

## Evolutionary hypotheses for a constraint to life-history resilience in depleted *Salmo salar* populations

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Phenotypic plasticity underlies much of the variation in life-history expression in fishes. An understanding of potential constraints on life-history plasticity thus may be critical for assessing the resiliency of populations or species to environmental change. Here, several evolutionary hypotheses are formulated for why a depleted lineage of Canadian Atlantic salmon *Salmo salar* populations continues to express an apparently maladaptive life history in the face of severe marine mortality. These hypotheses include: (1) reduced genetic variability for expressing plasticity, (2) constraints from genetic architecture, (3) constraints from gene flow, (4) phylogenetic constraints or irreversible evolutionary transitions, (5) environmental constraints to plasticity and (6) a restriction to population rescue from evolutionary-demographic feedbacks. This *S. salar* lineage is intriguing to consider for understanding resilience or the lack thereof, because it has life-history attributes that should favour resilience (*e.g.* a high degree of iteroparity, variable age at maturity and the presence of both long- and short-distance migration ecotypes). In particular, the discussion centres on the question of why *S. salar* females, in contrast to males, do not adopt a non-anadromous life history and mature in fresh water, given extremely high marine mortality among anadromous individuals of both sexes. A salient implication, with possibly significant conservation ramifications, is that fishes may exhibit substantial plasticity and potential for adapting to environmental change, but still be incapable of responding to certain environmental changes due to sex-specific constraints to life-history plasticity.

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### INTRODUCTION

A central theme of this special issue is that life-history diversity facilitates the resilience of a population or species to environmental change. To fully understand such life-history resilience or the lack thereof, as well as its conservation implications in fishes, this article hopes to illustrate the value of considering how constraints on life-history plasticity may affect individual fitness and ultimately population persistence (Stearns, 1989; Hutchings, 2004).

In the case of salmonids, such a discussion is informative for three reasons. First, there is mounting evidence that genetic variability in reaction norms (*i.e.* the variable phenotypic expression of the same genotype across an environmental gradient) underlies much of the life-history plasticity in these species (Hutchings, 2004, 2011). Good examples include population differences in age and size at maturity (Haugen

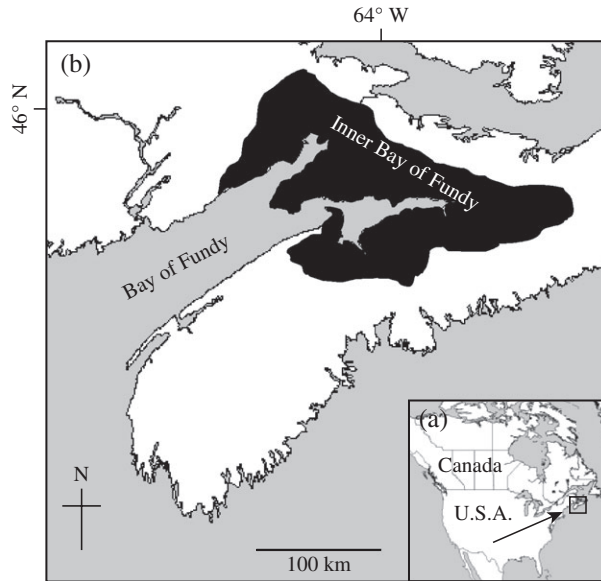


FIG. 1. Maps of (a) the general area inhabited by this case study's *Salmo salar* populations within eastern North America and (b) the location of inner Bay of Fundy *S. salar* populations (modified with permission from Fraser *et al.*, 2010a).

& Vollestad, 2000) and threshold body sizes for alternative maturation phenotypes associated with anadromy and non-anadromy (Myers *et al.*, 1986). Second, empirical work has shown that reaction norms for salmonid life-history traits may become invariant over short time scales (Haugen & Vollestad, 2000; Hutchings, 2004), a potential concern given the present rate of anthropogenic influence on salmonid populations. Third, although relatively underexplored, integrative analyses of fitness and life-history reaction norms have revealed that plastic changes in individual salmonid phenotypes probably affect population growth and abundance, and hence persistence (Hutchings, 2011).

