






An opinion piece: the evolutionary and ecological consequences of changing selection pressures on marine migration in Atlantic salmon

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Abstract

There are strong signals that the selection forces favouring the expression of long-distance sea migration by Atlantic salmon (*Salmo salar*) are changing. Unlike many other behavioural traits, the costs of migration are incurred before any fitness benefits become apparent to the migrant. The expression of this behaviour has thus been shaped by selection forces over multiple generations and cannot respond to short interval (within a single generation) environmental change as many other behavioural traits can. Here we provide a framework to examine the evolutionary and ecological consequences of a sustained increase in migration cost. We argue that Atlantic salmon may have entered an *evolutionary trap*, where long-distance sea migration has become maladaptive because of shifting environmental conditions. We predict that if higher migration costs (affecting survivorship and ultimately fitness) persist, then shifting selection pressures will result in continuing declines in population size. We suggest, however, that in some populations there is demonstrable capacity for *evolutionary rescue* responses within the species which is to be found in the variation in the expression of migration. Under a scenario of low to moderate change in the selection forces that previously promoted migration, we argue that disruptive, sex-based selection would result in partial migration, where females retain sea migration but with anadromy loss predominantly in males. With more acute selection forces, anadromy may be strongly selected against, under these conditions both sexes may become freshwater resident. We suggest that as the migration costs appear to be higher in catchments with standing waters, then this outcome is more likely in such systems. We also speculate that as a result of the genetic structuring in this species, not all populations may have the capacity to respond adequately to change. The consequences of this for the species and its management are discussed.

KEYWORDS

anadromy loss, fitness change, life-history strategy, migration evolution

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1 | LONG-DISTANCE MIGRATION

Long-distance migration is a common feature of the behaviour of animals (Baker, 1978). Billions of individuals, from thousands of species, from across the spectrum of animal phyla, migrate significant distances each year (Bowlin *et al.*, 2010). There is overwhelming evidence that migratory behaviour has evolved repeatedly, in parallel and in multiple discrete lineages (Cresswell *et al.*, 2011). The widespread nature and convergent evolution of this behaviour strongly points to its fitness advantages across a wide range of environmental circumstances and species.

For long-distance migration to be expressed and then maintained, clearly the fitness benefits must be greater than the fitness costs (Mangel & Satterthwaite, 2008). Where the benefits of migration have been examined in detail, they have frequently been linked to increased access to food resources (Dingle & Drake, 2007), but also to predator avoidance and reduced disease/parasite acquisition risk (for a more complete review see Alerstam *et al.*, 2003).

Some migration costs are obvious and ubiquitous. Almost always, there is considerable energetic cost directly associated with movement from one place to another (Bonte *et al.*, 2012). Migration is time consuming, which may limit other important activities (Dingle, 1996). Other costs are more probabilistic. There is a risk of navigational error during migration, resulting in a failure to reach the intended location. There is further risk arising from the uncertainty of finding suitable habitat during, and following, a migration (Cresswell *et al.*, 2011; Dingle, 1996; Rankin & Burchsted, 1992), as well as the risk of increased mortality from both natural and anthropogenic causes during migration (Furey *et al.*, 2015; Hard *et al.*, 2008). Thus it is not surprising that, where it has been measured, mortality rates are frequently higher during, and after, migration than they are at other periods in their life cycle (Cresswell *et al.*, 2011; Guillemain *et al.*, 2010; Owen & Black, 1991; Sillett & Holmes, 2002; Strandberg *et al.*, 2009).

As a class of phenotypic characteristics, behaviour plays an important role in the evolutionary processes for many species (Skulason *et al.*, 1999; West-Eberhard, 1989, 2005). Behavioural traits are among the most labile of trait types. Species often express multiple alternative behavioural phenotypes in response to any given set of environmental conditions (Sih *et al.*, 2004). Numerous field and laboratory studies have shown expressed behaviour to be adaptive, highly plastic and able to respond to short-term environmental change (McCleery, 1978). Optimal foraging theory, for example, predicts that predators should adjust their foraging tactics in response to prey abundance, size, handling time, predation risk and foraging profitability, and that they should do this in response to their immediate foraging experiences. There is considerable support from empirical studies suggesting that they do respond in this way (see Krebs, 1978 for a review of this topic).

