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Ollscoil na hÉireann, Corcaigh

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Natural selection, evolution, and demography of salmonine populations experiencing intrusion from non-local stock

Thesis presented by

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Table of contents

Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism and intellectual property.

Ronan O'Sullivan
University College Cork

Ronan James O'Sullivan

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The first time I met Tom Reed I was a 2nd year undergraduate student who had his whole career planned out – I was going to be an ornithologist no matter what. Tom joked that if I should ever want to work with fish, call him. “Not a hope”, I thought. Six years and one thesis on Atlantic salmon later, I can’t thank you enough. I doubt there are many supervisors that would give as much freedom to their students as you gave me, Tom, and that freedom has allowed me to become a scientist, but more importantly, a person that I am proud to be. Thank you.

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“No efforts of mine could avail to make the book easy reading”

-Ronald A. Fisher

Stylistic note

To maintain a consistent formatting and citation style throughout this thesis, I have standardised how subsections in each chapter are delineated and how previous research is referenced to throughout. Additionally, all figures and tables are found within the text rather than at the end of each chapter. This has affected the layout of the two published data chapters and, therefore, their presentation here differs from the copies of record available on the websites of their respective journals. Finally, the citations referenced herein are listed in their own section at the end of the thesis. This was done to avoid the unnecessary duplication of citations that would have arisen if each chapter had its own separate reference list.

Abstract

Many salmonine taxa experience intrusion into their wild, free-living populations from non-local conspecific and heterospecific individuals. Such intrusion arises most commonly as a result of releases from captive breeding programmes for conservation, or to provide a demographic excess that can be exploited commercially or recreationally. Furthermore, the relocation of conspecific individuals from one population to another, the deliberate stocking of sexually compatible foreign taxa into areas outside of their natural range, and domesticated individuals escaping from fish farms provide additional pathways for intrusion. The relative fitness of non-local to local fish, as well as the effects intrusion has on wild populations, is highly dependent on the ecological context that both types of fish experience and the level of adaptation displayed by the introduced fish. In this thesis, I examine how natural selection and, thus, evolution affect the performance of free-living salmonine populations that have experienced intrusion from non-local (captive-bred, translocated, domesticated) stock. Exploring this interplay can help to identify what conditions allow for, and the extent to which, non-local fish successfully breed in a given wild setting, as well as to determine the effects their breeding has on the demography of the recipient wild population. A better understanding of the roles natural selection and evolution have on demography and population viability is crucial for designing better captive breeding programmes and mitigating against the negative effects sexually compatible foreign taxa and fish farm escapees can have when they spawn in the wild.

In Chapter 2, I use a molecular pedigree to estimate the lifetime reproductive success of individual Atlantic salmon and demonstrate that captive-bred fish are 64% less fit than their wild-bred conspecifics when both spawn together in the wild. Furthermore, I found evidence of a transgenerational carry-over effect from the hatchery where the wild-spawned offspring of two captive-bred salmon experienced lower survival to adulthood than the offspring of two wild-bred fish. Finally, I used 43 years of population census data to determine that in years where the proportion of spawners that were captive-bred was larger, the productivity of the whole population was reduced.

In Chapter 3, I used the molecular pedigree to explore the evolutionary dynamics of female body size at spawning in Atlantic salmon by applying the variance decomposition methods of quantitative genetics. Female (but not male) salmon experienced positive directional selection for the trait but displayed no phenotypic or evolutionary response despite the trait being genetically heritable and, via the Breeder's Equation, being predicted to evolve towards larger sizes. By utilising a Bayesian regression technique for decomposing the selection gradient into genetic and environmental components, I determined that the female univariate selection gradient used to predict evolution was upwardly biased by one or more unmeasured, but genetically correlated, traits. This highlights the need to measure more than just the focal trait when examining the evolutionary trajectories of populations as management decisions for intruded populations based on biased predictions could result in unforeseen, negative consequences. Chapter 4 is a review of 91 genetically-explicit eco-evolutionary models in fisheries science, with a particular focus on the genetic architecture employed in the models. With relevance to my thesis, only 15 studies (16.5%) examined captive-wild interactions. 14 of these studies were parameterised for or motivated by the effects of captive-bred releases into wild salmonine populations. Five of these modelled trait inheritance through quantitative genetic architectures, nine used explicit Mendelian models of inheritance, and one study allowed for the independent inheritance of both a quantitative trait and a biallelic locus. Together, the results from Chapters 3 and 4 informed the design of my own genetically-explicit eco-evolutionary model in Chapter 5.

In Chapter 5, the aforementioned genetically-explicit eco-evolutionary model was used to explore how soft and hard selection interacted to affect evolution and demography in a salmonine population that had experienced intrusion from non-local stock. Non-local alleles were purged faster from the population when soft selection was stronger. Soft selection also indirectly influenced the strength of hard selection. By limiting the number of maladapted individuals that could breed, soft selection reduced introgression from maladapted alleles into the wild population. This caused a reduction in the number of fish displaying maladaptive phenotypes that would be selected against by hard selection, thus, weakening the strength of hard selection. Furthermore, the weakening of hard selection buffered against the demographic declines associated with this form of natural selection. The results of this chapter demonstrate how unexpected evolutionary dynamics can emerge in populations and how variation in the ecological context (in this case, the form and strength of both soft and hard selection) affects evolution and demography.

This thesis emphasises how variation in natural selection and the extent of intrusion/introgression impacts the evolutionary dynamics observed in salmonine populations that experience intrusion/introgression from non-local fish. Chapter 2 adds to the ever-growing list of studies describing reduced fitness for captive- relative to wild-bred fish while also providing a known example of how increasing numbers of captive-bred fish lead to a concomitant reduction in population productivity. The genetically-explicit eco-evolutionary model resulting from work done for Chapters 3, 4, and 5 stresses how the form and strength of natural selection can vary depending not just on prevailing ecological conditions but also on the genotypic/phenotypic composition of both the wild population and introduced individuals. A greater understanding of how evolutionary dynamics emerge and what conditions lead to a particular set of dynamics is critical in mitigating against the negative impacts arising from the deliberate or accidental release of non-local individuals into wild populations.

Chapter 1 General Introduction

1.1 Conservation and resource management in the Anthropocene

Understanding the interplay between evolution and ecology is increasingly important in the Anthropocene as populations of animals are subject to novel, often rapidly changing, selection pressures (Hendry 2017); pressures to which they might not be able to adapt (Radchuk et al. 2019). Studying these dynamics is further complicated by uncertainty with regards to what ecological and genetic processes might actually drive such change (Kinnison et al. 2015). Anthropogenically-mediated selective pressures and their emergent dynamics do not occur in isolation to pre-existing selection regimes. Rather, both regimes operate and influence a population simultaneously, with the potential for antagonistic (Kane et al. *Submitted*) or synergistic effects. Additionally, the strength and form of novel and pre-existing selective pressures likely vary over time, mediated by, but also influencing, the ecology and genetic composition of populations. Such temporal and state-dependent variation impedes our ability to predict how a given population might react to a specific insult. A better mechanistic understanding of how such processes operate and why certain dynamics emerge has practical implications for conservation biology (Kinnison et al. 2007) and wild resource management. Interventions that are beneficial to one population might have no, or even a deleterious, effect in another. Furthermore, interventions that were once beneficial might not be so in the future as the eco-genetic context, and therefore, dynamics of the population have changed over time (c.f. Schindler and Hilborn 2015).

1.2 Anthropogenic change and salmonine fishes

The salmonine fishes, consisting of salmon, trout, and charr, are those which belong to the subfamily Salmoninae. Salmonines are poikilothermic with a natural distribution in the northern hemisphere ranging from polar to subtropical, though with a distinct preference for colder waters. Many populations of salmonines have declined markedly over the past 200 years as a result of various human-induced environmental insults. The destruction and fragmentation of their freshwater habitat is particularly common and occurs on continental scales. Belletti et al. (2020) reported that there are over 1,000,000 barriers to fish movement across Europe. In estuarine and marine environments, wild salmonines are negatively impacted by pathogenic diseases (Shea et al. 2020) and parasites (Thorstad et al. 2015) potentially spreading from commercial fish farms. Numerous collapses of sea trout populations (*Salmo trutta* L. 1758) due to infestation by sea lice originating from fish farms have been documented over the past 40 years (Thorstad et al. 2015). Climate change likely imposes selective pressure on thermal tolerance during the freshwater life stages of salmonines while also affecting marine growth rate (Jonsson and Jonsson 2009). Negative effects on abundance due to increasing temperatures are known (Almodóvar et al. 2012), with the potential for both local stock declines (Tillotson et al. 2019) and ecosystem-level impacts (Kovach et al. 2013). Predictive modelling suggests that populations might not be able to evolve in response to climate change, likely leading to their extinction (Ayllón et al. 2019).

Two common interventions for beleaguered populations include translocations (Crotti et al. 2021) and supplemental captive-breeding (Cross et al. 2007; Fraser 2008). However, the release of captive-bred/non-local fish into the wild is now recognised as another novel, human-induced selective pressure ('genetic load') that wild salmonine populations must endure. Additionally, farmed salmon escaping from aquaculture facilities also impose selection pressures on wild populations. The release or escape of non-local, often domesticated, fish into the wild where they potentially breed alongside/interbreed with local fish is associated with depressed population productivity (Araki et al. 2009; O'Sullivan et al. 2020), driving traits from their evolutionary optima (Le Cam et al 2015), the formation of hybrid swarms with endangered taxa (Muhlfeld et al. 2009), and inducing changes in expressed life history strategies (Bolstad et al. 2017).

1.3 Captive breeding: hatcheries and farms

1.3 (a) Hatcheries

Intrusion and introgression from captive-bred individuals is of particular relevance to salmonine fishes as their populations are often subject to both deliberate and accidental influxes of non-local individuals via conservation breeding programmes, commercial stocking (Cross et al. 2007), and domesticated fish escaping from farms (Diserud et al. 2020).

Hatchery breeding programmes are the oldest form of captive breeding strategy for salmonine fishes. There are two main types: stocking programmes and ocean ranching. Stocking consists of rearing fish in captivity and releasing them into the wild during the freshwater portion of their lifecycle, as ova, fry or parr. Ocean ranching involves rearing fish in captivity up to the point of smolting (the physiological transition from freshwater- to saltwater-tolerant). These 'smolts' are released alongside their wild conspecifics who are also undergoing the smoltification process and migrating seaward. For both stocking and ocean ranching, the aim is to increase overall lifetime survival from ova to spawning by escaping the limitations of density dependent regulation in the river. For stocking, this is done to increase the wild-spawning abundance of a population. For ocean ranching, it is to provide a demographic excess for recreational, artisanal, or small-scale commercial exploitation. Generally, returning adult stocked fish are allowed to migrate up a catchment to spawn alongside their wild conspecifics, whereas ranched individuals are usually removed at a fish trap, therefore, being excluded from wild spawning habitat (Cross et al. 2007).

Despite the apparent demographic benefits of releasing captive-bred fish from hatcheries, there is little evidence that hatchery releases have aided in the sustainable recovery of wild salmonine populations. Hatchery programmes are often associated with a loss of fitness in the wild (Fraser 2008) and accompanying negative effects on population viability through reduced productivity (Chilcote et al. 1986; Leider et al. 1990; Miller et al. 2004; Araki et al. 2007a,b,c, 2009; Bordeleau et al. 2018; Jonsson et al. 2019; O'Sullivan et al. 2020). Furthermore, even a single generation in captivity can induce maladaptation in salmonines (Christie et al. 2009; Fraser et al. 2018), thus, calling into question many incidences where stocking from hatcheries was used as a conservation measure. A striking example of the failure of hatcheries is presented by King et al. (2021). They demonstrated that a conservation hatchery designed to help save sea trout populations in the Shetland Islands from collapsing played no part in the observed recovery. See Glover et al. (2018) for a similar result.

1.3 (b) Farms

Atlantic salmon, *Salmo salar* L. 1758, were the first fully domesticated fish with a dedicated captive breeding programme specifically selecting for commercially desirable traits (Gjedrem 2010). The Atlantic salmon farming industry has spread to countries both within and outside the natural distribution of the taxon, with Norway and Chile being the largest producers (FAO 2020; Iversen et al. 2020). Each new generation of farmed salmon is created by stripping gametes and breeding from only those fish that display the best performance in captivity (i.e. fast growth, high somatic mass, disease resistance). After 50 years and more than 12 generations of artificial, truncating selective regimes (Glover et al. 2017), farmed Atlantic salmon are now highly divergent, both genotypically and phenotypically, from their wild counterparts. Further differences likely arise due to the different source rivers from which farmed lineages were established (Gjedrem 2010).

Atlantic salmon farming consists of two phases: (1) a freshwater phase in on-land tanks, and (2) a marine phase where the smolting farmed salmon are moved to sea cages in some sheltered bay or fjord. Fish are provided with food, medication, and (during the tank phase) controlled temperatures so to maximise growth rate, thus, shortening production time. Farmed fish have the opportunity to escape and enter wild salmon populations at both the freshwater (Clifford et al. 1998) and marine (Sylvester et al. 2019) life stages. The threats posed to wild salmonine populations by farmed escapees include reduced productivity through juvenile displacement and low fitness (McGinnity et al. 1997, 2003, 2007), out-competing local salmon for breeding sites (Fleming et al. 2000), increased predation risk via introgression between wild and farmed genotypes (Houde et al., 2010; Solberg et al. 2020), evolution towards maladaptive trait values (Bolstad et al. 2017), and inadvertent domestication selection in hatcheries designed to supplement local populations (Hagen et al. 2019). However, the performance of wild-farmed hybrids and backcrosses is complicated by the ancestry of farmed fish as well as environmental conditions (Fraser et al. 2008). In areas of intense salmon farming, the ‘wild’ local populations can display very high levels of admixture with domesticated farmed genotypes (Karlsson et al. 2016), often accompanied by a reduction in genetic diversity within populations (Skaala et al. 2006). The Norwegian Institute for Nature Research (NINA) found that of the 239 rivers they surveyed, 159 contained salmon with domesticated elements in their genotypes, indicative of wide-scale introgression arising from farmed fish escaping and breeding in the wild (Diserud et al. 2020). Gilbey et al. (2021) found introgression was most common in those populations near fish farms.

1.4 Translocation of non-local taxa

The movement of non-local taxa into areas outside of their natural range is known as translocation. Translocation is often used as a conservation measure with individuals moved from a healthy to a threatened population in order to increase abundance or genetic diversity. The stocking of lakes or rivers with non-local fish for recreational purposes is also a form of translocation. Like hatchery and escaped farmed salmon, translocated individuals are rarely adapted to the novel environment into which they are placed, displaying low fitness. Wild Atlantic salmon experimentally transplanted into non-natal catchments have lower fitness relative to local salmon as do their F_1 hybrids (McGinnity et al. 2004, 2007), even if the local and non-natal catchments are geographically close (O’Toole et al. 2015). This holds true for naturally-dispersing salmon that stray into and breed in a different catchment from the one they themselves hatched in (Mobley et al. 2019), thus, highlighting the importance of local adaptation to the fitness of salmon in a given catchment (Fraser et al. 2011).

The translocation of fish to novel habitats for recreational purposes is most commonly done to provide fish for anglers. However, introducing a taxon into a habitat where it has never naturally occurred carries the risk that its introduction has a negative effect on any pre-existing occupants of the habitat. Rainbow trout, *Oncorhynchus mykiss* Walbaum 1792, is a species of salmonine native to the northern Pacific. Its popularity as a sport fish and for consumption has seen it introduced into many areas outside of its natural range where it now threatens the viability of local taxa. Hybridisation between non-local rainbow trout and local westslope cutthroat trout, *Oncorhynchus clarki lewisi* Suckley 1865, is leading to the collapse of many westslope populations into hybrid swarms, with even small levels of admixture causing significant declines in the fitness and abundance of the native trout (Muhlfeld et al. 2009).

1.5 Ecological context and genetic background: a framework for a better understanding of intrusion

The number of conservation-orientated hatchery programmes for salmonine fishes is likely to increase over the coming decades as climate change and habitat degradation negatively affect their ability to survive in the Anthropocene (Jonsson and Jonsson 2009; de Eyto et al. 2016; Belletti et al. 2020). This will likely occur in tandem with an expansion of the salmon farming industry due to its worth (FAO 2020) and increased demand from a growing global population. Furthermore, the accidental spread via translocation of non-local taxa into areas outside of their native ranges is predicted to increase (Seebens et al. 2021), and by extension, so too the probability of deleterious consequences arising from such translocations. The negative effects on local populations induced by releasing captive-bred/non-local taxa into them is well established (see sections 1.3 and 1.4). What is less clear is why some release and escape events cause population declines and genetic introgression while some appear to have no discernible effects.