This article specifically considers, as a case study, evolutionary hypotheses for the apparent lack of life-history resilience in a depleted Atlantic salmon *Salmo salar*, L. 1758 population complex found at the southern part of the species' north-west Atlantic range. Phylogeographic, life-history and demographic studies have suggested that *S. salar* spawning in rivers of the Inner Bay of Fundy, Canada (iBoF) is differentiated from other *S. salar* population complexes in North America (DFO, 2002; Verspoor *et al.*, 2002; COSEWIC, 2006) (Fig. 1). A chief known distinction between iBoF and adjacent population complexes is migratory behaviour. Most iBoF *S. salar* reportedly undergo localized migrations between river and marine feeding areas in the Bay of Fundy, whereas adjacent populations exhibit longer-distance migrations to the west of Greenland (Jessop, 1976, 1986; COSEWIC, 2006; Hubley *et al.*, 2008).

A host of factors are implicated in the decline of iBoF *S. salar* observed since the late 1980s, including freshwater habitat degradation or loss (DFO, 2003) and ecological or genetic interactions with escaped farmed salmonids (Morris *et al.*, 2008). Overall, however, it is widely accepted that a combination of still largely undetermined factors

in the marine phase of the life cycle is hindering population growth (COSEWIC, 2006, 2011; O'Reilly & Doyle, 2007). For example, historically, smolt-to-adult survival commonly ranged between 5 and 10%, whereas now it is <0.3%, in some cases zero (COSEWIC, 2006).

Despite iBoF population declines, one might argue that several life-history features of the iBoF *S. salar* lineage should have made it more resilient to environmental change. First, *S. salar* in general exhibit male alternative maturation phenotypes where some males mature as parr in fresh water (Myers *et al.*, 1986). This attribute should provide some degree of buffer against marine mortality by retaining genetic diversity across different cohorts. Second, the iBoF lineage exhibits a high degree of iteroparity for *S. salar* (in some populations >40%), and at least some populations exhibit variable age at maturity (Jessop, 1976, 1986; COSEWIC, 2006). These attributes should increase the likelihood of continuity in recruitment within populations. Third, the iBoF lineage is characterized by multiple migration ecotypes, chiefly short-distance migrants, but some populations have a mix of short and long-distance migrants or just long-distance migrants (Lacroix *et al.*, 2005; COSEWIC, 2006). In theory, this attribute should also provide some resilience, if one migratory ecotype suffers an extreme marine mortality event.

The non-mutually exclusive hypotheses explored to account for the continued expression of an apparently maladaptive life history in the iBoF lineage in the face of marine environmental change are as follows: (1) reduced genetic variability in reaction norms *per se*, (2) constraints from the genetic architecture of traits, (3) constraints from gene flow, (4) phylogenetic constraints or irreversible evolutionary transitions, (5) environmental constraints to phenotypic plasticity, (6) a lack of population rescue *via* evolutionary-demographic effects and (7) multiplicative interactive effects of several of these mechanisms.

What emerges from the discussion of these hypotheses is a general question: to what degree do sex-specific constraints on life-history plasticity ultimately affect population persistence? Arguably, the most obvious way for a salmonid to be resilient to marine mortality approaching 100%, irrespective of its causes, is to have both sexes adopt a non-anadromous life history and mature in fresh water. This can occur in *S. salar*, but in females it is almost uniquely associated with particular environmental conditions, specifically a migration shift from ocean to lacustrine habitat that still permits fast growth and thus achievement of large body size (Berg, 1985; McConnell & Gibson, 1989; Klemetsen *et al.*, 2003). Indeed, the positive relationships between anadromy, faster growth, larger body size, greater fecundity and greater fitness in females are a customary explanation for the routine expression of anadromy in *S. salar* females (Fleming, 1996; Hutchings & Jones, 1998). Many anadromous populations, however, including the vast majority in the iBoF, do not have access to such lacustrine habitat. Furthermore, although males commonly exhibit the most extreme expression of a non-anadromous life history, where individuals mature as parr in a riverine habitat, this is extremely rare in *S. salar* females (Table I).