Long-distance migration, however, differs qualitatively from behaviours that can be modulated in real time in response to changes in the environment. Although animals may be able to assess the costs and benefits of not migrating, using cues from the environment in

which they are currently living (Chapman *et al.*, 2011), by definition, migrants are not able to assess *a priori* the potential benefits of migration. This is because any benefits do not accrue until after most of the costs have been incurred. In general, any individual initiating long-distance migration behaviour does so blind to many of the costs, and all of the benefits. It has no cues to directly assess the future resource availability, predation risk, parasite or disease threat, in the habitat to which it is migrating. It also has no means to directly estimate the energetic burden of the journey or the navigational risks. Thus, unlike many other behavioural traits, migration might be regarded as an instinctive behaviour.

Instinctive (or innate or unlearned) behaviours, often defined as those which are not, or only slightly, dependent upon context, are somewhat controversial as a concept. Such behaviours are at one end of a continuum of behaviours, the other extreme of which are highly plastic behaviours that are shaped by learning through interactions with the environment (Avital & Jablonka, 2000; Marler, 2004; Tierney, 1986). Examples of true innate behaviour are generally difficult to find but include singing behaviour in some bird species (Kroodsma & Konishi, 1991) and chick pecking behaviour in gulls (Tinbergen & Perdeck, 1950). The expression of these behaviours is shaped more by evolutionary processes than they are by phenotypic plasticity (Tierney, 1986). Hardwired migration behaviour, where all individuals migrate, can thus be regarded as closer to the innate end of the spectrum of behaviours.

2 | MIGRATION IN ATLANTIC SALMON

Atlantic salmon typically make long-distance migrations from their natal rivers to feed in the open ocean (Thorstad *et al.*, 2011). Migration to sea for this species confers higher fitness for females (when compared with freshwater residency), which is accrued through higher growth, resulting in larger body size and consequential effects on reproductive output (Kinnison *et al.*, 2003; Sandlund *et al.*, 2014). The same marine migration benefits can also be true for males. Large body size in anadromous male salmon leads to higher mating and fertilisation rates and less individual variation in fertilisation success (Hutchings and Myers, 1994). Nonetheless, there is good reason to believe that marine migration for Atlantic salmon carries considerable costs, and that these costs have increased in the recent past.

The complex processes comprising smolting prepare fish for migration to sea water (Hoar, 1988). Seaward migration begins with active movement down river, often through freshwater lakes, then the hyperosmotic waters of estuaries, fjords and near-shore coastal zones before entering the open sea. On entering sea water, salmon consume prey items and encounter predators that they have never previously experienced. Over the course of a few weeks, seaward-migrating salmon are exposed to multiple habitat shifts and undergo a series of fundamental changes in physiology, growth, diet, behaviour, colouration, body shape, feeding ecology and parasite and predation risk (Rikardsen & Dempson, 2011). There is clear evidence that the early phase of sea migration is associated with relatively high

mortality (Gregory *et al.*, 2020; Thorstad *et al.*, 2021). Atlantic salmon seaward migration across lower river reaches, estuaries and coastal marine zones has been shown to result in high loss rates (losses of up to 25%.km⁻¹ have been reported), but mortality rates are habitat specific and highly variable (Thorstad *et al.*, 2012). There is now a growing body of evidence that migration through freshwater systems within which there are standing waters has a particularly high rate of mortality, indicating a greater cost of migration in such systems for Atlantic salmon (Aarestrup *et al.*, 1999; Hansen *et al.*, 1984; Honkanen *et al.*, 2018; Thorstad *et al.*, 2012; Lilly *et al.*, 2021).

3 | CHANGING MIGRATION COSTS

There is good reason to believe that the costs of sea migration for Atlantic salmon have changed as a result of human activity. Where either directly or indirectly, human activity imposes additional costs to the expression of traits in a species, then an ecological change and an evolutionary response in that species is to be expected (see Allendorf & Hard, 2009; Tillotson & Quinn, 2018 and references therein).