Understanding the ecological and genetic conditions that mediate such outcomes is crucial to designing captive breeding programmes that are less likely to lead to maladaptive introgression or population declines when fish are released/escape into the wild. Such an increased understanding will also benefit mitigation scenarios where translocated fish threaten local taxa (see Sato 2007 and Muhlfeld et al. 2009). Theoretical work by Baskett and Waples (2013), Baskett et al. (2013), and Tufto (2001, 2017) finds that the degree of maladaptation between local and captive-bred/non-local fish is instrumental in causing demographic declines in the recipient wild population. However, Baskett and Waples (2013) and Baskett et al. (2013) both found that the timing and scale of release/escape events with respect to ecological processes like density dependence in the lifecycle of the recipient wild population also mediated such outcomes. Experimental work has found that captive-bred stocked fish from hatcheries that replicate natural ecological conditions displayed higher post-release survival than those reared under standard captive breeding regimes (Hyvärinen and Rodewald 2013; Harbicht et al. 2020), with the advantage still apparent in their wild descendants (Evans et al. 2014). In this thesis, I explore how variation in such ecological conditions and genetic provenance of captive-bred/escaped salmonine fishes affects the selective landscape that populations experience and how differences in selective landscapes affect genetic introgression and demography.

1.6 Thesis objectives

In order to understand the interplay between selective landscape, introgression, and their effects on demography, I conducted analytical statistics on ecological and genetic data sets, performed a review of relevant modelling literature, and developed a predictive model. Specifically;

(a) I analysed a multigenerational molecular pedigree as well as long-term fish trap data sets to investigate the relative fitness of ranched and wild Atlantic salmon when both spawned alongside each other in the wild and how variation in the number of potentially breeding ranched fish affected population productivity. I also performed quantitative genetic analyses to explore how trait evolution and associated evolutionary dynamics were influenced by genetic architecture (Chapter 2 and Chapter 3).

(b) For Chapter 4, I conducted an extensive literature review and performed a synthetic analysis of 91 genetically-explicit eco-evolutionary models that have been published on topics of fisheries science. I did so in order to better understand how questions concerning the release of captive-bred individuals and foreign taxa have been treated thus far in the literature i.e. modelling approach used, genetic architectures assumed, traits studied.

(c) Using knowledge gained from Chapters 3 and 4, I built a genetically-explicit eco-evolutionary model designed to explore how ecological processes such as hard selection and soft selection affect genetic introgression and population viability in a generic salmonine population (Chapter 5).

Chapter 2

Captive-bred Atlantic salmon released into the wild have fewer offspring than wild-bred fish and decrease population productivity

This chapter has been published in the *Proceedings of the Royal Society B: Biological Sciences*. It is presented here ‘as published’ except for minor stylistic changes.

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Captive-bred Atlantic salmon released into the wild have fewer offspring than wild-bred fish and decrease population productivity

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Author contributions: **RJOS**, TER, PMcG, and EdE conceptualized the paper. **RJOS** and TER designed the LRS and productivity analyses, with **RJOS** conducting the analyses. PMcG, CRP, TA, SEJ, RP, and PAP conceived the original Burrishoole pedigree construction project. PMcG, GR, and RP facilitated data collection and PMcG, GR, RP, and EdE provided access to historical datasets. TA, SEJ, and CRP generated the molecular data and constructed the pedigree. **RJOS** and TER wrote the first draft of the manuscript, with all co-authors contributing to subsequent drafts.

2.1 Abstract

The release of captive-bred animals into the wild is commonly practised to restore or supplement wild populations but comes with a suite of ecological and genetic consequences. Vast numbers of hatchery-reared fish are released annually, ostensibly to restore/enhance wild populations or provide greater angling returns. While previous studies have shown that captive-bred fish perform poorly in the wild relative to wild-bred conspecifics, few have measured individual lifetime reproductive success (LRS) and how this affects population productivity. Here, we analyse data on Atlantic salmon from an intensely studied catchment into which varying numbers of captive-bred fish have escaped/been released and potentially bred over several decades. Using a molecular pedigree, we demonstrate that, on average, the LRS of captive-bred individuals was only 36% that of wild-bred individuals. A significant LRS difference remained after excluding individuals that left no surviving offspring, some of which might have simply failed to spawn, consistent with transgenerational effects on offspring survival. The annual productivity of the mixed population (wild-bred plus captive-bred) was lower in years where captive-bred fish comprised a greater fraction of potential spawners. These results bolster previous empirical and theoretical findings that intentional stocking, or non-intentional escapees, threaten, rather than enhance, recipient natural populations.

2.2 Introduction

The active management of populations to mitigate against anthropogenic change or increase opportunities for commercial or recreational exploitation occurs for many species (Walters et al. 2010; Simón et al. 2012; Tosi et al. 2015). Wild population management often incorporates captive breeding programmes, where reintroduction after extirpation (Seddon 1999; Hirzel et al. 2004) or supplementation of existing populations (Naish et al. 2007; Fraser 2008; Kozfkay et al. 2019) are the conservation goals. However, evidence suggests that the deliberate (stocking) or accidental escape of captive-bred conspecifics may depress the productivity of wild populations through ecological (Almodóvar et al. 2001; McGinnity et al. 2009), genetic (Lynch and O'Hely 2001; Araki et al. 2007a,b,c; Araki 2008; Araki and Schmid 2010; Ferchaud et al. 2018; Jonsson et al. 2019) or epigenetic mechanisms (Evans et al. 2014; Le Luyer et al. 2017; Rodriguez Barreto et al. 2019), as well as impacting other species (Bradbury et al. 2020) thus raising questions regarding the viability of wild populations that experience inputs of captive-bred individuals. Indeed, the lifetime fitness of released individuals relative to wild individuals is rarely directly measured.

The release of captively bred salmonine fish has been practised for over 150 years for the purposes of reintroduction, arresting population declines or providing increased opportunities for commercial harvest or recreational angling (Cross et al. 2007). 'Sea ranching' refers to situations where captive-bred fish are released as smolts (the life stage at which fish are physiologically ready to enter the marine environment) and then captured on their return migration as adults, either in a fishery or for use as broodstock for the next captive-bred generation. Sea ranching programmes aim to recover all the fish released into the wild as adults as part of either a commercial fishery or an experimental scientific programme. This is in contrast with 'stocking', where hatchery-produced fish may be released as eggs, juveniles or smolts, and intentionally allowed to spawn naturally in the wild once they have returned to the rivers as adults. However, some ranched fish may be released intentionally or may escape inadvertently, thus affording them the opportunity to spawn in the wild.

Salmonine fishes experience a severe survival bottleneck in the wild, with average egg-to-smolt survival rates in Burrishoole Atlantic salmon ranging from 0.3 to 1.1% (Salmon Research Trust/Agency of Ireland, including the Marine Institute, 1970 – 2018). By contrast, the hatchery environment with its absence of predators, food ad libitum and disease prevention can lead to very high cumulative survival of captive-bred fish. Therefore, stocking and ranching can provide more fish for angling, and/or increase commercial catches (McDermott et al. 1996). However, the intentional stocking or inadvertent release of captive-bred fish into the wild may threaten the long-term viability of recipient wild populations (Araki et al. 2009; McGinnity et al. 2009), thus creating a vicious circle, whereby artificial propagation increases the population's reliance on future interventions. In the past, captive-bred fish were assumed to be ecologically equivalent to wild-bred fish. However, mounting evidence (Supplementary Material, Table S1) demonstrates that hatchery fish have lower survival post-release, relative to wild-bred fish (Chilcote et al. 1986; Christie et al. 2009; Bordeleau et al. 2018; Milot et al. 2013) and are less likely to obtain and defend breeding sites or mates (Araki et al. 2007a,b; Leider et al. 1990; Morán et al. 1991; Fleming et al. 1997; Miller et al. 2004; Thériault et al. 2011). The longer a given individual spends in captivity, the more its phenotype diverges from that of wild-bred fish, and hence the worse its performance in the wild is expected to be, with a trade-off between higher cumulative survival and reduced wild performance post-release. Therefore, the numerical gains of stocking may be marginal or even negative, which argues against stocking even purely on demographic grounds (Cross et al. 2007; McGinnity et al. 2009; Perrier et al. 2013a; Young 2013; Waters et al. 2015; de Eyto et al. 2016). The inferior post-release survival and spawning behaviour of captively bred fish, coupled with negative demographic consequences, raises two questions—does the poor performance of individual captive-bred fish translate into reduced overall fitness for the captive-bred group relative to wild-bred fish? If so, do spawning captive-bred fish affect population productivity?

Any potential short-term demographic benefits of stocking or ranching must be weighed against longer term impacts owing to transgenerational carry-over effects (Araki et al. 2009; Christie et al. 2009; Evans et al. 2014; Bordeleau et al. 2018; Milot et al. 2013). Experiments with Atlantic salmon *Salmo salar* L. have shown that the parental hatchery environment can affect the survivorship of wild-bred offspring (Evans et al. 2014), which can occur via genetic responses to domestication selection in captivity, or via non-genetic effects of the captive environment, including maternal effects and epigenetic inheritance. Classic studies (Araki et al. 2007a,b; Araki 2008) on steelhead trout, *Oncorhynchus mykiss* Walbaum, have demonstrated that even a few generations of captive-rearing can reduce the performance of captive-bred individuals and their offspring in the wild via genetic changes that occurred in captivity, even when broodstock were obtained from the local wild population (McGinnity 1997; Baily et al. 2010). Therefore, interbreeding between captive- and wild-bred fish entails evolutionary risks for the wild population, as introgression of 'hatchery alleles' can negatively affect the fitness of hybrids in the wild, potentially depressing population size or productivity (Lynch and O'Hely 2001). Natural selection in the wild should select against wild-bred individuals with high levels of captive ancestry (Ford 2002), which in turn should purge hatchery alleles. However, this purging process would still incur a demographic cost to the wild population (Baskett and Waples 2013), while continued influx of hatchery fish would lead to further introgression and fitness depression. We use lifetime reproductive success (LRS) data from the Burrishoole catchment in Ireland to (i) compare lifetime fitness in nature of wild- and captive-bred Atlantic salmon that had the opportunity to spawn naturally and (ii) quantify the resulting impacts on population productivity of annual intrusions of captive-bred fish. We then compare the LRS of captive-bred fish against that of wild-bred fish to test the hypothesis that hatchery-induced genetic or environmental effects reduced the fitness of captive- bred fish relative to wild-bred fish when both spawned naturally in the wild. Finally, we use a density-corrected measure of overall lifetime productivity (adult recruits per adult spawner) to test the prediction that population productivity is lower in years where captive-bred fish comprise a greater fraction of the potential spawning population.

2.3 Methods

(a) Lifetime reproductive success data

An experimental ranching programme has operated in Burrishoole since the 1960s, where captive-bred fish are tagged and released as smolts. The ranching programme was established using primarily local broodstock, but also with the inclusion of non-local brood in the earlier years of the programme. In the Burrishoole system (see de Eyto et al. 2016), the majority (approx. 90%) of wild-bred fish migrate to sea at age 2+, a little over 2 years after hatching with a small fraction (approx. 10%) migrating as either age 1+ or age 3+ juveniles. Similarly, captive-bred individuals migrate at ages 1+ or 2+. Prior to release, captive-bred fish are microtagged and their adipose fin is clipped, so as to distinguish them from wild-bred fish upon their return as adults. Microtagging refers to the procedure of injecting a coded wire tag (a length of magnetized stainless steel wire 0.25 mm in diameter) into the nose of fish. The majority of captive- and wild-bred fish return from the ocean to breed after one full 'sea-winter' as so-called grilse, with the remainder returning as multi-sea-winter (MSW) fish (Metcalfe and Thorpe 1990). Upon their return, captive-bred fish are either caught in a rod fishery, retained as broodstock, released up the catchment due to hatchery constraints or for enhancement/angling, under the assumption that these fish are recaptured before spawning. Most fish of both provenances return from the ocean during May to September, but do not spawn until late winter (November–January), with peak spawning in mid-December. Fish that survive spawning return to the sea early in the following calendar year. Individual fish in our data that did not display the conventional 2+-grilse life cycle had their LRS appropriately indexed to the correct years across which they spawned (see lines 280–693 in Code text file available at

http://data.marine.ie/geonetwork/srv/eng/catalog.search#/metadata/ie.marine.data:dataset.4346).

A total trapping system on the catchment has allowed for censusing and tissue sampling of all anadromous Burrishoole salmon that were potential spawners. Trapped fish are measured for fork-length, with scale samples taken for molecular parentage assignment and sexing. Whether a fish is caught pre-spawning (i.e. in the upstream traps on their return from the ocean) or post-spawning (i.e. in the downstream traps on their migration back to the ocean) was also recorded. 94.21% of wild-bred fish were tissue sampled as kelts in the downstream traps, while 94.74% of captive-bred fish were sampled pre-spawning in the upstream traps. Captive- and wild-bred salmon in Burrishoole have similar propensities for male precociality (McGinnity et al. 2007) so we do not believe their absence from our data biases our estimates of relative reproductive success (RRS), as our estimates of absolute LRS for each provenance are expected to be equally biased by failing to account for mature male parr. This trapping regime has allowed for the collection of annual census data based on total counts, phenotypic and genetic sampling of the potential anadromous wild-spawning population (Supplementary material, Table S2) which, in combination with molecular parentage assignment, has facilitated the estimation of lifetime fitness for individual fish using a molecular pedigree. See Aykanat et al. (2014) and O'Sullivan et al. (2019a) for details of tissue sampling procedures, identity and parentage analysis, sex determination and pedigree reconstruction. Pedigree data available at O'Sullivan et al. (2019b).

The discrepancy in when each provenance was sampled (upstream versus downstream) could bias LRS estimates downward for wild-spawning, captive-bred fish, due to the higher cumulative in-river mortality risk inflating their expected number of zero LRS records relative to wild-bred parents. We explored this by comparing non-zero LRS records between the provenances. The mean LRS was still significantly lower for captive- bred relative to wild-bred fish, demonstrating that this source of bias was not driving the main results (in qualitative terms) from the analyses. See Supplementary Material, Text S1 for further details.

(b) Productivity data

We estimated annual productivity of the population as the average contribution of adult offspring to the next generation by fish that had an opportunity to breed in the wild (i.e. the combined number of wild- and captive-bred potential spawners). To quantify the total number of recruiting offspring produced by a spawning cohort we assumed, for simplicity, that all wild-bred fish smolted at age 2+ and then returned as adults after either one or two winters at sea. Therefore, the total recruits produced by spawning cohort t was estimated by summing the number of wild-bred grilse returning in year t+4 and the number of wild-bred MSW fish returning in year t+5. This was then divided by the number of spawners (wild-bred + captive-bred) in year t, providing us with a ratio of adult recruits per spawner, giving us an adult-to-adult productivity measure. We estimated productivity for all years where complete life cycle data were available (43 years; 1970–2012). Since female MSW salmon and female grilse differ in their fecundity (de Eyto et al. 2015), variation in the annual grilse:MSW ratio could affect productivity if estimated using ova deposition. To explore this, we calculated an alternative productivity measure that involved 'converting' adults into eggs, using an unpublished relationship between female length and fecundity (Marine Institute 1992–2012, unpublished data; Supplementary Material, Text S2).