Similar sex disparities in the degree of non-anadromy and precocial maturation in fresh water occur in several other salmonids (Quinn, 2005; Thériault *et al.*, 2008; Dodson *et al.*, 2013). Similar recent marine environmental changes have occurred in regions other than the iBoF (Welch *et al.*, 2009). Furthermore, significant captive breeding efforts of iBoF *S. salar* are into their fourth generation now with few signs that the populations are re-establishing self-sustaining populations in the wild (COSEWIC,

TABLE I. Documented cases of female non-anadromy with maturation at the parr stage in *Salmo salar* (modified and updated from Hindar & Nordland, 1989). Other kinds of examples of non-anadromy in *S. salar* are reviewed in Klemetsen *et al.* (2003)

River	Geographical coordinates	<i>n</i>	Length (mm)	Age (years)	<i>F</i>	Reference
Vltava, Czech Republic	50° 21' N, 14° 30' E	1	—	8	—	Schafema, 1934
Terne, U.K.	52° 20' N, 2° 20' W	1	229*	2	—	Regan, 1938
Gave D'Oloron, France	58° 34' N, 5° 49' W	1	138*	2	—	Fontaine & Vibert, 1950
Whale, Canada	58° 00' N, 67° 30' W	10	275–305*	5–8	—	Power, 1969
Scorff, France	48° 00' N, 3° 20' W	6	150–211*	1–2	—	Bagliniere <i>et al.</i> , 1981; Bagliniere & Maisse, 1985
Elorn, France	48° 30' N, 4° 20' W	1	225*	3	—	Prouzet, 1981
Namsen, Norway	64° 28' N, 11° 31' E	—	136–228*	—	—	Berg, 1985
Fuglestadana, Norway	58° 34' N, 5° 49' E	1	188*	3	58	Hindar & Nordland, 1989
Avon, U.K.	50° 45' N, 1° 46' W	1	186†	2	82	Moore & Riley, 1992
Ouananiche Beck, Canada	46° 40' N, 53° 10' W	46	82–123‡	1–4	33§	Gibson <i>et al.</i> , 1996

*F*, fecundity.

\*Total length.

†Length not defined.

‡Fork length.

§Mean.

2011) and similar captive and supplementation programmes are being implemented in a number of other regions (Fraser, 2008). Therefore, insights gained from an evolutionary consideration of life-history resilience in iBoF populations may be relevant to other conservation programmes.

## DISCUSSION

### REDUCED GENETIC VARIABILITY IN REACTION NORMS

#### *PER SE*

Genetic variability underlies the plastic expression of life-history phenotypes in different environments (Hutchings, 2011), so its depletion could account for a lack of resilience in the iBoF *S. salar* lineage. For most traits, this hypothesis does not appear very plausible. The evolutionary potential of the iBoF lineage appears to be quite high: iBoF populations exhibit lots of genetically based phenotypic expression under a range of controlled or natural environmental conditions, including in poor *v.* ideal growth regime treatments, over a wide gradient of pH, under different competitive conditions with farmed iBoF hybrids, under different stream gradients and under varying turbidities (Fraser *et al.*, 2007a, 2008; Houde *et al.*, 2010, 2011; Debes *et al.*, 2012). Furthermore, the iBoF lineage appears to harbour a similar amount of genetic diversity at a variety of quantitative traits relative to adjacent, less affected population groups of *S. salar* (Fraser *et al.*, 2010a, b; Tymchuk *et al.*, 2010; Debes *et al.*, 2013). Nonetheless, a caveat to this overall hypothesis is that the amount of genetic variability underlying reaction norms might not adequately depict a population's ability to adapt to environmental change (Hutchings, 2011). Although rich genetic variability has been demonstrated in the reaction norms for studied traits, these trends may not extend to key life-history traits implicated in individual survival, fitness and perhaps population growth.