Over the past three to four decades, adult Atlantic salmon abundance has declined markedly (Chaput *et al.*, 2019; Dadswell, 2000; Kocik & Brown, 2002; Mills *et al.*, 2013; Potter & Crozier, 2000). Long-term tagging studies have shown a generally consistent and marked decline in the proportion of salmon returning from migration to sea (Chaput, 2012; Chaput *et al.*, 2019; Dadswell *et al.*, 2021). For example, adult return rates in the River Corrib, Ireland, declined from 10% to 20%.y⁻¹ before 1990 to 4%-8%.y⁻¹ after 1990 (Potter & Crozier, 2000); the River Esk, Scotland, showed an adult return rate of 1.0%-6.9%.y⁻¹ for 1 SW and 0.5%-3.0%.y⁻¹ for 2 SW fish before 1985 which declined to 0.2%-1.0%.y⁻¹ for both age classes after 1988 (Friedland *et al.*, 2000). Although declining migration survivorship appears to be a general pattern across the species, see Pardo *et al.*, 2021 for an example of an alternative pattern. The mechanisms that lie behind declining migration success are not fully understood, but it is clear that in recent years the anthropogenic pressures that have the potential to impact upon migration success in Atlantic salmon have increased. These have been more comprehensively reviewed elsewhere (Forseth *et al.*, 2017; Parrish *et al.*, 1998; Thorstad *et al.*, 2012). Here we briefly outline three such pressures.

In many parts of its range, coastal marine aquaculture for Atlantic salmon has established and rapidly increased since the 1970s (Martinez-Porchas & Martinez-Cordova, 2012). Salmon aquaculture has been shown to impact on wild salmon during their migration to sea in Norway and Scotland (Bøhn *et al.*, 2020; Finstad *et al.*, 2011; Ford & Myers, 2008). This is a new pressure on salmon migration that did not exist in the first half of the 20th century.

Warmer ocean conditions negatively affect population sizes of Atlantic salmon broadly across North America (Mills *et al.*, 2013). Climate change effects have been observed in several populations throughout its range, and these impacts have increased over the past few decades (Baisez *et al.*, 2011; Boylan & Adams, 2006;

Friedland, 1998; Jonsson & Jonsson, 2009; Todd *et al.*, 2011; Todd *et al.*, 2012).

Riverine impoundments cause direct mortality for migrating salmonids as fish are forced to pass through, or over, structures (Aarestrup & Koed, 2003; Marschall *et al.*, 2011). There are also indirect barrier effects which can extend the duration of the migration (Gauld *et al.*, 2015) and have the potential for anthropogenic trait selection (Lothian *et al.*, 2020). In a study on a Chinook salmon, *Oncorhynchus tshawytscha*, population from the Snake River, Williams *et al.* (2008) demonstrated rapid evolution of migration patterns related to the construction of a hydropower dam. Although river impoundment has occurred over many centuries, dam construction increased markedly during the 20th century (Gleick, 2003). Thus, this is a relatively new cost to migration for salmon.

4 | EVOLUTIONARY TRAP

Here we argue that the costs of marine migration for Atlantic salmon have increased over the past decades. As long-distance migration behaviour is unresponsive to short-time interval environmental change, it is thus highly plausible that Atlantic salmon have become caught in an *evolutionary trap* (*sensu* Robertson *et al.*, 2013). This occurs when a previously adaptive expressed phenotype becomes maladaptive, as the wider environmental conditions change at a pace that is faster than the evolutionary response by the organism concerned (Robertson *et al.*, 2013).

If indeed Atlantic salmon are now caught in an *evolutionary trap*, what evidence exists to suggest that this is the case? A decrease in the proportion of emigrating fish returning to spawn in fresh water compared to a few decades ago has been recorded worldwide (Chaput, 2012 and references therein). This reduced probability of any individual surviving migration indicates an increased cost of long-distance migration, without an obvious equivalent increase in the benefits of migration. This strongly points to a change in the operational selection pressures occurring at a rate that is faster than an evolutionary response in a trait (migration) that is primarily shaped by evolutionary processes (as opposed to those emerging from environmentally driven plasticity).