(c) Relative reproductive success between provenances

Fitness, measured as LRS, was estimated by counting the number of adult fish returning in subsequent years that could be assigned genetically as offspring of a focal parent. Thus, LRS was an individual-level analogue of our population-level productivity (recruits per spawner) measure. RRS of each provenance was then estimated for each spawning cohort by dividing their arithmetic mean LRS by that of wild-bred fish. Thus, wild-bred fish have an RRS value of 1 in any given spawning cohort, and RRS values of less than 1 for captive-bred fish indicate lower fitness compared to wild-bred fish. Parentage assignment errors and incomplete sampling of parents and offspring were accounted for as per Araki and Blouin (2005), yielding an unbiased estimator of RRS for each cohort (Supplementary Material, Table S3). The method of Araki and Blouin (2005) involved: (i) subtracting the number of offspring successfully assigned back to a parent from the number of offspring sampled; (ii) dividing this difference by the total number of potential parents; (iii) multiplying by the pedigree-derived assignment error, divided by one minus the assignment error; and (iv) subtracting the result from the arithmetic mean LRS. This was done separately for each provenance, with the result being an unbiased estimate of the mean LRS for both wild- and captive-bred salmon. Dividing captive-bred mean LRS by wild-bred mean LRS yielded the unbiased RRS estimator. This allowed us to examine variation in the RRS of captive-bred fish across six cohorts (1977, 1978, 1980, 1981, 1985 and 1989). Separate one-tailed permutation tests were used to test for significant differences in the mean LRS between captive- and wild-bred salmon for each of the six cohorts. The permutation tests generated 1 000 000 estimates of the difference in arithmetic mean LRS between captive- and wild-bred fish. p-values for each test were calculated as the proportion of the permuted samples greater than the observed difference in the mean LRS between the provenances. One-tailed tests were chosen as we had an a priori expectation for lower LRS in captive-bred fish based on previous work (Araki et al. 2007a,b; Araki 2008). Permuting the difference between the mean LRS estimates is mathematically equivalent to testing if the RRS of captive-bred fish is different from one—one being the relative fitness of wild-bred fish. To assess evidence for the hypothesis that, across all cohorts, there was an overall pattern of captive-bred salmon displaying lower LRS than wild-bred salmon, we combined the p-values from each of the six permutation tests using Fisher's combined probability test (FCPT). FCPT relies on taking the natural logarithms of the permuted p-values. In cases where the permuted p-value was zero, we used the 'independence_test' function in the 'coin' R package to derive a non-zero p-value for use in the FCPT (Hothorn et al. 2008; R Core Team 2019). When the permuted and 'coin'-derived p-values were on opposite sides of the arbitrary 0.05 significance threshold, the more conservative p-value was chosen. This analytical pipeline was also used to assess evidence for the hypothesis that captive-bred fish displayed lower LRS than wild-bred fish when data were separated by sex. Again, the sex-specific comparisons were done for each cohort separately, as well as across all cohorts. For overall provenance and sex comparisons, the weighted geometric mean of relevant cohort-specific RRS estimates was calculated.

Lower LRS in captive-bred fish relative to wild-bred could be explained by reduced survival of their offspring in the wild due to transgenerational effects of the hatchery on offspring phenotypes (Evans et al. 2014) via genetic (Baily et al. 2010) or epigenetic inheritance (Rodriguez Barreto et al. 2019). However, captive-bred fish could simply have lower spawning success (Miller et al. 2004) or, in the case of females, higher rates of egg retention (de Eyto et al. 2015). If that were the case, one would expect that a higher fraction of captive-bred fish would have an LRS equal to zero due to never having spawned. We thus tested whether captive-bred fish in our pedigree had a higher proportion of zero LRS than wild-bred fish using the 'prop.test' function in R. Having found a significantly higher proportion of zero LRS in captive-bred fish (Supplementary Material, Text S3), we then restricted our dataset to records where LRS > 0 and performed a one-tailed permutation test as above. A significant difference between captive-bred and wild-bred fish would be consistent with transgenerational effects of the hatchery environment on the survival of offspring of captive-bred parents. The fecundity of captive-bred females is approximately 1.4 times that of wild-bred females in the Burrishoole system, as captive-bred fish have a higher number of smaller eggs per kilogram of maternal bodyweight in comparison with wild-bred fish (Marine Institute 1970–2012, unpublished data). Thus, in the case of females, lower LRS, having excluded the zeros, for captive-bred fish relative to wild would be despite the fact that they can deposit more eggs per capita. Finally, we estimated the reduction in the mean individual LRS across the six cohorts relative to a hypothetical pure wild-bred population, as the result of intrusions by captive-bred fish. This was estimated by multiplying the number of captive-bred fish in a given cohort by their estimated RRS that year, doing the same for wild-bred fish, and then summing these products across cohorts and dividing by the grand total of captive-bred and wild-bred fish. This result was then subtracted from one and multiplied by 100 to give the percentage reduction in the mean individual LRS in the mixed population in the parental generation relative to a hypothetical pure population.

(d) Effect of intrusions of captive-bred fish on population productivity

As a measure of hatchery intrusion, we used the proportion of the total number of returning wild- and captive-bred adults that had an opportunity to spawn in the wild, that were captive-bred. This figure ranged from 0.01 to 0.61. Population productivity was calculated as recruits per spawner, as explained above, with spawners indexed to year t, as per the hatchery influence measure. Regressing population productivity on proportion captive-bred fish would be problematic as it ignores potential density dependence, which can be strong in Atlantic salmon (Jonsson et al. 1998; Einum and Nislow 2011). We approximated annual population density by the total annual return of fish, assuming the area of spawning and rearing habitat within the catchment was relatively fixed across years. While this density measure was only poorly correlated with the annual proportion of captive-bred fish (Pearson's correlation: $r = 0.057$, $t = 0.37$, $d.f. = 41$, $p = 0.72$), failing to account for density dependence could still obscure the relationship between hatchery intrusion and population productivity. In fisheries science, nonlinear productivity relationships are typically assumed (e.g. Beverton–Holt or Ricker functions [Hilborn and Walters 2013]). Rather than choosing an arbitrary stock–recruit function, we instead fit a generalized additive model (GAM) assuming Gaussian errors using the 'mgcv' (Wood 2010) R package, where the natural logarithm of population productivity was regressed onto total annual numbers of fish that had the opportunity to spawn in the wild, with the latter set as a smoothing term with nine knots (Supplementary Material, Figure S1). The residuals from this model are equivalent to a density-corrected productivity measure, as they represent a density-independent stock–recruitment relationship. Using a linear model, we then regressed these residuals against the proportion of captive-bred fish in a spawning cohort, with the prediction that population productivity would be lower in years of stronger hatchery intrusion. This analysis was repeated using our alternative 'ova-per-ovum' productivity measure and proportion ova contributed by captive-bred fish as the explanatory variable to check that the results were robust to converting adults into eggs (Supplementary Material, Text S2). Visual inspection of diagnostic plots showed that all model assumptions were met (Supplementary Material, Figures S2 and S3). All analyses were conducted in R version 3.6.1.

2.4 Results

One-tailed permutation tests revealed significantly reduced LRS for captive-bred compared to wild-bred fish in all but one of the six spawning cohorts (Figure 1a and Table 1). FCPT revealed an overall effect of reduced RRS in captive-bred fish across the six cohorts (FCPT: $X^2 = 117.94$, *d.f.* = 12, $p < 0.001$; Figure 1a and Table 1). For female-specific comparisons, captive-bred females displayed lower LRS than wild-bred females in all six cohorts, with the reduction being significant in four cohorts (Supplementary Material, Figure S4). RRS of captive-bred females ranged from 0.13 to 0.38, with an average RRS of 0.30 ($X^2 = 107.67$, *d.f.* = 12, $p < 0.001$; Table 1). Captive-bred males displayed lower LRS than wild-bred males in three of the six cohorts, with the reduction being significant in two cohorts (Supplementary Material, Figure S4). RRS of captive-bred males ranged from 0 to 20.92, with an average RRS of 0.67 (FCPT: $X^2 = 37.10$, *d.f.* = 12, $p < 0.001$; Table 1). Having excluded LRS records equal to zero, captive-bred fish again displayed significantly lower fitness relative to wild-bred fish (one-tailed permutation test: RRS = 0.81, $p < 0.001$). The average reduction in the mean LRS in the mixed population calculated across the six cohorts, compared with a theoretical population of purely wild-bred fish, was 22.2%. We report the variance in LRS for both provenances across all cohorts in the Supplementary Material, Table S4.

The population-level analysis revealed a significant negative relationship between our density-independent population productivity measure and the proportion of captive-bred fish in a spawning cohort (adjusted $R^2 = 0.09$, $F_{1,41} = 5.15$, p-value = 0.0285; Figure 1b). Population productivity at the mean value of the proportion captive-bred fish across the 43-year period (0.15) was reduced, on average, by 9.52% (back-transformed from the log scale), relative to a hypothetical pure population (proportion captive-bred fish = 0). For the six cohorts where we had LRS data, the mean captive-bred proportion was 0.19 and the reduction in population productivity was 12.4%. Similar results were found using our alternative ‘ova-per-ovum’ productivity measure.

Table 1. Cohort- and sex-specific, and overall estimates of unbiased RRS for Atlantic salmon. For cohort- and sex-specific estimates, *p*-values were determined by one-tailed permutation tests. For overall comparisons, RRS was estimated using the weighted geometric mean of cohort- or sex-specific estimates of RRS, and a *p*-value determined using FCPT, assuming a X^2-distibution with 12 degrees of freedom. Significant *p*-values in bold.

	Overall		Female		Male	
Cohort	RRS	*p*-value	RRS	*p*-value	RRS	*p*-value
1977	1.54	0.76	0.21	0.14	20.92	0.99
1978	0.27	<**0.001**	0.15	<**0.001**	1.68	0.48
1980	0.10	<**0.001**	0.20	0.08	0.00	0.07
1981	0.15	<**0.001**	0.13	<**0.001**	0.17	<**0.001**
1985	0.41	<**0.001**	0.38	<**0.001**	0.42	<**0.001**
1989	0.61	**0.001**	0.17	<**0.001**	1.28	0.72
Overall	0.36	<**0.001**	0.30	<**0.001**	0.67	<**0.001**

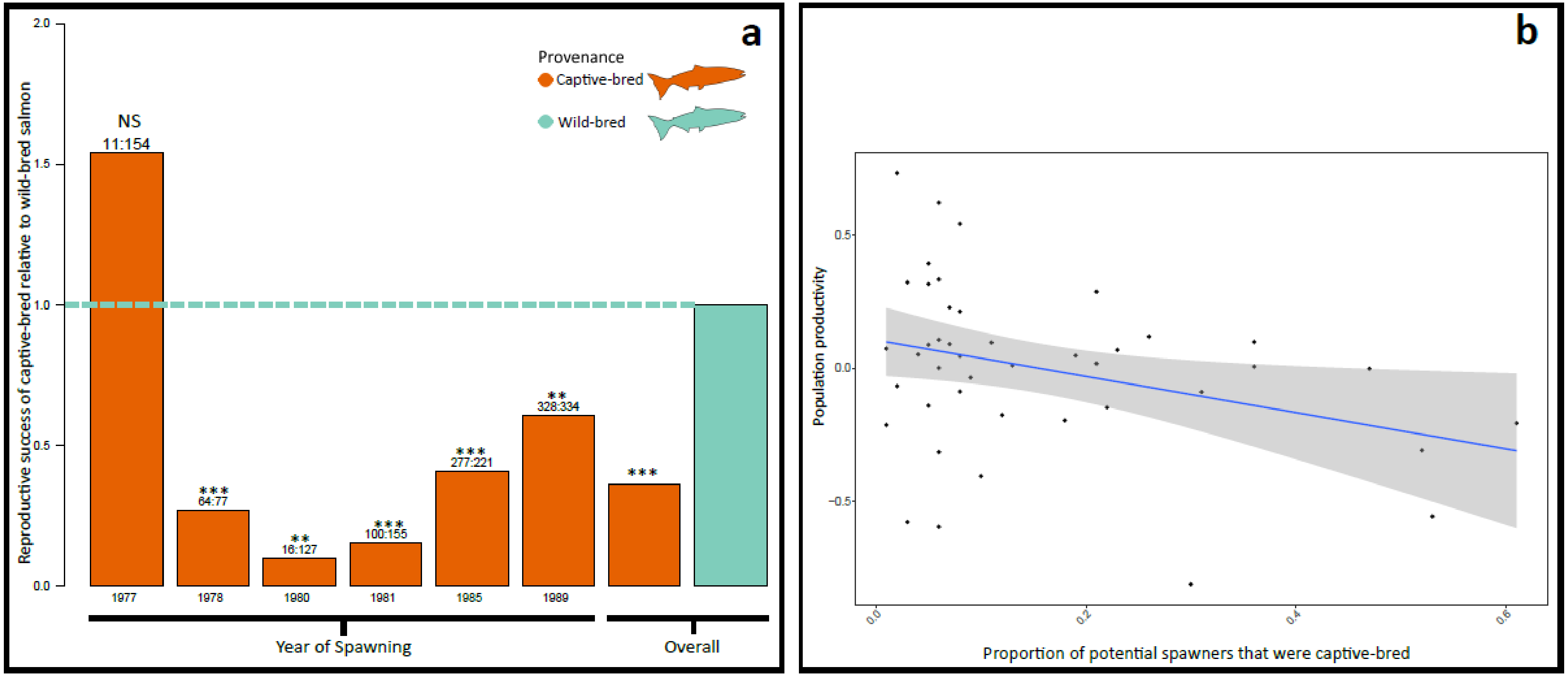

Figure 1: (a) Overall and cohort-specific comparisons of RRS for captive- and wild-bred Atlantic salmon in the Burrishoole catchment, Ireland. Overall RRS comparison estimated as the weighted geometric mean of the six cohort point estimates. Significance of the overall comparison determined using FCPT, where $X^2 = 117.94$ with 12 degrees of freedom. Significance of cohort-specific comparisons was determined using one-tailed permutation tests. Horizontal line for emphasis of increase/decrease in reproductive success of captive-bred fish relative to wild-bred fish. Numbers on top of bars represent the number of captive-bred (left number) salmon and wild-bred (right number) salmon used in cohort-specific comparisons. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. (b) Productivity of the mixed population as a function of the annual proportion of potentially spawning fish that were captive-bred. The solid line represents the line-of-best fit from a linear model, and shading represents the 95% confidence interval.

2.5 Discussion

Numerous studies have consistently revealed the reduced ability of captive-bred salmonines to survive and breed successfully in the wild (Fraser 2008) (Supplementary Material, Table S1), but few studies have been able to estimate the lifetime contribution of captive-bred fish to subsequent generations relative to wild-bred fish. This information is vital as it quantifies the net fitness impacts of captive-rearing at the individual level, which in turn can inform population-level analyses and eco-evolutionary modelling studies. We demonstrate that captive-bred Atlantic salmon, predominantly of local origin, that had the opportunity to spawn in the wild exhibited lower LRS than wild-bred conspecifics, that this fitness reduction was apparent for both females and males and that the inferior performance of captive-bred fish depressed overall population productivity. These findings mirror those of the steelhead trout studies (Araki et al. 2007a,b; Araki 2008). The steelhead studies were seminal as they provided some of the first multi-generational, pedigree-derived, unbiased RRS estimates between wild-spawning captive- and wild-bred fish. To the best of our knowledge, this has not been shown before for any population of Atlantic salmon. As such, our results have implications for ranching and stocking programmes across the native range of Atlantic salmon, where these practices are often used for either angling gains, mitigation for dam-impounded rivers, or as a conservation strategy.

The significantly lower LRS of captive-bred compared to wild-bred salmon remained after we excluded LRS records equal to zero, consistent with transgenerational effects of the hatchery environment on the survival of offspring produced by captive-bred parents. To further explore this, we used our pedigree to estimate the LRS of wild-bred offspring as a function of whether they had zero, one or two captive-bred parents (Supplementary Material, Figure S5). That is, we compared the mean number of grandchildren produced by captive-bred × captive-bred matings, captive-bred × wild-bred matings and wild-bred × wild-bred matings across the six cohorts. Statistical power was limited but we did find a non-significant trend where wild-bred fish with either one or two captive-bred parents had decreased LRS relative to fish with two wild-bred parents (Supplementary Material, Figure S5). This pattern is consistent with findings in both steelhead (Araki et al. 2009) and Atlantic salmon (Evans et al. 2014) that demonstrated transgenerational carry-over effects from the hatchery environment. However, neither Evans et al. (2014) nor our study were able to disentangle if such transgenerational effects reflect genetic or non-genetic inheritance. Studies on steelhead (Araki et al. 2007a,b; Araki 2008; Araki et al. 2009) and brook trout (Fraser et al. 2019), *Salvelinus fontinalis*, Mitchill 1814, show that one or two generations of captive-rearing are sufficient to induce maladaptation in captive-bred fish, or their descendants. This may reflect inadvertent domestication selection, relaxed natural and sexual selection, or epigenetic inheritance. While studies of salmonines are beginning to reveal epigenetic effects of hatchery rearing (Le Luyer et al. 2017; Rodriguez Barreto et al. 2019), further study is required before generalizations can be made regarding the relative importance of genetically versus epigenetically mediated maladaptation.

In our study, we could only assign parents to offspring that themselves survived to recruit as adults and in the majority of cases (78.68%), only a single parent could be assigned, owing to incomplete sampling of candidate parents. For the minority of cases in which two parents could be assigned, 28.68% involved captive-bred × captive-bred matings, 20.59% involved captive-bred × wild-bred matings and 50.74% involved wild-bred × wild-bred matings. The mean LRS of captive-bred × captive-bred pairs (n = 39) was 0.26, for captive-bred × wild-bred pairs (n = 28) was 0.64, and for wild-bred × wild-bred pairs was 0.57. These numbers were too low to undertake meaningful statistical analysis, but the pattern is consistent with transgenerational effects of the hatchery environment on offspring survival, with possible non-additive effects of parental provenance.