### A CONSTRAINT FROM GENETIC ARCHITECTURE

The high levels of genetic variation underlying many different traits highlighted above do not preclude that a constraint from genetic correlations in trait architecture might exist within the iBoF lineage and account for a lack of life-history resilience. This has not been investigated but could relate to linkages between growth, migration and maturation. For instance, if selection for the fast growth required for parr maturation also selects for individuals that migrate (or migrate at earlier ages), this could impede selection for non-anadromy. In a non-anadromous rainbow trout population *Oncorhynchus mykiss* (Walbaum 1792) derived from an anadromous ancestor above a waterfall, for example, growth and maturation were positively correlated but less strongly than the negative genetic correlation between migration (smolting) and maturation (Thrower *et al.*, 2004). The result was that despite strong selection against migrants who could never return to spawn (analogous to the present-day iBoF), a high incidence of migration still persisted (Thrower *et al.*, 2004). Such a phenomenon might especially arise in females; there is substantial evidence in salmonids suggesting that very rapid growth is associated with early smoltification among predominantly females (Dodson *et al.*, 2013).

## A CONSTRAINT FROM GENE FLOW

As suggested above, in the face of strong selection against anadromy, selection might favour non-anadromy of both sexes in iBoF *S. salar*. Nevertheless, gene flow from outside populations, whether from wild (Fraser *et al.*, 2007b), farmed (O'Reilly *et al.*, 2006) or hatchery sources (O'Reilly & Doyle, 2007), could overwhelm such selection. Gene flow could thereby act as a constraint to non-anadromy, especially because remaining iBoF populations are very small. For example, escaped farmed *S. salar* have been found to comprise a considerable proportion of the wild spawning run in some iBoF rivers (Morris *et al.*, 2008) and they can successfully interbreed with wild iBoF *S. salar* (O'Reilly *et al.*, 2006). These farmed *S. salar* have been strongly artificially selected for delayed maturation and earlier smoltification (Debes *et al.*, 2012), which could plausibly contribute to a constraint to non-anadromy in iBoF populations.

## PHYLOGENETIC CONSTRAINT OR IRREVERSIBLE EVOLUTIONARY TRANSITION

Another, non-mutually exclusive hypothesis for an apparent lack of life-history resilience in iBoF *S. salar* is that a phylogenetic constraint exists in the lineage that prevents responding to contemporary environmental change. Or, similarly, an irreversible evolutionary transition may have taken place in the expression of some specific trait since the colonization of the iBoF, and this trait is integral to the present-day resilience of the population complex.

It is difficult to assess whether a pre-existing phylogenetic life-history constraint existed when *S. salar* first colonized the iBoF. Yet, historical data on iBoF divergence from other *S. salar* populations suggest that the colonization process of the iBoF did not involve genetic bottlenecks (Verspoor *et al.*, 2002), and, as discussed above, the lineage appears to be quite rich in genetic variability. Moreover, gene flow with outside populations over time (Fraser *et al.*, 2007b) might have had a positive effect in this case by reducing the probability of an intraspecific phylogenetic constraint in the iBoF lineage, though not necessarily a species-level or sex-specific one.

More likely is that an irreversible evolutionary transition has arisen through strong selection. Again, one obvious trait expression that would render the iBoF lineage resilient to strong and rapidly increasing marine mortality would be an ability of both males and females to mature in fresh water, either by not migrating out to sea or by maturing as parr. At a first glance, it would appear that the possibility of a rapid, plastic expression of non-anadromy in iBoF females exists. Indeed, the evolutionary transition from anadromy to non-anadromy in female *S. salar* has occurred independently multiple times in North American and European lineages (Behnke, 1972; King *et al.*, 2001; COSEWIC, 2011), suggesting that at least low levels of genetic variability exist in many populations for expressing female non-anadromy. This includes the lineage that colonized the iBoF after the last deglaciation 10 000–12 000 years ago, because one iBoF population occupies a large lake (Shubenacadie Grand Lake). Moreover, female offspring of anadromous *S. salar* have matured in fresh water following introductions into isolated ponds (McConnell & Gibson, 1989), and captive-reared *S. salar* females provided with sufficient food readily mature in fresh water.