5 | EVOLUTIONARY RESPONSE

Assuming that the magnitude and direction of the new selection forces are not so severe as to result in widespread extirpation of migrants, then we may expect to see an evolutionary response, sometimes referred to as *evolutionary rescue* (Barrett & Hendry, 2012; Carlson *et al.*, 2014; O'Dea *et al.*, 2016). Any evolutionary response is most likely to be context-dependant. If long-distance migration in the Atlantic salmon is subject to moderate magnitude changes in the selection forces operating, then we might expect one response to be a change in the sex ratio of sea migrants. Common in species producing large eggs, the energetic cost of gamete production in Atlantic

salmon is greater for females than for males (Hendry *et al.*, 2004). In a selective environment where energetic gains, high growth and consequently large body size are the principal benefits derived from long-distance migration (Gross *et al.*, 1988; Hendry *et al.*, 2004), then the accrued benefits of migration are likely greater for females than for males (Myers, 1984). For any selection pressure acting against sea migration, or where the selection pressure for either a marine migration strategy or its alternative (freshwater residency) is reaching parity, the effect is likely to be greater for males than females. A logical consequence of a weak to moderate change in the selection pressure

promoting long-distance sea migration is that sex-based, disruptive selection would result in the expression of partial migration (Chapman *et al.*, 2011). As a result, sea migrants should comprise mostly females and the non-anadromous component of the population would be predominantly males. Change over time in the sex ratio of sea migrants will be an important metric of evolutionary change; nonetheless, there is a paucity of sites for which these data are currently collected.

An alternative scenario, under low to moderate selection pressure against migration to sea, is that salmon might respond by making short-distance migrations, only as far as near-shore coastal zones. The