Previous studies of Burrishoole salmon (McGinnity et al. 2009; de Eyto et al. 2016) demonstrated that increased captive-born intrusion depressed the freshwater productivity of the overall population. A similar result is known for Scottish salmon (Bacon et al. 2016). Our study goes further, using recruits per spawner as a measure of productivity. Crucially, this productivity measure incorporates the marine life stage (lacking in McGinnity et al. [2009] and de Eyto et al. [2016]), which accounts for potential provenance-specific variation in marine survival. This facilitated meaningful comparison of fitness across the entire life cycle. Given the higher fecundity of captive- relative to wild-bred fish (Marine Institute 1970–2012, unpublished data), it might be expected that larger proportional intrusion from captive-bred fish would increase the productivity of the mixed population. However, as this study (as well as McGinnity et al. [2009] and de Eyto et al. [2016]) demonstrated, the opposite response was observed. This was corroborated by our pedigree- derived, individual-level, LRS data: we estimated a reduction in mean LRS of 22.2% across the six cohorts for the mixed population relative to a hypothetical pure wild-bred population. One potential explanation is that in years with more captive-bred fish—which are more fecund than wild-bred fish—there are more initial fry in total and hence there is stronger competition among offspring for feeding territories and, hence, lower juvenile survival for both provenances. However, our population-level analysis of productivity accounted for density dependence (Grossman and Simon 2020) and still found an effect of captive-bred intrusion, which implies that either a higher fraction of captive-bred fish fail to spawn successfully, or their offspring survive less well relative to the offspring of wild-bred parents (Jonsson et al. 1998). Tentative evidence for the latter explanation was provided by our additional analysis where LRS records of zero were excluded, and the analysis of grand-offspring numbers presented in Supplementary Material, Figure S5. Another potential route for the intrusion of captive-bred genes into the wild population is via a higher tolerance by captive-bred females to matings with subdominant males (Thompson et al. 1998).

Even if offspring of captive-bred fish are initially competitively superior to offspring of wild-bred fish (as has been found for wild-bred offspring of farmed salmon, McGinnity et al. [2003]), this advantage is more than outweighed by processes that reduce their overall survival. For example, captive-bred females produce smaller eggs than wild-bred females, potentially due to relaxed selection (Thompson et al. 1998) that may be associated with a correlated increase in egg number. In the wild, fry emerging from smaller eggs are likely to suffer higher early mortality (Heath et al. 2003; Einum et al. 2004), and hence this could contribute to the overall lower LRS of captive-bred fish. McGinnity et al. (2009)

further speculated that various bio-energetic and phenological mechanisms (e.g. winter energy use and timing of fry swim-up) could lead to the offspring of captive-bred fish having lower freshwater survival than offspring of wild-bred fish. Additionally, the offspring of captive-bred fish may perform less well during the smolt/oceanic life stage, again, reducing population productivity. As stated earlier, a potential source of bias in our data stems from the fact that captive-bred fish were predominantly sampled as upstream migrants, whereas wild-bred were predominantly sampled as downstream migrants. While this may have impacted our findings quantitatively, we believe our overall results to be robust in qualitative terms to this potential source of bias (Supplementary Material, Text S1).

In conclusion, our results bolster the consensus that captive-bred animals often have lower fitness in wild environments than wild-bred conspecifics and their interbreeding can depress the productivity of the recipient populations. This raises questions regarding whether supplementation represents a viable mitigation strategy. McGinnity et al. (2009) found that, under projected future climate regimes, high levels of hatchery influence have the potential to depress productivity to an extent that threatens population persistence. Moreover, reductions in population productivity may be accompanied by concomitant reductions in effective population size and the loss of adaptive traits (Le Cam et al. 2015) which negatively impacts long-term evolutionary potential. Considering this, and given the scale with which Atlantic salmon are subjected to stocking and ranching across their range, there is the potential for wide-scale population declines if stocking and ranching continue without due consideration to what causes captive-bred fish or their descendants to perform poorly relative to wild-bred fish.

2.6 Supplementary Material

Table S1: Studies of salmonine fishes that have examined differences in fitness or components of fitness between wild- and captive-bred conspecifics. ‘Local’ and ‘non-local’ stock refers to whether the captive-bred fish used in a study were derived from brood collected locally or from brood collected from a different system i.e. a neighbouring catchment. ‘Y’ = Yes, ‘N’ = No, ‘NA’ = Not applicable. Details from this study highlighted in bold.

Publication	Species	Local stock	Non-local stock	Parentage assignment	Cohort number	Molecular markers	Fitness measure(s)	Fitness difference
Fleming et al. 1997	*Salmo salar*	Y	N	N (tagging)	NA	NA	Male attendance at redds, female redd construction	Y
McGinnity et al. 2003	*Salmo salar*	Y	N	Y	1	6 microsatellites	Viability of young	Y
Milot et al. 2013	*Salmo salar*	Y	N	Y	1	8 microsatellites	Fry assigned back to parent	Y
Bordeleau et al. 2018	*Salmo salar*	Y	N	N (tagging)	NA	NA	Survival to repeat spawning	Y
Jonsson et al. 2019	*Salmo salar*	Y	N	N (tagging)	NA	NA	Smolts per increasing proportion of wild females	Y
O'Sullivan et al. 2020	***Salmo salar***	**Y**	**Y**	**Y**	**6**	**30 microsatellites**	**Lifetime reproductive success**	**Y**
Morán et al. 1991	*Salmo trutta*	Y	Y	N (Detection of a specific allele)	NA	allozymes	Lack of introgression of *LDH-5*90* allele into wild population	Inferred
Hansen 2002	*Salmo trutta*	Y	Y	N (population assignment)	NA	9 microsatellites	Estimated admixture proportion	Y
Dannewitz et al. 2004	*Salmo trutta*	Y	N	Y	1	11 microsatellites	Fry and parr assigned to parent	N
Reisenbichler and McIntyre 1977	*Oncorhynchus mykiss*	Y	NA	N (marking/experimental design)	NA	allozymes	Survival, growth rate	Y
Chilcote et al. 1986	*Oncorhynchus mykiss*	Y	Y	N (Detection of a specific allele)	NA	allozymes	Proportional offspring survival	Y
Leider et al. 1990	*Oncorhynchus mykiss*	Y	Y	N (Detection of a specific allele)	NA	allozymes	Proportional offspring survival	Y
McLean et al. 2004	*Oncorhynchus mykiss*	Y	Y	N (population assignment)	NA	8 microsatellites	Smolts per female	Y
Miller et al. 2004	*Oncorhynchus mykiss*	N	N	Y	1	4-6 microsatellites	Offspring survival	Y
Araki et al. 2007a, b, c	*Oncorhynchus mykiss*	Y	Y	Y	3, 2	6 microsatellites	Lifetime reproductive success	Y
Araki et al. 2009	*Oncorhynchus mykiss*	Y	N	Y	2	6 microsatellites	Lifetime reproductive success	Y
Ford et al. 2006	*Oncorhynchus kisutch*	Mixed	Mixed	Y	1	6-7 microsatellites	Lifetime reproductive success	N
Thériault et al. 2011	*Oncorhynchus kisutch*	Y	N	Y	2	10 microsatellites	Lifetime reproductive success	Y
Berejikian et al. 2009	*Oncorhynchus keta*	Y	N	Y	1	8 microsatellites	Adult-to-fry survival	N
Hess et al. 2012	*Oncorhynchus tshawytscha*	Y	N	Y	13	15 microsatellites	Lifetime reproductive success	N
Williamson et al. 2010	*Oncorhynchus tshawytscha*	Y	N	Y	1	11 microsatellites	Estimated fitness based on fractional assignment	Y

Table S2: Provenance- and sex-specific, and overall numbers of wild-bred and captive-bred, Atlantic salmon used for the RRS comparisons. For sex, $F_{\text{Wild-bred}}$ = 'Female wild-bred', $M_{\text{Captive-bred}}$ = 'Male captive-bred', etc.

	Provenance		Sex			
Cohort	Wild-bred	Captive-bred	$F_{\text{Wild-bred}}$	$F_{\text{Captive-bred}}$	$M_{\text{Wild-bred}}$	$M_{\text{Captive-bred}}$
1977	154	11	133	8	21	3
1978	77	64	69	39	8	25
1980	127	16	120	9	7	7
1981	155	100	133	63	22	37
1985	221	277	160	153	61	124
1989	334	328	195	209	139	119
Overall	1068	796	810	481	258	315

Table S3: Overall and sex-specific estimates of captive- and wild-bred Atlantic salmon mean absolute fitness used to estimate relative reproductive success, RRS, for each cohort. Numbers presented of offspring sampled, offspring assigned, parents sampled, and False Discovery Rate, FDR, were those used to correct RRS estimates as per Araki et al. (2007).

Overall

Cohort	Captive-bred fitness	Wild-bred fitness	Offspring sampled	Offspring assigned	Parents sampled	FDR
1977	0.727	0.481	192	82	267	0.055
1978	0.344	1.180	213	113	172	0.055
1980	0.063	0.504	140	65	307	0.055
1981	0.170	0.974	296	168	293	0.055
1985	0.408	0.995	364	333	594	0.055
1989	0.223	0.365	242	195	696	0.055

Female

Cohort	Captive-bred fitness	Wild-bred fitness	Offspring sampled	Offspring assigned	Parents sampled	FDR
1977	0.125	0.534	192	72	267	0.036
1978	0.205	1.280	213	96	172	0.017
1980	0.111	0.517	140	63	307	0.030
1981	0.143	0.962	296	137	293	0.036
1985	0.399	1.031	364	226	594	0.058
1989	0.177	0.451	242	125	696	0.067

Table S3 (cont.)

Male

Cohort	Captive-bred fitness	Wild-bred fitness	Offspring sampled	Offspring assigned	Parents sampled	FDR
1977	2.333	0.143	192	10	267	0.046
1978	0.560	0.375	213	17	172	0.082
1980	0.000	0.286	140	2	307	0.297
1981	0.216	1.045	296	31	293	0.053
1985	0.419	0.902	364	107	594	0.140
1989	0.303	0.245	242	70	696	0.132

Table S4: Overall and cohort-specific variation in lifetime reproductive success (LRS) for wild-bred and captive-bred Atlantic salmon.

Year of Spawning	Wild-bred	Captive-bred
1977	1.0356	2.0182
1978	2.9402	0.8958
1980	0.6964	0.0625
1981	1.6097	0.1829
1985	1.9500	0.6627
1989	0.8211	0.3387
Overall	1.4226	0.5022

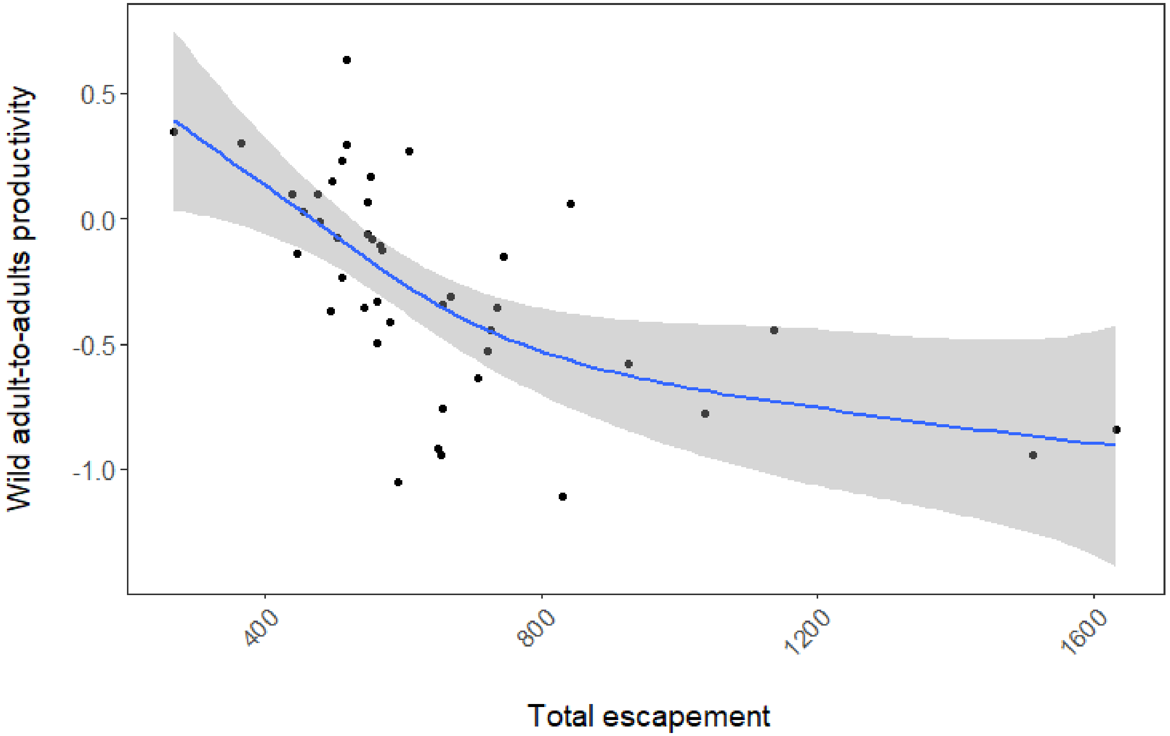

Figure S1: Stock-recruitment relationship between the total escapement (potential number of spawners) of wild- and captive-bred Atlantic salmon for a cohort and the natural logarithm of the productivity of that cohort, measured as recruits per spawner, giving an adult-to-adults productivity measure. The solid line represents the line-of-best fit from a GAM model, and shading represents the 95% confidence interval. Adjusted $R^2 = 0.41$, Deviance explained = 44.4%, $F_{2.3} = 10.6$, $p < 0.001$; note for F, reported degrees of freedom are estimated.

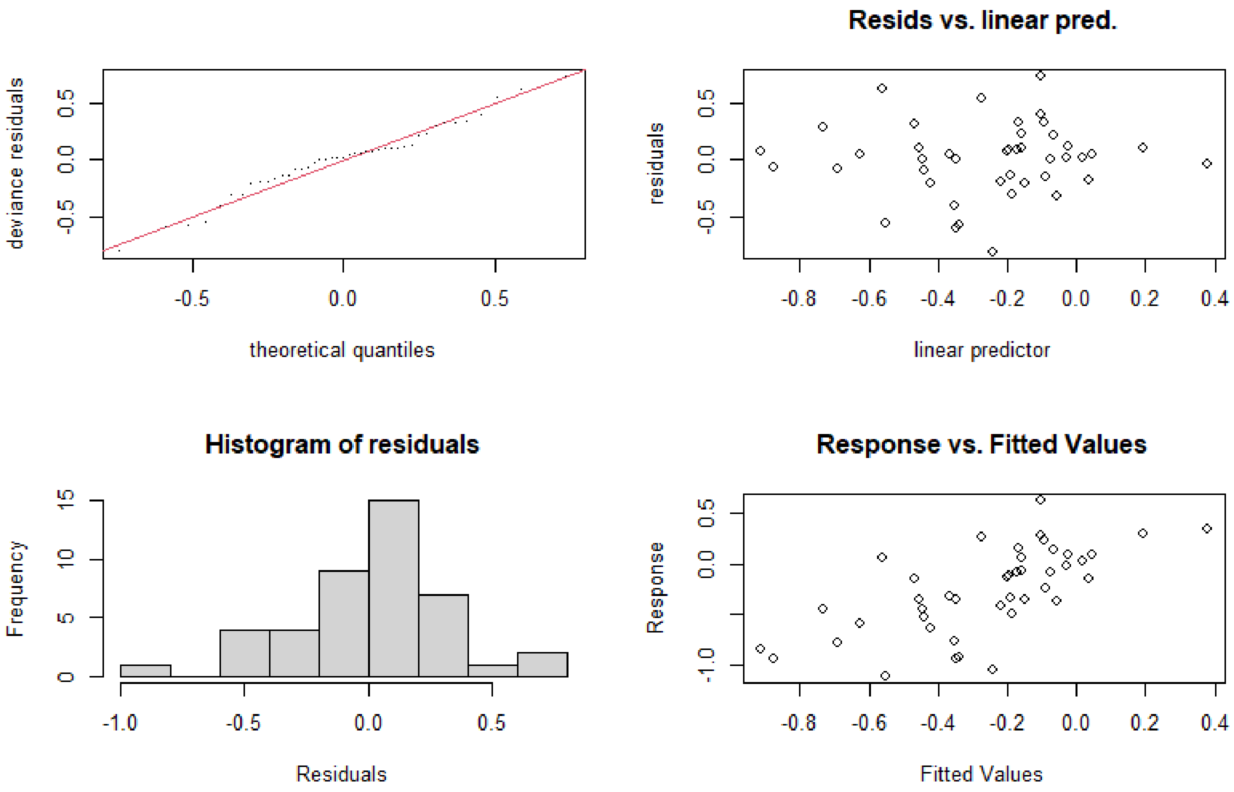

Figure S2: Diagnostic plots for stock-recruitment model.