At a second glance, however, the evolutionary transition from anadromy to non-anadromy in *S. salar* has often been associated with a migration shift from the ocean to lakes to obtain fast growth and a larger body size (Berg, 1985; McConnell &



Gibson, 1989). Female maturation in riverine environments, which would be required for present-day resilience in the majority of iBoF populations that occupy river drainages lacking lakes, is uncommon (Power, 1969; Berg, 1985; Hindar & Nordland, 1989; Gibson *et al.*, 1996). Furthermore, historically, strong selection in favour of anadromy in iBoF females is likely to have occurred up to the period of recent, drastic marine environmental change given the high degree of iteroparity in iBoF females (Jessop, 1976, 1986; COSEWIC, 2006). Such a high degree of iteroparity implies high interannual survival across multiple excursions in the marine environment and this may have had a profound, disproportionate influence on individual female fitness relative to the fitness that could be obtained by a female remaining in fresh water. Namely, iBoF reaction norms relating to growth, migration and maturation might have become invariant for an anadromous life history. Indeed, as the rate of female parr maturation observed in *S. salar* populations (Table I) is comparable to mutation rates that alter phenotypic traits ( $10^{-5}$  or less), Hindar & Nordland (1989) hypothesized that in some locations, recurrent mutation alone might explain the expression of female parr maturation. The iBoF lineage may very well exemplify such a situation.

Although an irreversible evolutionary transition to female anadromy appears more plausible than a phylogenetic constraint *per se*, the switch from anadromy to non-anadromy (or *vice versa*) is a particular type of plasticity involving a threshold trait and expression of two alternative phenotypic states. In such cases, strong directional selection can shift the phenotypic proportion of one of the two alternative tactics towards fixation (*e.g.* anadromy in iBoF females), but it may not erode all the underlying genetic variation, which can remain hidden owing to the threshold nature of the trait (Roff, 1992; Dodson *et al.*, 2013). Therefore, overall, it appears likely that females in iBoF populations still possess the ability to adopt a non-anadromous life history. Given the very low reproductive success of non-anadromous females, however, selection may not be able to dislodge anadromy from fixation and express non-anadromy, even in low proportions.

## ENVIRONMENTAL CONSTRAINTS TO PHENOTYPIC PLASTICITY

Another related evolutionary hypothesis for a lack of life-history resilience in iBoF *S. salar* is that an environmental constraint to phenotypic plasticity exists. If genetic fixation to anadromy in iBoF females has not occurred, then some other demographic and environmental factors must explain the lack of plastic expression of female non-anadromy. For example, in the specific case of female parr maturation, there are only two documented cases where *S. salar* females routinely exhibit this trait in freshwater streams or rivers (Berg, 1985; Gibson *et al.*, 1996). In both cases, the anadromy to non-anadromy transition occurred rapidly after the last deglaciation and subsequent isostatic rebound of streams and rivers, perhaps in less than a few hundred years (Berg, 1985; Gibson *et al.*, 1996).

Berg (1985) hypothesized that the transition to female parr maturation would have been facilitated by very cold water temperatures near glacial margins, which extended parr residency (*i.e.* delayed migration) and which may have reduced the competitive advantage of anadromy (Berg, 1985). If true, then this leads to the intriguing hypothesis

that iBoF females cannot express parr maturation because the overwintering temperatures they experience at the southern part of the species range are too high to promote a longer parr residency.

A perhaps more plausible, non-mutually exclusive environmental constraint to the plastic expression of female non-anadromy could be attainment of a sufficiently large body size in fresh water as a trigger, either through optimal habitat conditions for fast growth or through increasing residency before a migration to sea took place. For example, freshwater maturation was environmentally induced in offspring of anadromous *S. salar* introduced to pond environments more optimal for growth relative to their less productive home stream (McConnell & Gibson, 1989).