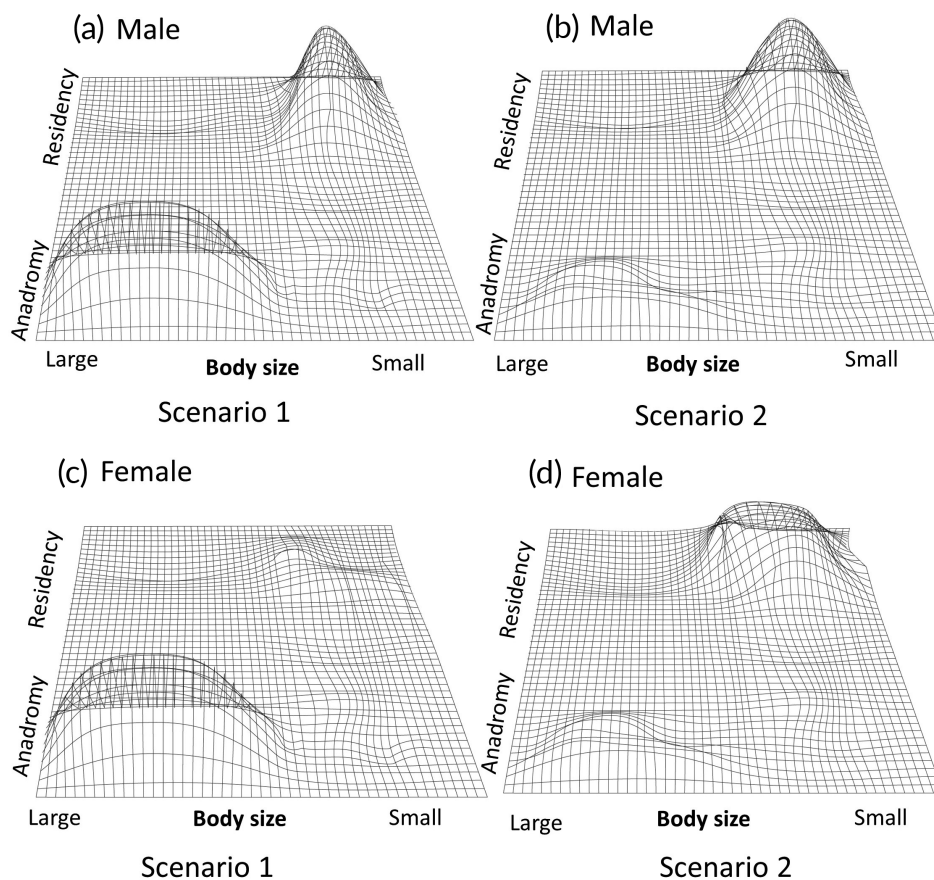


FIGURE 1 A three-dimensional, hypothetical fitness landscape for Atlantic salmon under two alternative selection regimes, differing in the strength of the selection for anadromy. Migration strategy is presented as binary (anadromy or freshwater residency) on the Y-axis; body size at sexual maturation is a continuous variable on the X-axis, and the Z-axis represents the probable fitness outcome for alternative combinations. Males and females are presented separately. (a) and (c) depict scenario 1 (the assumptive historical condition) where anadromy is under moderately strong positive selection pressure for males and females respectively. In this scenario, high fitness in males (a) is gained both by migration to sea, thus achieving large body size and becoming sexually mature at small body size while resident in fresh water. Both strategies have around equal fitness outcomes. The range of body sizes that achieve high fitness is greater among large body size, anadromous fish than for resident, small-bodied fish as a result of body size constraints of the sneaking reproductive strategy employed by small fish. In contrast, female fish (c) only achieve high fitness under scenario 1 at large body size following migration to sea. Because of the strong relationship between body size and gamete number in females, high fitness is not achieved at small body size in females that do not migrate to sea. Under the alternative scenario 2 (the possible future selection pattern) (b) and (d), increased migration costs result in selection against anadromy for both males and females. Thus, high fitness is retained in males (b) at small body size in freshwater residents but lost for fish that undertake marine migration. For females (d) high fitness of anadromous individuals, with consequent large body size, is also lost and now residency and small body size yields the highest fitness outcomes. For resident females (unlike males) the relationship between body size and gamete number remains, and thus there will be selection for larger body size females among freshwater residents. As a consequence females are likely to exhibit larger body size at maturity than males under this scenario. Nonetheless, the relatively low energy availability in freshwater systems will constrain the maximum body size achievable

relative benefits of anadromy likely decrease as migration distance increases (Ohms *et al.*, 2014). This effect has been shown for brown trout, *Salmo trutta*, (Bohlin *et al.*, 2001), sockeye salmon, *Oncorhynchus nerka*, (Wood, 1995), and Arctic charr, *Salvelinus alpinus*, (Finstad & Hein, 2012) suggesting that a similar effect is possible for Atlantic salmon.

Atlantic salmon do have the capacity to express a sex-based disruptive migration pattern. Males are less likely to migrate to sea to fulfil their fitness and are regularly recorded as becoming sexually mature at small size, in the parr stage (Figure 1a) (see, e.g., Baum *et al.*, 2004; Myers *et al.*, 1986). Such males have a higher probability of surviving to sexual maturity, which increases the rate of turnover of their genes into the next generation (Hutchings and Myers, 1994). The fitness costs for males that become sexually mature as parr include a lower egg fertilisation rate, increased variation in fertilisation rate and a lower probability of subsequently migrating to sea when compared with individuals that migrate to sea without becoming mature as parr (Hutchings, 2011). In contrast, females are only rarely recorded as becoming sexually mature without undertaking a sea migration (Figure 1c) (Bagliniere & Maisse, 1985; Mills, 1971). The incidence of mature parr in Atlantic salmon is known to vary spatially (Dalley *et al.*, 2011) and across time (Myers *et al.*, 1986), which strongly points towards environmental mediation of the expression of maturation without anadromy. Under a scenario of a decrease in the cost: benefit ratio of sea migration and a resulting moderate selection pressure acting against sea migration, then the incidence of mature male parr is likely to increase (Figure 1b).