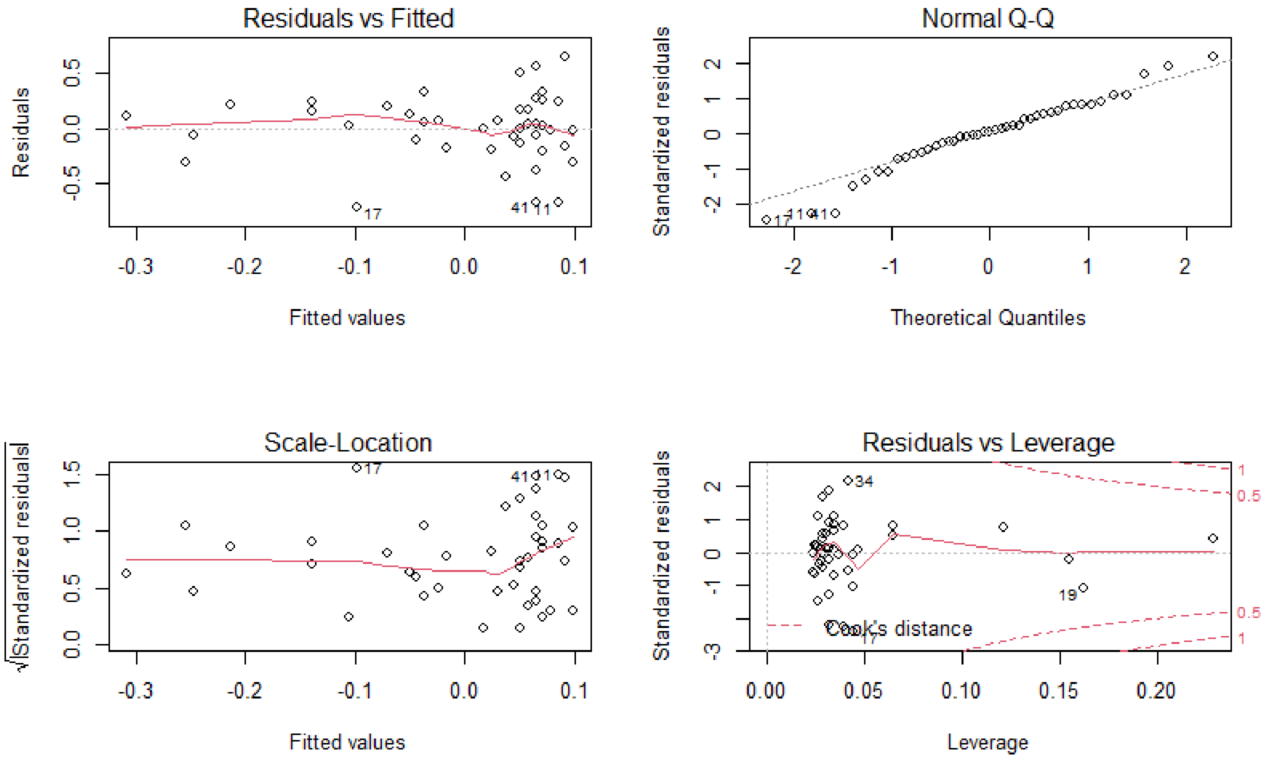

Figure S3: Diagnostic plots for linear model examining how larger proportions of captive-bred Atlantic salmon in the total number of fish that can potentially spawn reduces the productivity of the wild population.

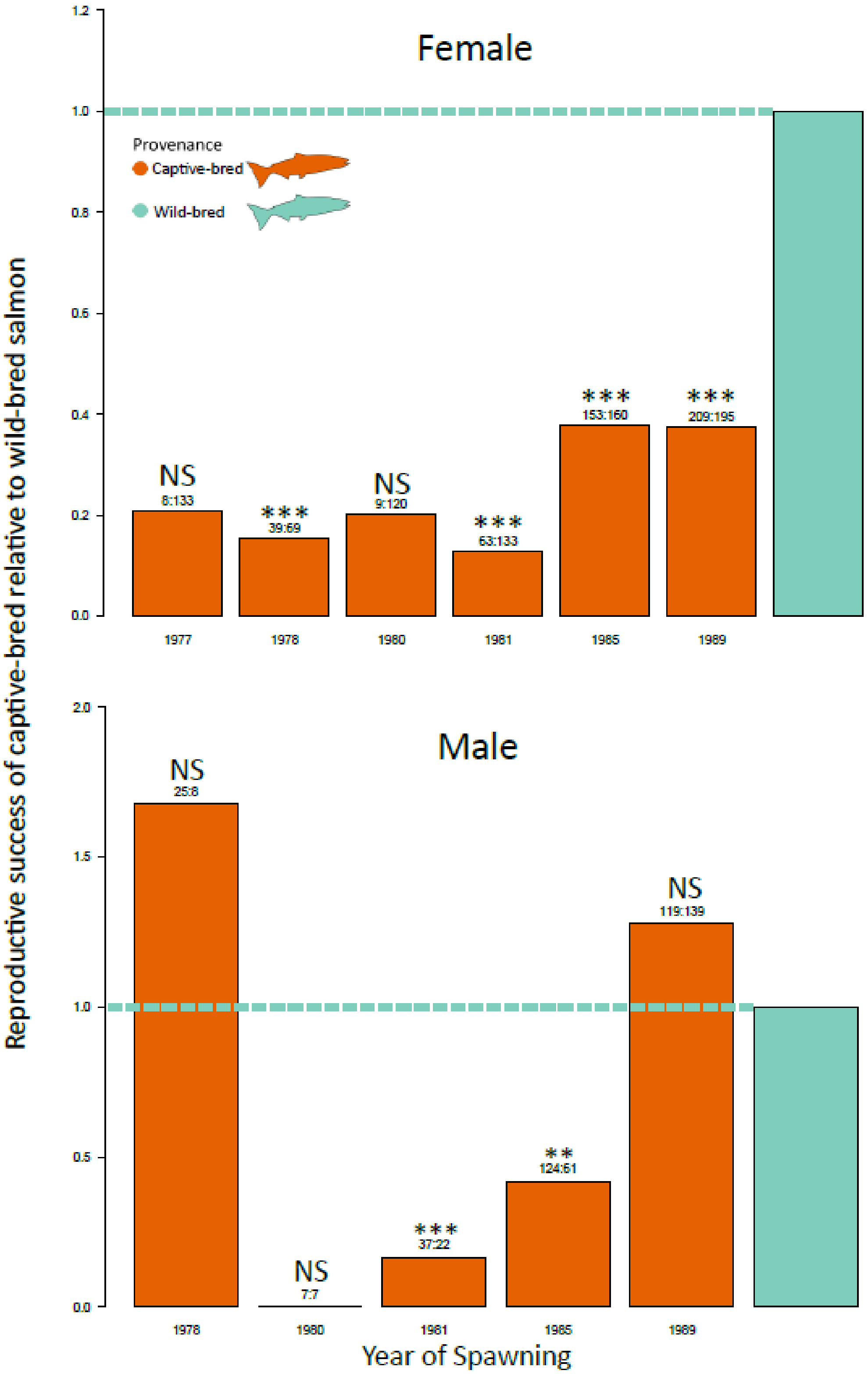

Figure S4: Cohort- and sex-specific comparisons of relative reproductive success, RRS, for captive-bred and wild-bred Atlantic salmon in the Burrishoole catchment, Ireland. Significance of cohort-specific comparisons determined using one-tailed permutation tests. Horizontal line for emphasis of increase/decrease in reproductive success of captive-born fish relative to wild-born fish. Numbers on top of bars represent the number of captive-bred (left number) salmon and wild-bred (right number) salmon used in cohort-specific comparisons. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$. Note, to improve the figure's readability, the male 1977 cohort is not displayed due to a very large (20.92) RRS estimate with large uncertainty bounds owing to a very low sample size for captive-bred males.

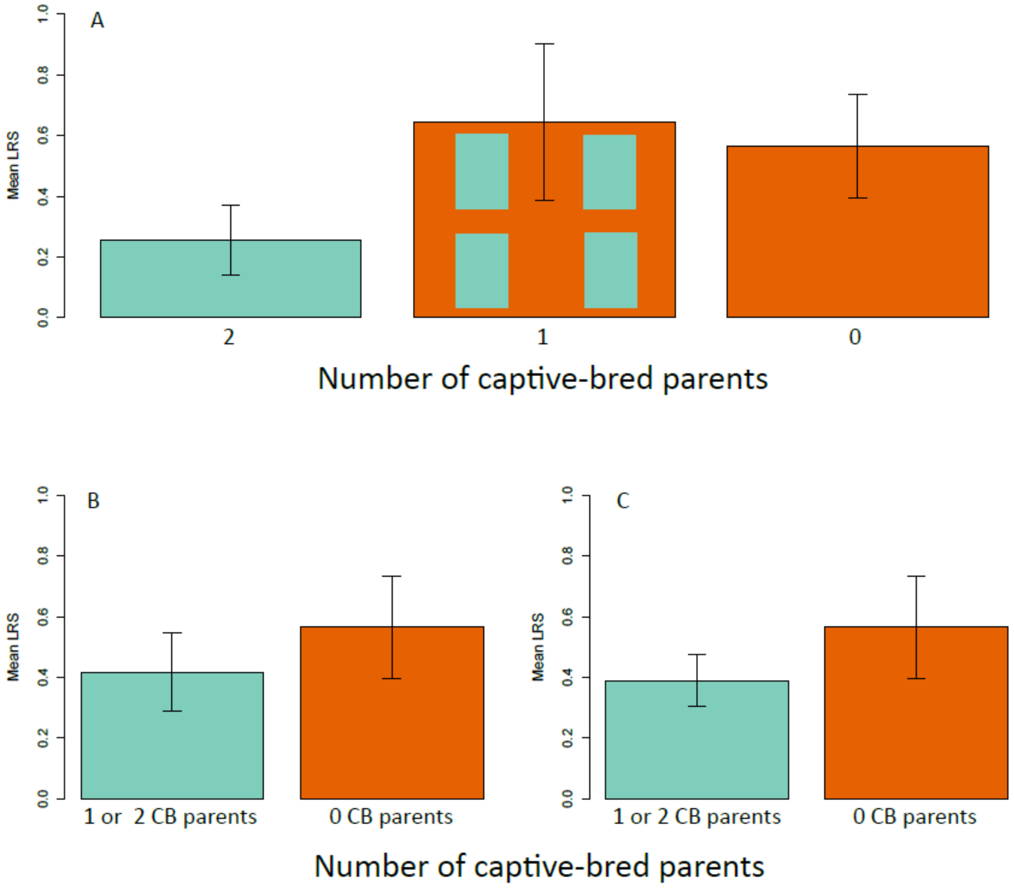

Figure S5: (A) Transgenerational effects of captive ancestry on the fitness of wild-bred Atlantic salmon in the Burrishoole catchment, Mayo, Ireland. Barplots represent the mean absolute fitness (measured as lifetime reproductive success, LRS) of wild-bred salmon for which both parents were known, separated into three categories: two captive-bred parents, one captive-bred parent (the other being wild-bred), no captive-bred parents (i.e. two wild-bred parents). One-tailed permutation tests revealed no significant difference in fitness between any of the categories (p-values; 1 captive-bred parent vs 0 captive-bred parents: 0.59, 2 captive-bred parents vs 0 captive-bred parents : 0.08, 2 captive-bred parents vs 1 captive-bred parent: 0.06). (B) Difference in mean LRS between wild-bred salmon with zero captive-bred parents versus those with one or two captive-bred parents. One-tailed permutation test revealed no significant difference in mean LRS between the two categories ($p = 0.17$). (C) Same as B but adding into the green category wild-bred salmon with one captive-bred parent and the other parent unknown. One-tailed permutation test revealed no significant difference in mean LRS between the two categories ($p = 0.14$). Error is represented by ±1 standard error.

Text S1: Bias caused by different sampling times for captive- and wild-bred fish

In the Burrishoole catchment, most captive-bred fish were sampled as upstream migrants (USM) on their return migration to spawn (94.74% USM, 5.26% DSM). Captive-bred fish were identified by an adipose fin clip that had been removed upon their release from the hatchery as ranched smolts. Similarly, most wild-bred fish were sampled as downstream migrants (DSM) post-spawning (94.21% DSM, 5.79% USM). If a captive-bred fish attempted to spawn, any resulting offspring would have to survive until they themselves were kelts for them to be sampled and, thus, assigned back to captive-bred parents (since the offspring would be wild-bred). That is, the offspring of wild-bred fish were sampled at the same life stage as their parents (both DSM), whereas the offspring of captive-bred parents were sampled at a later life stage than their parents (USM for parents, DSM for offspring). Therefore, any mortality that may have occurred in captive-bred adults (potential parents) between entry into fresh water (upstream migration) and subsequent re-entry into salt water as a kelt (downstream migration post-spawning) has the potential to bias downward the lifetime reproductive success, LRS, of captive-bred fish. To explore the extent of this bias, we performed a one-tailed permutation test comparing the non-zero reproductive success of captive- and wild-bred fish, that is, we removed records of fish that had zero LRS as these were potentially biasing downward the overall captive-bred LRS estimate. While many of these zeros are likely true zeros (that is, many captive-bred fish had zero LRS because they failed to spawn or none of their offspring survived to adulthood), we believed it pertinent to check whether removing such records changed the results in qualitative terms, which it did not. Therefore, this shows that captive-bred fish have lower fitness even after removing cases where $\text{LRS} = 0$, which removes this bias related to captive-bred fish and wild-bred fish being sampled at different times, and also discounts the fact that a higher fraction of captive-bred fish may have simply failed to spawn (and hence left no offspring). This gives us confidence that our overall result – that captive-bred fish have lower fitness in the wild than wild-bred fish – is not entirely driven by a potential bias due to differential sampling times. However, removing the LRS = 0 cases also makes for a more conservative test of fitness differences, given that many of these were likely true zeros. We do, however, acknowledge that the RRS estimate based on including the zeros may be an overestimate. We arrived at the same qualitative result whether using individual-level (pedigree-derived LRS) data or population-level (productivity) data: namely, that the expected mean fitness of the mixed population is lower than that of a hypothetically "pure" population. The population-level data indicated a percentage reduction here of ~22%, while the individual-level data indicated a reduction of ~10%, with the discrepancy likely related to differences in time-series length (43 cohorts for the population-level analysis; 6 cohorts for the individual-level analysis), incomplete sampling for the individual-level analysis, and the fact that the population-level analysis involved correcting for density dependence.

Text S2: Ova-per-ovum productivity

We 'converted' adults into eggs by summing the estimated ova deposition by wild-bred grilse recruits in year $t+4$ and wild-bred MSW recruits in year $t+5$, and dividing by the estimated ova deposition of wild-bred and captive-bred spawners in year t. This 'ova-per-ovum' measure of productivity was strongly correlated (Pearson's correlation: $t = 18.77$, $df = 41$, $r = 0.95$, $p < 0.001$) with our recruits per spawner productivity measure. The productivity of a given Atlantic salmon cohort can be estimated as the number of adult recruits divided by the number of potential breeders in year t that produced those recruits. Since wild-bred Atlantic salmon in our system typically exhibit either a '2+,grilse' or '2+,1MSW' lifecycle, we assume this population structure for all analyses. However, this difference in sea age means that not all offspring originating from a given spawning cohort will themselves recruit into the same future spawning cohort. Therefore, the total wild-bred productivity for a given spawning cohort could be estimated as

(Eqn.1) $$P_{Wild\text{-}bred\,t} = (\Sigma Ngrilse_{t+4} + \Sigma Nmsw_{t+5}) / Nspawners_t$$

where $P_{Wild\text{-}bred\,t}$ is the productivity of a wild-bred cohort at t, $Ngrilse_{t+4}$ is the number of salmon recruiting at $t+4$, $Nmsw_{t+5}$ is the number of salmon recruiting at $t+5$, and $Nspawners_t$ is the total number of salmon (both captive-bred and wild-bred) spawning at t. However, MSW salmon and grilse do not contribute equally to productivity due to female MSW salmon having greater fecundity than female grilse (de Eyto et al. 2015). Therefore, using the fecundity of grilse and MSW salmon at $t+4$ and $t+5$, respectively should provide a more accurate estimate as it effectively examines the number of zygotes produced by a given cohort.