A last environmental constraint might be availability of oviposition habitat in relation to female body size as originally proposed by Dodson *et al.* (2013). For example, salmonids typically spawn in gravel beds of approximate diameter equal to 10% of their body length (Kondolf & Wolman, 1993). This suggests that a smaller, non-anadromous iBoF female would exploit smaller gravel sizes. Either such oviposition habitat might not be sufficiently available in iBoF rivers or perhaps the smaller, co-occurring competitor species, brook trout *Salvelinus fontinalis* (Mitchill, 1814) already occupies such habitat.

#### LACK OF POPULATION RESCUE VIA EVOLUTIONARY-DEMOGRAPHIC FEEDBACKS

Perhaps neither a lack of genetic variability underlying phenotypic plasticity nor an environmental constraint to phenotypic plasticity exists in the iBoF lineage as hypothesized above. Perhaps instead, female non-anadromy can be expressed, at least at very low frequencies (Hindar & Nordland, 1989). Even if this scenario was true, female reproductive output might still be insufficient to rescue iBoF populations from extirpation by demographically boosting recruitment. Indeed, individual fecundities would be drastically lower in non-anadromous females than in anadromous ones (Bagliniere & Maisse, 1985; Hindar & Nordland, 1989). If it is assumed in this scenario that a genetic component to expressing female non-anadromy exists (as it does for males), for a positive evolutionary-demographic feedback on population growth to occur, rapid evolution occurring over a few generations towards increasing frequencies of female non-anadromy could be envisaged, ultimately rescuing iBoF populations from extreme marine mortality. Such a positive feedback may be very difficult to initiate if it is overridden by demographic or environmental stochasticity (Gomulkiewicz & Holt, 1995).

A similar challenge to facilitating resilience *via* the initiation of a positive evolutionary-demographic feedback could be envisaged at other life-history traits, such as migratory ecotypes. For instance, the specific geographic areas of localized marine migration of most iBoF *S. salar* may be largely responsible for severe marine mortality. In addition to non-anadromy, a way to potentially avoid such areas would be to adopt the long-distance migration strategy to Greenland exhibited by adjacent *S. salar* population groups (including a few iBoF population members such as the Gaspereau River; O'Reilly & Doyle, 2007). Such intraspecific variation in marine migration often has a partial genetic basis and may evolve under natural selection (Kallio-Nyberg *et al.*, 2000). Within populations, marine migration can be a relatively invariant trait (Waples *et al.*, 2004) and adjacent *S. salar* population groups with long-distance migrations are also experiencing increased marine mortality (though not



as high as the iBoF; Gibson *et al.*, 2011). This implies that long-distance migrations would probably incur additional energy costs to iBoF individuals adopting this strategy, perhaps countering the possible advantages of avoiding critical areas of marine mortality closer to natal iBoF rivers. Collectively, a combination of environmental and genetic constraints to increasing the frequency of long-distance migration in iBoF populations, and hence the likelihood of resilience, might reinforce low survival and stochasticity.

## OTHER CONSIDERATIONS AND MULTIPLICATIVE EFFECTS

Much of the discussion up to now has implicitly assumed that local selection should favour female non-anadromy in iBoF *S. salar* given the strong selection against anadromy, or in other words, that a non-anadromous existence is now adaptive. Although smolt-to-adult survival in the iBoF is zero or at best *c.* 0.3% (COSEWIC, 2006), it might be argued that the potential relative fitness of a successfully returning anadromous female in the iBoF might on average still be greater than that of a female adopting non-anadromy. Average female fecundity of anadromous iBoF females is *c.* 3500–4000 eggs (COSEWIC, 2006). Female fecundity and annual survival rates of any non-anadromous iBoF females are uncertain, but based on other works of riverine maturing fish or geographically close populations, fecundities might be 30–33 eggs (Hindar & Nordland, 1989; Gibson *et al.*, 1996) and annual survivorship *c.* 25–50% (Whelan *et al.*, 2000). Assuming similar juvenile survival rates, the highest possible relative fitness of an anadromous female in comparison to a non-anadromous female might in fact exceed one (1.6:1, based on  $4000 \times 0.003$  *v.*  $30 \times 0.25$ ). Undoubtedly, this survival-fecundity trade-off could in part explain why non-anadromy has not evolved in iBoF females, though even a drop in marine survival to just 0.2% in the comparison makes non-anadromy equally advantageous to anadromy. Furthermore, reduced reproductive success in non-anadromous females could be exacerbated by lower early life-history survival either through limited oviposition habitat or competition with *S. fontinalis*.

