Gjedrem and Baranski 2010), in addition to selection for survival in the hatchery environment, which could lead to further evolution along the fast-slow continuum.

Table 1. Schematic differences of slow vs. fast pace of life in life-history, behavioural and physiological traits (from Reale *et al.* 2010). High growth rate is highlighted as this has been the focal trait in the selective breeding programmes of Atlantic salmon.

Slow pace of life	Fast pace of life
<i>Life history:</i>	
Long life	Short life
Delayed reproduction	Precocious reproduction
Low growth rate	High growth rate
Fewer offspring of higher quality	More offspring of lower quality
<i>Behaviour:</i>	
Philopatry	High dispersal
High level of parental care	Low level of parental care
Low aggressiveness	High aggressiveness
Shy	Bold
Thorough exploration	Superficial explorer
Low activity	High activity
High sociability	Low sociability
<i>Physiology:</i>	
High HPA axis reactivity	Low HPA axis reactivity
Low sympathetic system reactivity	High sympathetic system reactivity
Low metabolism	High metabolism
Low sensitivity to oxidative stress	High sensitivity to oxidative stress
High immune response	Low immune response

The effect of introgression on wild salmon

Documenting phenotypic changes following farmed salmon introgression in wild salmon populations is difficult. Molecular markers can be used to estimate the farmed genetic relatedness of wild fish (Karlsson *et al.* 2014). However, at the individual level these estimates are imprecise due to the close relatedness between farmed and wild salmon and lead to a conservative estimate of the effect of introgression (Bolstad *et al.* 2017). Despite these

challenges we have documented decreased egg size when controlling for body size (Hagen *et al.* 2019), changes in the number of years spent at sea (sea age) and increased size at maturity within sea age (Bolstad *et al.* 2017) following farmed genetic introgression. In my talk, I present a continuation of this work with a new analysis on the effect of introgression on both early and late life-history traits in wild Atlantic salmon. Here, I summarise the main points.

The new analysis is based on more than 7,000 salmon caught by anglers in 105 Norwegian salmon rivers. In addition to obtaining a scale sample, the anglers recorded mass, total length and sex. The scales were read by professional scale readers to infer freshwater age and sea age as well as back-calculated growth from the growth pattern in the scales. Genetic analysis and quantification of farmed genetic relatedness of the fish followed the method used by Bolstad *et al.* (2017). Because the escaped farmed salmon in the material was excluded based on the growth pattern in the scales, all fish included in the study were wild born but varied in their farmed genetic relatedness. All rivers in the study belonged to the Eastern Atlantic phylogenetic group (i.e. the northernmost rivers in Norway were not included) (see map in Bolstad *et al.* 2017).

The new analysis revealed that increasing farmed genetic relatedness in wild fish increased probability of smolting and migrating out to sea at age 2+, and therefore a decreased smolt age. There was no effect of introgression on size at outmigration, meaning that the body-length growth increased with increasing farmed genetic relatedness. For the later life-history traits, there was an increased probability of maturing after two sea winters (SW) for males in rivers dominated by 1SW salmon, and for females in rivers dominated by multi sea winter (MSW) salmon. For males in rivers dominated by MSW salmon and females from rivers dominated by 1SW salmon we found little effect of introgression on sea age at maturity. Combining the effect of probability of smolting and probability of maturing revealed that farmed genetic introgression reduces age at first reproduction. This was mostly due to a decreased smolt age.

Growth at sea also increased with increasing introgression. The effect of introgression on growth seemed to be largest in the first year compared to later years at sea and was particularly strong on growth during the return migration in salmon from 1SW dominated rivers.

A faster pace of life following farmed genetic introgression in wild salmon populations

The main conclusion of the above analysis is that wild fish with high genetic relatedness to farmed fish grow faster and mature at a younger age than genetically wild fish. This supports the prediction that selective breeding for fast growth leads to a faster pace of life following farmed genetic introgression in wild salmon populations. Our results are in general supported by the findings of the experiments of controlled releases of farmed salmon, wild salmon and their hybrid offspring in natural rivers (Fleming *et al.* 2000; McGinnity *et al.* 2003; Skaala *et al.* 2012; Skaala *et al.* 2019) and in experiments performed under hatchery conditions (Glover *et al.* 2017).

The POLS hypothesis predicts that an increased pace of life would lead to changes in suites of behavioural and physiological traits in addition to life-history traits. Experiments have shown that farmed compared to wild fish have higher levels of aggression (Einum and Fleming 1997; Fleming and Einum 1997; Houde *et al.* 2010a) more boldness in terms of shorter emergence time after exposure to an artificial predator (Einum and Fleming 1997; Fleming and Einum 1997; Houde *et al.* 2010b) and increased dispersal (Jonsson *et al.* 2003; Jonsson and Jonsson 2017), all being traits associated with the fast end of POLS. Selection for increased growth has led to a higher susceptibility to predators (Solberg *et al.* 2020), which can, at least partly, explain the observed lower juvenile survival in the wild (McGinnity *et al.* 1997; Fleming *et al.* 2000; McGinnity *et al.* 2003; Skaala *et al.* 2012; Skaala *et al.* 2019). Studies of gene

transcription have shown that immune related genes are upregulated in wild compared to farmed salmon (Bicskei *et al.* 2014; Bicskei *et al.* 2016), while protein synthesis and metabolism are downregulated in wild compared to farmed salmon (Roberge *et al.* 2006; Bicskei *et al.* 2014), both supporting the POLS hypothesis. A comparison of structural genetic variation in wild and farmed Atlantic salmon have shown allele frequency changes in farmed salmon show evolution of genes underlying behavioural traits during domestication, as well as immunity and metabolism genes (Bertolotti *et al.* 2020). Taken together, the empirical evidence strongly supports our hypothesis that functional genetic differences between wild and farmed salmon can largely be explained by POLS.

The evolution towards a faster pace of life during the domestication of Atlantic salmon is not surprising because of the strong selection for faster growth. However, it could have dire consequences for the wild salmon populations strongly affected by farmed genetic introgression. We would expect changed foraging behaviour following a faster pace of life which probably has cascading effects in the river ecosystem. We would also expect demographic consequences and a more stochastic population dynamic. Increased stochasticity leads to reduced long term population growth rate (Lande *et al.* 2003) and together with increased maladaptation of life-history traits this would lead to lowered population viability.

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