Atlantic salmon fecundity can be estimated from either length or weight data, using the well-documented relationship between fish size and fecundity (de Eyto et al. 2015). In Burrishoole, lengths of grilse (either as upstream migrating spawners or downstream migrating kelts) are documented every year, with fecundity estimated using the nonlinear function

(Eqn.2) $$F_i = e^{(5.79+0.035\,length_i)}$$

where F and *length* are the estimated fecundity and measured length in centimetres for the *ith* female, respectively (Marine Institute, unpublished data). A sex ratio of 55% female : 45% male is used. The fecundity of MSW fish was calculated using a standard value of 4274 ova per female, with a sex ratio of 70% female : 30% male. The fecundity of captive-bred fish was calculated using an average number of ova per female, based on actual ova counts in the broodstock, and a sex ratio of 55% female : 45% male.

Equation 1 can now be alternatively parameterized as

(Eqn.3) $$P_{Wild\text{-}bred\,t} = (\Sigma Fgrilse_{t+4} + \Sigma Fmsw_{t+5}) / Fspawners_t$$

where $Fgrilse_{t+4}$ and $Fmsw_{t+5}$ are the estimated fecundities of individual grilse and MSW salmon at $t+4$ and $t+5$, respectively, and $Fspawners_t$ is the total fecundity of all spawning females (both captive-bred and wild-bred) at t. $P_{Wild\text{-}bred\,t}$ is now a measure of ova-per-ovum productivity that is robust to both variation in lifecycle and fecundity. We estimated productivity for all years where data were available. Due to the stocking of captive-bred ova within the catchment for experimental purposes in some years, $Fspawners_t$ was corrected as necessary (Marine Institute, pers. comm.). We repeated the population-level analyses using ova per ovum productivity instead of recruits per spawner. The results were qualitatively unchanged.

Text S3: Results of the test for a higher proportion of zero LRS for captive-bred than wild-bred Atlantic salmon.

The proportion of captive-bred and wild-bred fish that displayed zero LRS was 0.82 and 0.67, respectively. The 95% confidence interval for these estimates was 0.12 – 1.0. $X^2 = 72.45$, $df = 1$, $p < 0.001$

Chapter 3

Evolutionary stasis of a heritable morphological trait in a wild fish population despite apparent directional selection

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Evolutionary stasis of a heritable morphological trait in a wild fish population despite apparent directional selection

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Author contributions: **RJOS**, TER, and AK conceptualized the paper and designed the analyses, with **RJOS** conducting the analyses. PMcG, PAP, TA, SE, and CRP conceived the original Burrishoole pedigree construction project. PMcG, GR, and RP facilitated data collection and provided access to historical datasets. TA, SE, and CRP generated the molecular data and constructed the pedigree. **RJOS**, TER, and AK wrote the first draft of the manuscript, with all co-authors contributing to subsequent drafts. TA wrote the text of the Supplementary Material and made Figures S2 and S3.

3.1 Abstract

Comparing observed versus theoretically-expected evolutionary responses is important for our understanding of the evolutionary process, and for assessing how species may cope with anthropogenic change. Here we document directional selection for larger female size in Atlantic salmon, using pedigree-derived estimates of lifetime reproductive success as a fitness measure. We show the trait is heritable and, thus, capable of responding to selection. The Breeder's Equation, which predicts microevolution as the product of phenotypic selection and heritability, predicted evolution of larger size. This was at odds, however, with the observed lack of either phenotypic or genetic temporal trends in body size, a so-called 'paradox of stasis'. To investigate this paradox, we estimated the additive genetic covariance between trait and fitness, which provides a prediction of evolutionary change according to Robertson's secondary theorem of selection (STS) that is unbiased by missing variables. The STS prediction was consistent with the observed stasis. Decomposition of phenotypic selection gradients into genetic and environmental components revealed a potential upward bias, implying unmeasured factors that covary with trait and fitness. These results showcase the power of pedigreed, wild population studies – which have largely been limited to birds and mammals – to study evolutionary processes on contemporary timescales.

3.2 Introduction

The process of adaptive evolution can be split conceptually into inheritance on the one hand, and phenotypic selection on the other, i.e. the effect of phenotype on relative fitness. Selection can be thought of as the 'bridge' between ecology and evolution (Hendry 2017) and, indeed, changing patterns of selection on functional traits lie at the heart of many applied eco-evolutionary problems (Kinnison and Hairston 2007; Hanski 2012; Alberti 2013; Smallegange and Coulson 2015; Fugère and Hendry 2018). A better understanding of which traits are under selection, the form such selection takes (stabilizing, disruptive, fluctuating, directional), and the extent to which genetic constraints influence actual responses to selection is required to obtain deeper insights into the evolutionary process.

The theoretical groundwork for the study of phenotypic selection in the wild was in place by the 1980s (Price 1970; Lande 1980; Lande and Arnold 1983; Arnold and Wade 1984), and since then a wealth of empirical studies have reported estimates of selection differentials or gradients in natural populations (Hoekstra et al. 2001; Kingsolver et al. 2001; Kingsolver and Pfenning, 2007; Siepielski et al. 2009, 2013). At the same time, increasing numbers of studies using powerful, flexible statistical approaches such as the "animal model" (Kruuk 2004; Wilson et al. 2010) report estimates of key quantitative genetic parameters that influence microevolutionary responses. A general finding is that abundant genetic variation exists in natural populations for traits under selection (Mousseau and Roff 1987; Lynch and Walsh 1998) and hence, it would be expected that adaptive evolutionary responses should be commonly observed. However, among those studies that have estimated actual microevolutionary trends, a majority have found a lack of observed response to selection, despite evidence for directional selection and heritability; the so-called "paradox of stasis" (Merilä et al. 2001; Kruuk et al. 2008; Stinchcombe et al. 2013; Pujol et al. 2018).

Accurately estimating the form, direction, strength of selection, and predicting a trait's evolutionary response also has practical applications with the potential to inform management policy for exploited species experiencing harvest-induced selection (i.e. Allendorf and Hard 2009), or conservation policy for populations where *in situ* adaptation to anthropogenic change may be the sole route to persistence (Visser 2008; Martins et al. 2018). Explanations for mismatches between observed and expected responses to selection, including the special case of evolutionary stasis, can be grouped into biological versus statistical (Pujol et al. 2018). On the biological side, inaccurate microevolutionary predictions can result by failing to account for various phenomena such as age structure, indirect genetic effects, genotype-by-environment interactions, fluctuating selection at unmeasured times and/or places, and genetic correlations between the focal trait and unmeasured traits also under selection (Etterson and Shaw 2001; Morrissey et al. 2012). Statistical explanations invoke biased and/or imprecise estimates of quantitative genetic parameters; e.g. failure to account for environmental sources of phenotypic resemblance among relatives (Kruuk and Hadfield 2007), or bias in phenotypic selection estimates caused by covariance between some unmeasured variable with both the focal trait and fitness (Fisher 1958; Hadfield 2008; Morrissey et al. 2010; Stinchcombe et al. 2014; Reed et al. 2016).

Here we explore patterns of phenotypic selection, inheritance, and evolution of body size in a wild, pedigreed population of Atlantic salmon *Salmo salar* L., 1758. Body size is a key phenotypic trait generally theorised to be under natural and/or sexual selection. Empirical studies of wild animal populations have found a range of patterns, including positive directional (Boag and Grant 1981; Schluter and Smith 1986; Brown and Brown 1998; Milner et al. 1999; Kruuk et al. 2001; Husby et al. 2011), negative directional (Price et al. 1984; Bonnet et al. 2017), stabilising (Schluter and Smith, 1986; Preziosi and Fairnbairn 2000), disruptive (Gross 1985) and fluctuating (Gibbs and Grant 1987; Seamons et al. 2007; Bonnet and Postma 2018) selection on body size or related traits. Salmonid fishes provide excellent model systems in this regard since many of their populations are intensively studied, body size metrics are often routinely measured, and fitness components can be measured directly (Quinn et al. 2001a; Carlson and Quinn 2007; Kendall and Quinn 2009; Carlson et al. 2009; Morrissey and Ferguson 2011) or estimated indirectly using molecular pedigrees (Aykanat et al. 2014; Seamons et al. 2007; Naish et al. 2013; Reed et al. 2019; this study).

Large size is generally expected to be advantageous to both female and male anadromous salmonids, but for different reasons. Larger females can produce more and larger eggs (Beacham and Murray 1993; Bacon et al. 2012; de Eyto et al. 2015), can dig deeper nests so that their eggs are less susceptible to scouring in high river flows (Steen and Quinn 1999), and compete better for limited nest sites (Holtby and Healey 1986). Selection pressure in males, on the other hand, may be more influenced by sexual selection for access to mates, with larger males better able to court and defend females (Fleming and Gross 1994; Fleming 1996). However, small 'sneaker' males persist as an evolutionarily stable strategy in some systems, as they are able to 'steal' fertilizations from larger, more socially dominant males (Fleming and Einum 2011). Previous studies on Pacific salmonids have found sex differences in the form and magnitude of selection on adult body size (Fleming and Gross 1994; Carlson and Quinn 2007; Seamons et al. 2007).

Using measures of total adult-to-adult fitness (individual lifetime reproductive success, *LRS*) inferred from a molecular pedigree for nine cohorts of spawning adult Atlantic salmon, our aims were to determine (i) if adult body size was, on average, under linear and/or nonlinear selection across the considered time period, and (ii) its evolutionary potential. Having shown the trait to be both heritable and under directional selection in females, our subsequent goals were to (iii) test for a microevolutionary trend in female body size over time and (iv) explore whether the observed evolutionary response was concordant with expected responses to selection predicted using two theoretical approaches: the Breeder's Equation (BE; Lush 1937) and the Robertson-Price Identity (Robertson 1966, 1968; Price 1970; also known as the secondary theorem of selection, hereafter STS). The BE can give biased predictions if there are variables missing from the analysis that covary with both the focal trait and fitness (Hadfield 2008; Morrissey et al. 2010). The STS provides an estimate of the expected evolutionary change in mean trait value per generation, given by the additive genetic covariance between trait and relative fitness, which is unbiased by missing traits or environmental variables (Hadfield 2008; Morrissey et al. 2010). A comparison of BE versus STS predictions can, therefore, be a useful indirect test of the presence of such missing traits or environments, particularly if observed evolutionary responses are more concordant with STS than with BE predictions. Our final aim was to (v) use the more direct method of Rausher (1992; see also Hadfield 2008, Morrissey et al. 2010, 2012, and Stinchcombe et al. 2014) to quantify the difference between genetic and non-genetic regressions of fitness on trait, which if present would bias evolutionary predictions based on the univariate BE.

3.3 Methods

(a) Study System

The Burrishoole catchment in the West of Ireland (Supplementary Material, Figure S1) drains an area of approximately 100 km^2 of varying topography and land use (de Eyto et al. 2016) and consists of three major lakes: brackish Lough Furnace, connected to the sea by the Burrishoole River, and the larger, freshwater Loughs Feeagh and Bunaveela, with Atlantic salmon spawning in a series of afferent rivers. A total trapping system operates on the catchment, where all upstream migrating pre-spawning adults, all downstream migrating post-spawning adults ('kelts'), and all downstream migrating juveniles ('smolts') are enumerated. Traps are located on two short rivers that connect Lough Feeagh to Lough Furnace (Supplementary material, Figure S1). A hatchery has operated on the catchment since the early 1960s as part of an experimental ocean ranching programme (McGinnity et al. 2009). The hatchery rears a core "ranched" salmon stock, that originated from wild Burrishoole fish, up to the smolt stage, at which point they are usually released into Lough Furnace and allowed to migrate to sea naturally (although historic releases into Lough Feeagh and directly into the estuary have also occurred). Starting in the 1960s, returning hatchery fish (identified by an adipose fin clip) were externally tagged and allowed to migrate upstream. Subsequent downstream homing behaviour allowed a proportion of these to be removed, with a sub-sample of these fish used as brood stock for the following generation of captive-reared salmon. In recent years, the management goal has been to reduce the proportion of hatchery fish to less than 5% of the spawning stock that is allowed to ascend the traps to spawn. Therefore, varying numbers of hatchery fish have been released above the traps over the years, some of which spawn in the wild (Thompson et al. 1998; McGinnity et al. 2009; Aykanat et al. 2014). Thus, there has been some gene flow from the hatchery to the wild population. This study focusses exclusively on wild-spawning fish i.e. fish who were born in the wild or in the hatchery, but who themselves spawned in the wild; the evolutionary dynamics within the hatchery are not examined.

(b) Pedigree construction

Microsatellite genotype data were used to construct a molecular pedigree of all returning fish, using the Cervus software 3.0.7 (Kalinowski et al. 2007). Full details on fish sampling, DNA extraction, genotyping, and pedigree construction protocols are provided in Aykanat et al. (2014) and in the Supplementary Material. The sex of returning fish was determined based on phenotypic characteristics and confirmed genetically with a sex marker (see Aykanat et al. 2014 and Supplementary Material for details).

The term "cohort" is hereafter used to refer to the year a fish returned from the sea on its spawning migration; note that fish may return over a range of months, from June to September, and most spawn in December, but some spawning may also occur the following year in January. While a pedigree was constructed from all available data (see Supplementary Material; Table S1), due to breaks and changes in the sampling regime since the 1960s, not all years could be included in the analyses described herein. We report identity analysis results and the false discovery rate for the entire pedigree (see Supplementary Material, Figure S2, Table S1). After data cleaning the pedigree used in this study comprised of wild-spawning fish for the following cohorts: 1977, 1978, 1979, 1980, 1981, 1982, 1984, 1985, and 1989 (see Supplementary Material, Figure S3). On average, 90% of fish in this system follow a four-year lifecycle (Piggins and Mills 1985): individuals will spend two years in freshwater, migrate to sea for one winter, and then return to the catchment in the following year to spawn. There is some generational overlap (see Supplementary Material, Figure S4 for a diagrammatic explanation of the typical four-year lifecycle). For example, fish spawning in 1989 represent the offspring of fish that would have spawned mostly in 1985, but with a small fraction coming from 1983, 1984 and 1986. The offspring of fish spawning in 1989 would themselves return and be sampled as adults predominantly in 1993. A gap in sampling in 1991, 1992 and post-1993 precluded us from being able to determine whether we missed any offspring spawned by the 1989 cohort that did not recruit in 1993, and so *LRS* may be underestimated for fish that spawned in 1989. Selection analyses were re-run excluding data from the 1989 cohort and the results were qualitatively unchanged, hence this potential source of bias was deemed unproblematic.

In this study system, up until 2011, upstream migrating adults were enumerated but not sampled for DNA or measured for phenotypes. Instead, they were sampled as kelts in the traps on their post-spawning downstream migration back to sea. This sampling regime aimed to avoid stressing the fish on their upstream spawning migration. However, periodic sampling of upstream migrating fish did occur in some years (e.g. 1977, 1978). Some mortality occurs in freshwater either prior to, during, or post-spawning, with mortality much higher in males, leading to a female bias in our sample (Aykanat et al. 2014). On average across the whole study, the number of fish measured for fork-length (hereafter referred to simply as body size) represented approximately 50% of the total numbers of upstream migrating pre-spawners. While adults lose mass between entering freshwater and leaving again after spawning, adult female skeletal size is not expected to change; thus, body size of female kelts can safely be assumed to reflect body size at spawning. As such, all sampled females from the relevant cohorts were used in the estimation of the female size selection gradient. Since male skeletal length is known to increase between freshwater entry and spawning, (due to the development of a secondary sexual characteristic of the jaw known as the 'kype'), selection analysis on male length was limited to only those males that were sampled as kelts. We also assume that kelts represent a random subset of original spawners with respect to body size and *LRS*, but we lack the data to formally test this, and explore in the Discussion the possible implications of violations to this assumption.

The *LRS* of each fish was measured by counting the number of offspring assigned genetically to that individual who themselves returned as adults in future years, and in turn were sampled. We acknowledge that this *LRS* measure is potentially an underestimate of lifetime fitness given that some returning adults (in particular males) die prior to being sampled as kelts, while a small fraction of adult offspring may 'stray' (i.e. return to rivers other than their natal river), but this need not lead to biased microevolutionary inferences (see Discussion). The final dataset consisted of 1185 records of female *LRS* and body size, and 302 records of male *LRS* and body size (with no repeat measures in either sex; note that while Atlantic salmon are capable of iteroparity, this is rare in our study system), measured across nine return cohorts (see Supplementary Material, Table S2).