If selection against anadromy is occurring now, or later becomes stronger, then it is highly plausible that long-distance sea migration may be selected against in both males and females, resulting in anadromy ceasing in both sexes. There is evidence of exactly this phenomenon from other species. The loss of anadromy has occurred frequently in populations of *S. trutta*. In areas of the Northern Hemisphere glaciated during the Pleistocene, many populations established from anadromous ancestors within in the last 12,000 are now wholly resident in fresh water (Ferguson *et al.*, 2019). Anadromy is also likely ancestral in Atlantic salmon (Crespi & Teo, 2002). Although not common, we also know that the Atlantic salmon has the capacity to lose anadromy (Adams *et al.*, 2016; Birt *et al.*, 1986; Palva *et al.*, 1989). The Atlantic salmon population in Lake Saimaa, Finland, is no longer anadromous (Palva *et al.*, 1989). A non-anadromous population of Atlantic salmon in Five Mile Pond East in Newfoundland, derived from anadromous populations nearby (Birt *et al.*, 1986), has lost its capacity to adapt to sea water (Burton & Idler, 1984). In the Nansen River, Norway, both males and females of a population exhibit facultatively non-anadromy where both sexes retain the capacity for migration to sea but do not migrate (Sandlund *et al.*, 2014). Hutchings *et al.* (2019) list 72 populations of non-anadromous salmon worldwide, of which 82% come from catchments with lakes, suggesting that selection for the abandonment of sea migration may be more likely in catchments with standing water bodies. For all of these populations, both sexes are typified by small body size relative to anadromous, long-distance migrant populations. Thus, an expected consequence of

a loss of sea migration would be that mean body size would decline markedly (Figure 1b,d).

6 | THE PACE OF CHANGE

If the changes in selection forces outlined above are occurring in salmon, how quickly might we see the patterns of migration in this species change? Sea migration is a highly heritable trait in salmonids (Thériault *et al.*, 2007), but evolutionary change may occur rapidly. Fraser *et al.* (2011) showed that adaptation to conditions experienced by populations exposed to different local environments can arise in as few as 6 to 30 generations in Atlantic salmon.

7 | ADAPTIVE CAPACITY

If, as we argue above, marine migration in Atlantic salmon is already being selected against and that salmon are currently in an evolutionary trap, then what are the broader consequences? In our view, there is sufficient evidence that Atlantic salmon is a species with both the adaptive capacity and phenotypic plasticity to adapt to changing selection pressures on anadromy. The occurrence of males, and records of females (albeit relatively rarely), becoming sexually mature, as so-called precocious parr, in populations that are primarily anadromous, suggests that there is sufficient phenotypic variation upon which selection may act to re-shape the expression of migratory traits. Nonetheless, there is at least one factor that may influence the capacity of Atlantic salmon to respond to changing selection pressures. As a result of the strong natal site fidelity shown in Atlantic salmon, there is considerable genetic structuring across the species (Gilbey *et al.*, 2018). Although the functional gene differences between relatively discrete populations of the species across the range are not yet well understood, it is highly plausible that some specific populations do not have the same level of capacity to adapt to changing selection pressures as others.

The consequences of a shift in the widespread expression of anadromy in this species would be considerable. Atlantic salmon are charismatic and have a cultural significance and economic value as a fishery throughout its range (Radford *et al.*, 2004). The desirability and allure of this species is largely a result of its large body size and its long-distance migration behaviour. The full global economic, social or cultural value of Atlantic salmon has never been evaluated, but it is generally assumed to be high (Myrvold *et al.*, 2019). For Canada the monetary value of wild salmon in 2011 was estimated at \$255 million (Pinfold, 2011), in Scotland alone, in 2004, salmon and other freshwater species were estimated to be worth £100 million (Radford *et al.*, 2004). If these migratory and body size characteristics of the species were lost, its social, cultural and economic importance would also be lost.

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AUTHOR CONTRIBUTIONS

C.E.A. and L.C. developed the original concept for this piece and created the initial draft; J.R.R., H.M.H., D.T. and M.P.N. contributed intellectually to the development of ideas and their refinement; all authors contributed to editing.

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