More generally, it is difficult to tease apart which of the hypotheses presented in this article are most plausible. From the standpoint of natural selection in the iBoF, if non-anadromy is not adaptive and anadromy still is adaptive, the latter is clearly insufficient to avoid extinction at the present time through demographic or environmentally stochastic events. If, however, non-anadromy is currently adaptive (or another trait relating to anadromy is such as shifts in spatial migration), multiplicative effects of several of the mechanisms proposed are probably jointly acting as a constraint to persistence. In particular, it might be that genetic correlations that constrain female non-anadromy or parr maturation, the disparate trade-off between fecundities produced between anadromous and non-anadromous females, and the unproductive freshwater environment in iBoF rivers (specifically, lacking lacustrine habitat) combine to inhibit evolutionary rescue of iBoF populations through non-anadromy.

Despite such a complicated array of possibilities, it is important to recognize the life-history flexibility and plasticity expressed by *S. salar* as a species (Hutchings & Jones, 1998; Klemetsen *et al.*, 2003). Something in the environment to sustain *S. salar* in the iBoF thus appears to be missing, and so a first-step focus on possible environmental constraints to the plastic expression of life-history types favouring persistence

(*i.e.* allowing both anadromy and non-anadromy) might be the most pertinent one for conservation.

## CONSERVATION IMPLICATIONS

On one hand, salmonids exhibit substantial phenotypic plasticity and potential for adapting to a range of environments (Garcia de Leaniz *et al.*, 2007; Carlson & Seamons, 2008; Fraser *et al.*, 2011; Hutchings, 2011; Dodson *et al.*, 2013). On the other hand, as argued here, some salmonids may be unable to express phenotypes that permit them to respond to certain environmental changes, such as the inability of both sexes to express maturation phenotypes in fresh water despite extreme marine mortality.

For iBoF *S. salar* populations, possible constraints to the expression of female non-anadromy, whether through an arrestment of migration to the sea or *via* parr maturation, raise interesting concerns for ongoing conservation initiatives and decision making. Should the marine environment not improve in the foreseeable future, female non-anadromy would be the only possible means of maintaining viable wild populations without perpetual captive breeding (which is not without severe biological and socioeconomic caveats; Fraser, 2008). Before exploring manipulations intended to promote non-anadromy, an important consideration is whether climatically driven shifts in environmental conditions are likely to far exceed the reaction norms for life-history traits in iBoF (or other southern) populations. If this is deemed to be unlikely, then the question of how to generate non-anadromy in the wild is a perplexing one, and might depend on the principal constraint underlying the expression of non-anadromy. If this constraint is environmentally driven, the habitat of iBoF rivers might require artificial enhancement with the addition of lacustrine habitat or nutrient enrichment to increase growth rates of juveniles. If it is genetically driven, such as an invariant reaction norm for an anadromous life history, then genetic material from external non-anadromous populations might be required. Either case poses significant risks, ethical concerns and uncertain probability of success. Furthermore, life-history resilience of iBoF *S. salar* based on a non-anadromous existence implies a discontinuation of any fisheries-related benefits to humans, because individuals of both sexes in fresh water, particularly if they mature as parr, are too small for human consumption. More generally, a better understanding of sex-specific constraints on life-history plasticity may be crucial for assessing the potential of different populations or species to persist or rebound following natural or human-induced environmental change.

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