(c) Phenotypic selection

Body size for each fish was mean and variance standardized (hereafter denoted as *Size'*) by subtracting the overall grand mean body size across the nine cohorts from each individual body size measure and dividing by the overall standard deviation. This yields a standardized size measure known as a 'z-score'. Using z-scores allows for the estimation of standardized selection coefficients which are directly comparable across studies (Lande and Arnold 1983). This was done separately for males and females, which varied in their means and standard deviations, and selection analyses were performed separately since selective regimes are known to differ between the sexes in salmonids (Fleming 1996; Seamons et al. 2007). Overall patterns of linear and nonlinear phenotypic selection across the whole study period were estimated for each sex separately using generalized linear mixed effects models (GLMMs) implemented in the 'MCMCglmm' R package (Hadfield 2010; R Core Team 2017), in which *LRS* was the response variable and the explanatory variables included linear and quadratic effects of *Size'*. Models were fit using a Poisson error structure and a log link function as MCMCglmm's Poisson error structure automatically accounts for overdispersion in the data. We derived linear and quadratic selection coefficients using the method of Morrissey and Goudie (bioRxiv). Briefly, this method estimates linear and quadratic selection coefficients from GLMMs that are equivalent to those estimated from standard Lande-Arnold regressions. We focus on a single trait expressed as *z*-scores and so regression coefficients in the selection analyses correspond to both standardised selection differentials and univariate standardised selection gradients (Postma 2006). Hereafter, these are referred to as selection gradients, but noting that they do not necessarily reflect true direct selection on body size, as correlated traits affecting fitness could be missing from the analyses (Lande and Arnold 1983). Selection analyses used MCMCglmm's default priors, equivalent to a Gaussian distribution for the fixed effects, and an inverse-gamma distribution for the variances.

(d) Animal models to estimate quantitative genetic parameters

Initial exploration of male quantitative genetic parameters was impeded by small sample sizes and large associated errors. As such, all further quantitative genetic analyses were conducted solely on females. First, we ran a univariate animal model with *Size'* as the response variable, an intercept as the only fixed effect, and random effects that included an additive genetic effect (with the variance in these corresponding to the additive genetic variance, V_A), a maternal effect (V_{dam}), a cohort effect (V_{cohort}), and a residual effect (V_{resid}). Narrow-sense heritability (h^2) was then calculated by dividing V_A by the sum of all variance components ($V_A + V_{dam} + V_{cohort} + V_{resid}$). No fixed effects were included in the analysis as no additional individual-specific information was available on environmental variables or traits that might influence body size, such as the date a fish was sampled. Female Atlantic salmon stop feeding once they return to freshwater and are therefore not expected to either gain or lose skeletal size during the adult freshwater phase. While there is variation in date of ocean exit, i.e. "run timing", which may be associated with variation in body size (Quinn et al. 2006), we had no individual-level information on this. Sea age – the number of winters spent at sea prior to freshwater return – is also correlated with body size at return and is itself heritable in Atlantic salmon (Barson et al. 2015; Reed et al. 2019). Given that over 90% of fish in this population return after a single winter at sea (known as 'grilse') and that the inclusion of heritable traits as fixed effects can affect estimates of V_A for the focal trait, sea age was not included as a fixed effect in the animal models. The animal model for *Size'* was initialised with a burn-in period of 500,000 iterations and then run for a further 2,000,000 iterations, with a thinning interval of 1000, giving a final MCMC sample size of 2000.

For a trait to respond to selection, there must be additive genetic variance in the trait, as well as a covariance between fitness and the trait (Fisher, 1930). As such, we estimated V_A and h^2 for *LRS* using an animal model with the same fixed and random effects structure as that used for *Size'*. The 'QGglmm' R package was used to integrate over the posterior distributions of the random effects for the animal model of *LRS*, in order to convert the estimated variance components from the latent scale to the observed scale of the data (de Villemereuil et al. 2016; Bonnet and Postma 2018). The animal model for *LRS* was initialised with a burn-in period of 1,000,000 iterations and then run for a further 14,000,000 iterations, with a thinning interval of 10,000, giving a final MCMC sample size of 1400. Univariate animal models used non-informative, parameter-expanded priors.

(e) Testing for observed microevolutionary change

Conceptually, a microevolutionary change occurs within a population when the mean breeding value – a measure of the 'genetic merit' (additive genetic effects) of individuals for the trait of interest – changes over time. Predicted breeding values for *Size'* for each individual were extracted from the female univariate animal model and the observed temporal change in mean breeding values (slope of mean annual breeding value versus cohort as a continuous variable) across the study period was calculated using a variant of the method described in Hadfield et al. (2010). We fitted *Cohort* as a random effect as per Postma (2006), rather than as a fixed effect as per the Hadfield method. This gave a posterior distribution of temporal slopes of estimated mean breeding values (EBVs) which corresponds to a distribution of estimates for the linear rate of evolutionary change. We *a priori* expected a positive microevolutionary trend, given that positive directional selection was found for females (see Results), and statistical support for this was assessed by calculating the fraction of the posterior distribution of temporal slopes that was greater than zero. The probability that the observed change in EBVs was different from a scenario of genetic drift was then calculated by simulating random breeding values for *Size'* down the pedigree using the *rbv*() function in MCMCglmm (Hadfield 2010) for each of the 2000 posterior samples of the univariate animal model for *Size'* based on the estimated V_A. Linear regressions were fitted to the cohort mean of these random breeding values to obtain the temporal slopes due to drift for each posterior sample. The fraction of the posterior distribution of observed temporal slopes that was greater than these "drift slopes" was then calculated. This provides an estimate of the probability that the observed microevolutionary trend was greater than expected due to genetic drift alone. Since *Size'* was a mean and variance standardized quantity and was regressed on years, the units for evolutionary change here were phenotypic standard deviations per year (PSD). The estimated rate of microevolution on an annual basis was converted to a per-generation rate, by multiplying the annual rate by four (the average generation time of fish in our study system). This is then equivalent to a change measured in 'haldanes' (PSD generation^{-1}).

(f) Comparing observed microevolutionary change against predictions from the BE and STS

The expected per-generation rate of adaptive evolutionary change for this population was first calculated based on the multivariate BE (Eqn.1):

(Eqn.1) $$R_{BE} = V_A\beta$$

where R_{BE} = the response to selection, i.e. the predicted genetic change in the mean trait value from one generation to the next based on the BE, and β is the univariate selection gradient, which in our case corresponds to the linear coefficient for body size on the latent scale in the phenotypic selection analysis. To obtain a full posterior distribution of R_{BE} that accounts for all uncertainties in the estimation procedures, we multiplied realizations of V_A and β_{Size} from their respective posteriors to obtain samples from the posterior of R_{BE} and then calculated the posterior mode and 95% credible intervals for R_{BE} from this. This allowed us to determine if the per-generation rate of *observed* microevolution, as calculated in the previous step, matched the *predicted* response derived from the BE.

The STS states that the additive genetic covariance (cov_A) between a trait (z), and relative fitness (w), is a direct measure of the expected per-generation evolutionary change of that trait, unbiased by unmeasured covariates (Robertson 1966; Price 1970; Stinchcombe et al. 2014). We call this an evolutionary "response" for linguistic consistency but recognise that the STS is agnostic regarding the drivers of evolutionary change, which could include drift or selection on a genetically correlated trait, in addition to direct selection on the trait itself.

$$R_{STS} = cov_A(w, z) \qquad \text{(Eqn.2)}$$

We defined a bivariate animal model with *Size'* and *LRS* as response variables to estimate the additive genetic covariance between them, which in this case corresponds to $cov_A(w, z)$ due to the log link function on *LRS* (Morrissey and Goudie bioRxiv). The bivariate animal model consisted of an intercept with random effects for additive genetic, dam, cohort and residual effects specified within an unstructured variance-covariance matrix, using non-informative, parameter-expanded priors. As before, this gives a full posterior distribution for R_{STS}, for which we report the posterior mode and 95% credible intervals. For all models, Markov chains were thinned so as to keep autocorrelation between successive draws below 10%. Alternative priors were specified for all models (selection and animal), with none proving sensitive.

(g) Quantifying bias in phenotypic selection gradients

Work by Rausher (1992), Hadfield (2008), Morrissey et al. (2012) and Stinchcombe et al. (2014) has shown that the difference between the "environmental selection gradient", β_E (which corresponds conceptually to the regression slope of environmental deviations for fitness on environmental deviations for trait) and the "genetic selection gradient", β_G (which corresponds conceptually to the regression slope of breeding values for fitness on breeding values for trait) provides a metric of so-called "environmental bias" to phenotypic selection. For example, a purely environmental variable such as nutritional status might influence both the focal trait and fitness, generating phenotypic covariance between them even if the trait does not necessarily causally influence fitness (Price et al. 1988). The phenotypic selection gradient would be biased, in the sense that there is no selection on underlying breeding values in this hypothetical example, nor would any response to selection be expected even if the trait were heritable (Rausher 1992). While this is typically referred to as "environmental bias", phenotypic selection estimates may be biased whenever there are unmeasured factors of any sort, be they genetic or environmental, which correlate with both focal trait and fitness (Hadfield 2008; Morrissey et al. 2012). The difference (in slopes) between non-genetic and genetic regressions of fitness on trait represents our 'bias statistic (hereafter, referred to as '$\Delta\beta$') and because we used a Bayesian approach, we could obtain a posterior probability that this bias statistic was greater than zero, which would imply stronger positive 'selection' at the non-genetic, compared to the genetic, level. This in turn can be interpreted as the probability that predictions from the univariate BE are biased by missing traits or environments.

We had only a single focal trait and so β_G and β_E could be calculated from the bivariate animal model of trait (*Size'*) and fitness (*LRS*) used to calculate R_{STS}. For β_G, this involved dividing $cov_A(w, z)$, equivalent to a genetic selection differential, by V_A, to give a univariate selection gradient. To calculate β_E, we summed all the environmental covariance terms in the bivariate animal model and divided by the sum of the corresponding variance components for *Size'*. The bias statistic, $\Delta\beta$, was then calculated as β_E - β_G, using full posterior distributions for each (Morrissey et al. 2012). When the 95% credible intervals of the resulting posterior distribution of $\Delta\beta$ do not include zero, there is sufficient evidence to state that there is bias in the phenotypic selection measure. If the credible intervals include zero, there is insufficient evidence to suggest bias, but equally one cannot conclude unequivocally that there is no bias in situations where statistical power may be low (Reed et al. 2016; this study).

The results for all parameter estimates from our Bayesian models are expressed as posterior modes and 95% highest posterior density (HPD) intervals. Variance components by definition cannot be negative but were deemed statistically not significant when the lower HPD interval overlapped zero.

3.4 Results

(a) Phenotypic selection

Phenotypic selection was positive in females, with credible intervals that did not overlap zero ($\beta_{Size} = 0.23$, 95% HPD: 0.08, 0.34), implying directional selection for larger body size (Figure 1, Table 1). The quadratic selection gradient was close to zero with credible intervals including both negative and positive values (Table 1), implying weak or no nonlinear selection in females. For males, the linear selection gradient was less than a third that of females, with credible intervals including a broad range of negative and positive values (Figure 1, Table 1), suggesting either a lack of consistent directional selection in males or insufficient statistical power to detect a real relationship (given that sample size for males was only 302, compared to 1185 for females). Similar to females, the quadratic selection gradient was close to zero in males with credible intervals including both negative and positive values (Table 1).

(b) Univariate animal models

The animal model for *Size'* revealed significant additive genetic variation in female *Size'*, as well as significant cohort and residual effects, with the maternal effect being very close to zero (Table 2). *LRS* showed significant cohort and residual effects, with the additive genetic and maternal effects being very close to zero. Heritability (h^2) of female *Size'* was estimated at 0.23 (95% HPD: 0.06, 0.41). After transformation from the latent to the data scale, h^2 for *LRS* was estimated as 0.0005 (95% HPD: <0.0001, 0.11).

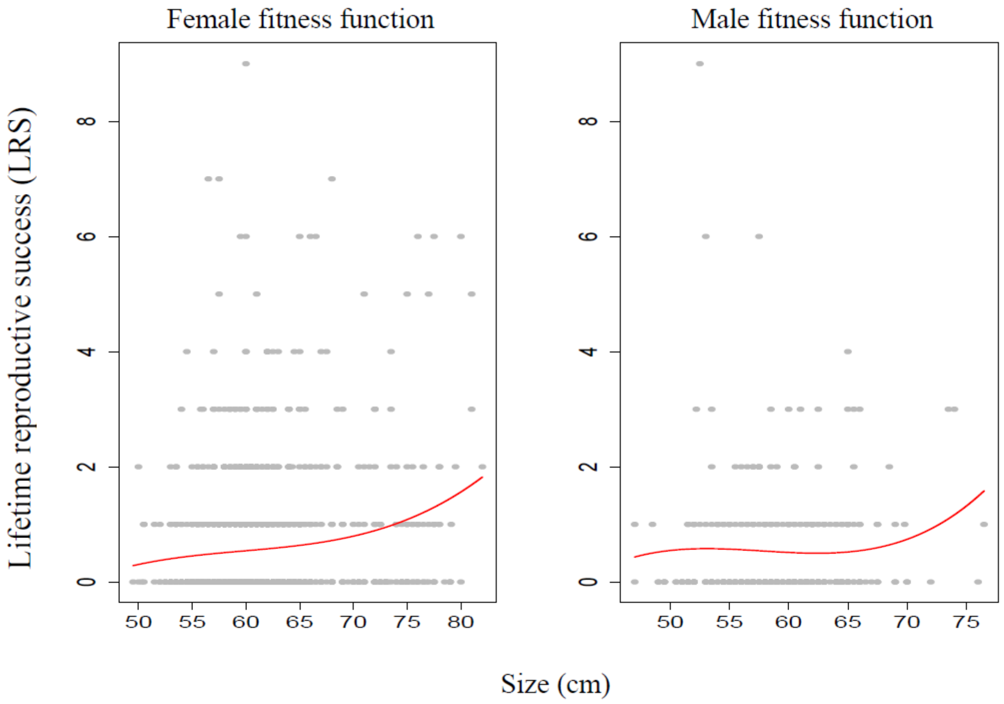

Figure 1: Phenotypic selection patterns (red curves) on body size measured in centimetres (cm) for female and male Atlantic salmon. Selection gradients were approximated for illustration purposes using univariate cubic splines c.f. Schluter (1988) and Wilson et al. (2005).

Table 1: Linear and quadratic standardised (univariate) selection gradients for female and male Atlantic salmon

	Female		Male	
	Posterior mode	95% HPD	Posterior mode	95% HPD
Linear selection	0.23	0.08-0.34	0.07	-0.18-0.26
Quadratic selection	0.1	-0.005-0.24	0.04	-0.12-0.56

(c) Comparing observed versus predicted evolution

There was no overall temporal trend in annual mean phenotype across the 1977 to 1989 study period (-0.18 cm yr^{-1}; 95% HPD: -0.55, 0.24; Figure 2a). Likewise, there was no genetic trend in EBVs for female body size (0.0005 PSD yr^{-1}, 95% HPD: -0.007, 0.01; Figure 2b), with the posterior probability of this trend being greater than zero being only 59%. The probability of the temporal trend being more positive than expected under a scenario of genetic drift was 57%. Re-expressed in phenotypic standard deviations per generation (haldanes) rather than per year, this corresponded to an observed per-generation evolutionary change of 0.002 haldanes (95% HPD: -0.03, 0.04; Figure 3). By comparison, the BE predicted a per-generation rate of evolutionary change in female body size of 0.05 haldanes (95% HPD: <0.001, 0.10; Figure 3), implying that female salmon were predicted to increase in size across the time period. The STS, on the other hand, predicted a rate of evolutionary change in female body size of -0.004 haldanes, with credible intervals broadly overlapping zero (95% HPD: -0.21, 0.10; Figure 3); that is, it predicted a lack of any consistent response to selection, which was concordant with the observed lack of temporal trend in estimated breeding values or mean phenotype.

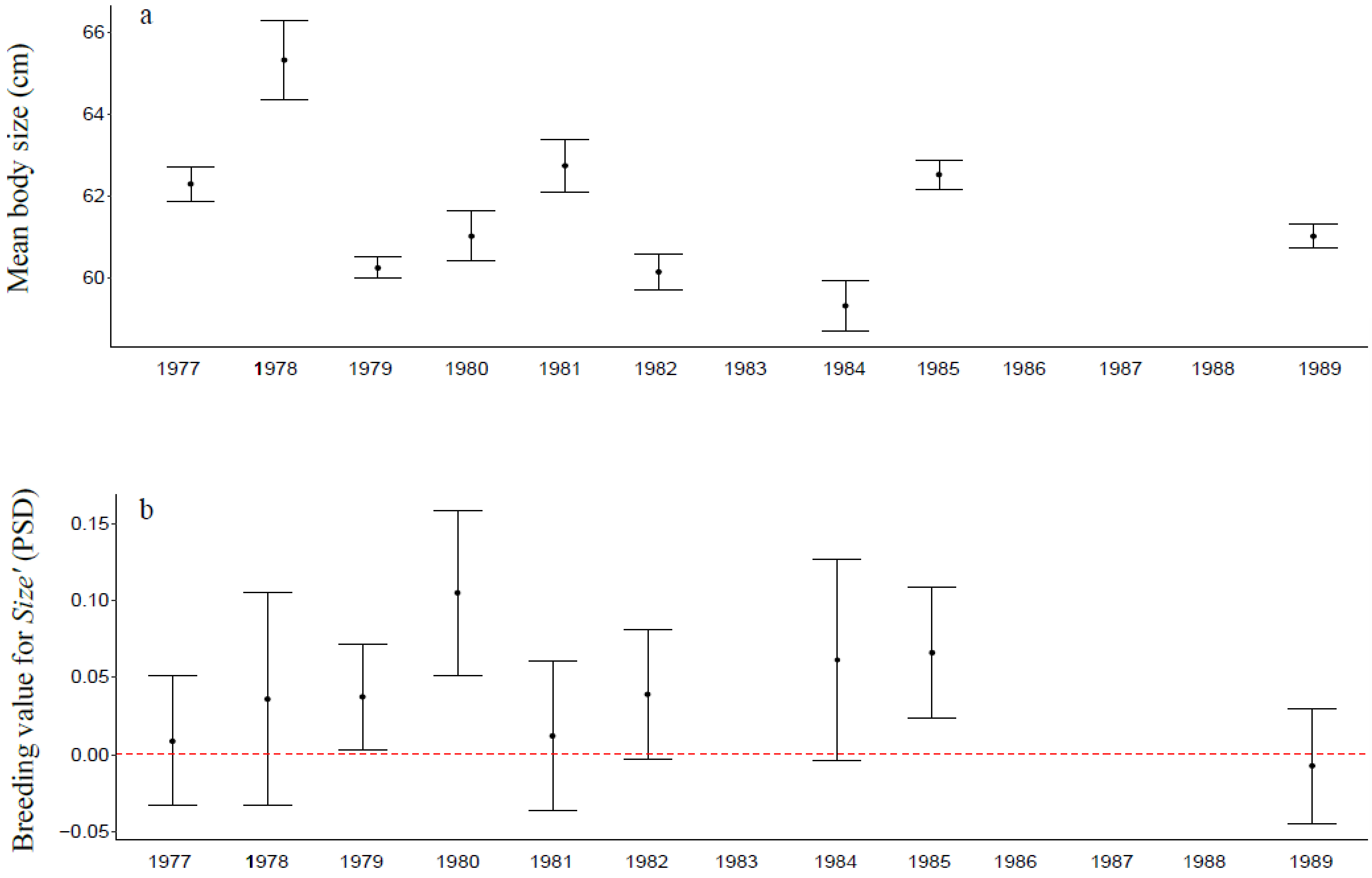

Figure 2: (a) Observed phenotypic trend in mean body size for female Atlantic salmon over the period 1977-1989. The upper and lower bounds of the whisker plots represent standard errors; (b) Observed evolutionary trend in cohort mean breeding values for Size' (measured in phenotypic standard deviations, PSD, with the standardization done using the global mean and standard deviation) in female Atlantic salmon over the period 1977-1989. The upper and lower bounds of the whisker plots represent standard errors.

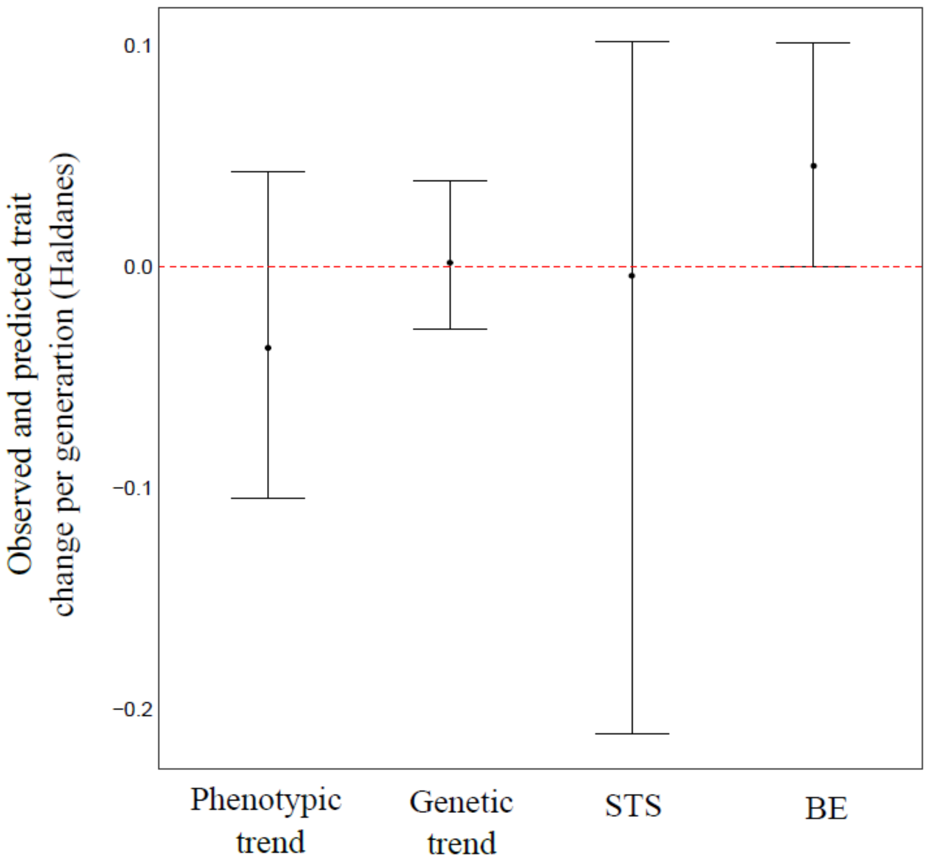

Figure 3: Comparison of observed and phenotypic trends in *Size'* in female Atlantic salmon, with predicted evolutionary trends in breeding values based on the multivariate Breeder's Equation (BE) and the Secondary Theorem of Selection (STS). The observed evolutionary change (Genetic trend) was determined by extracting estimated breeding values from the univariate animal model for *Size'* and testing for a temporal trend.

(d) Quantifying bias in selection gradients

The posterior mode estimate for $\Delta\beta$ was 0.43, indicating that missing traits or environmental variables contribute to a more positive association between trait and fitness than can be attributed to the effect of the trait alone on fitness. Credible intervals overlapped zero (95% HPD: -0.21, 1.7: Figure 4) with 94.2% of the slope estimates greater than zero.

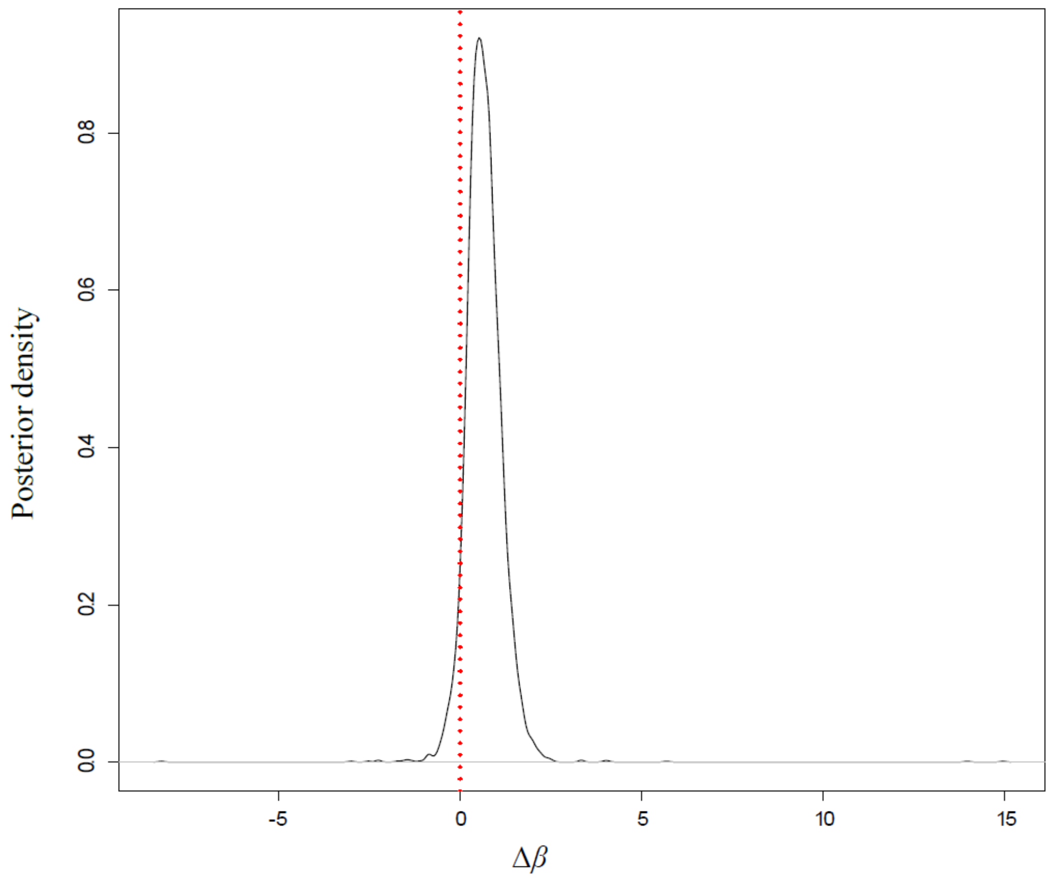

Figure 4: The posterior distribution of the bias statistic, $\Delta\beta$, between environmental and genetic selection gradients. 94.2% of the distribution lies above zero (right of the dashed vertical line), strongly suggesting bias in the female phenotypic selection gradient due to unmeasured trait(s) or environmental factors.

Table 2: Posterior modes and 95% HPD intervals for additive genetic variance (V_A), cohort (*Cohort*), maternal (*Dam*), and residual (*Residual*) variance component estimates from univariate animal models for *Size'* and *LRS* in female Atlantic salmon. Heritability (h^2) estimates were calculated as the quotient between V_A and the sum of V_A, *Cohort*, *Dam*, and *Residual*. For *LRS*, all parameter estimates are given on the latent scale, with the exception of h^2, which is on the data scale after integration over the variance components (see Methods).

	Size'					*LRS*				
Parameter	V_A	*Cohort*	*Dam*	*Residual*	h^2	V_A	*Cohort*	*Dam*	*Residual*	$h^2_{\text{Data scale}}$
Posterior mode	0.26	0.08	0.0003	0.68	0.23	0.003	0.33	0.001	0.93	0.0005
95% HPD	0.05-0.42	0.03-0.35	<0.0001-0.1	0.51-0.89	0.06-0.41	<0.001-0.57	0.1-1.21	<0.001-0.18	0.4-1.25	<0.0001-0.11

3.5 Discussion

(a) Selection analyses

Based on information derived from nine cohorts spanning three generations of our molecular pedigree, we found evidence for positive directional selection on female body size in Atlantic salmon. There was no evidence for directional selection on male body size, nor for nonlinear selection in either sex. Our finding of positive directional selection on female body size was consistent with predictions (Fleming 1996) that larger female salmon should experience greater reproductive success for myriad potential reasons (e.g. produce more eggs, produce larger eggs that give an early size advantage in offspring, more aggressive, secure better territories). While the ecological drivers of this positive selection in females remain unclear, size-mediated competition among the adults for suitable spawning sites and among offspring for territories are likely to be involved. Seamons et al. (2007) also documented positive linear selection on body size (fork length) in anadromous female steelhead trout (*Oncorhynchus mykiss* Walbaum 1814) using pedigree-derived *LRS* as the fitness measure. Adult-to-adult *LRS* for females can be decomposed into three components: mating success, fecundity, and offspring viability (egg-to-adult survival). Maternal body size could in theory affect all three components, but effects on offspring viability would be indirect and mediated via factors such as egg size and physical qualities of the nest site (Fleming 1996). As such, maternal effects on offspring survival are likely limited to early stages (egg to fry), attenuating thereafter at the juvenile, smolt, and marine phases (Reed et al. 2015). Stochastic environmental effects probably dominate variation in overall egg-to-adult survival and hence it is unsurprising that maternal body size explains so little of the variation in *LRS*. The theoretical and practical implications of assigning offspring viability as a component of maternal fitness are discussed further below.

For males, direct effects of body size on *LRS* likely act solely via mating success, although indirect effects may arise if there is positive assortative mating, where large males mated to large females sire more or better quality offspring (Fleming

1996). As such, the overall lack of evidence for selection on male body size in our study is intriguing. Theory suggests that male Atlantic salmon should experience disruptive selection: large ocean-going (anadromous) males and early-maturing males (sneakers) that spawn before going to sea are predicted to achieve higher fitness than intermediate-sized males, which cannot compete as successfully against larger anadromous males for access to females, nor adopt as effectively the sneaking tactic of smaller mature males (Hutchings and Myers 1994; Taborsky 2008). While these may be different 'traits' in the sense that different genes/developmental pathways might affect size-at-first-maturity of anadromous males versus early maturing males, recent work shows that the same QTL may influence both sea-age at maturity (Allyón et al. 2015; Barson et al. 2015) and early male maturation (Lepais et al. 2017). Our study was limited to anadromous males only, and while some may have spawned previously as sneaker males, these fish would not have been sampled at that stage. As up to 30% of paternities in Burrishoole may be attributed to sneaker males, approaching 60% in years of proportionally high hatchery spawning (Thompson et al. 1998), disruptive selection could well occur across the full range of male body sizes.

Another explanation for the lack of selection in males could simply be that there is little variation in male size in this population, and hence a reduced scope for selection. For example, Atlantic salmon in the River Teno/Tana in Finland/Norway exhibit a much larger range of male body sizes, and selection for larger males is known to occur there (Mobley et al. 2019; see also Fleming 1998). Anthropogenic changes over the past several decades, particularly in the marine environment, have reduced the prevalence of larger, older salmon in some populations across their range (Quinn et al. 2006; Chaput 2012; Reed et al. 2017), including the Burrsihoole (Nixon 1999), which may in turn limit the opportunity for ongoing selection.

Among anadromous males, we still expected to find positive directional selection given that larger males may have an advantage in intra-sexual competition in Atlantic salmon (Hutchings and Myers 1987) and other salmonids (Fleming and Gross 1994; Quinn et al. 2001a). Our sample size of 302 males may have been too small to detect subtle directional selection. Or it may be there are costs of larger body size (e.g. increased aggression from other males during establishment of dominance hierarchies, predation costs) that counteract any sexually-selected benefits. A further hypothesis is that females may choose males on the basis of traits which are uncorrelated with overall body size. Selection pressures are also likely to be context-specific; for example, Seamons et al. (2007) found that larger male steelhead trout had higher *LRS* on average than smaller males, but the strength of selection varied among years for unknown reasons. In contrast, Carlson and Quinn (2007) documented selection against larger male sockeye salmon (*Oncorhynchus nerka* Walbaum 1792) in an Alaskan study population, with the largest males (and females) being more susceptible to stranding at the mouth of the spawning river connected to a lake, particularly in years where lake levels were low. Larger fish in that system are also more susceptible to brown bear (*Ursus arctos* L. 1758) predation (Quinn et al. 2001b).

If straying rates in our system are correlated with both body size and fitness, then our estimates of selection on body size could be biased in a global sense, i.e. different relationships between size and fitness might have been found in either sex if the body size and *LRS* of strayers into non-natal rivers could be measured and included in the analysis. Conceivably, strayers may be a non-random subset of the local population in this regard, however, we have no reliable data on this. Selection estimates would only be biased if the relationship between trait and fitness was not the same in strayers versus non-strayers. Similar issues arise in nest-box population studies of passerine birds, where study areas typically represent only a small local sample of a much larger, widespread population. In such situations, selection estimates are best interpreted at a local scale, i.e. they represent the relationship between phenotype and *local* recruitment. Local selection pressures and their consequences for discrete, locally-adapted salmonid populations such as our study system (O'Toole et al. 2015) are arguably of more interest than estimates of global selection, unless one is interested specifically in meta-population dynamics.

A second source of methodological bias could arise from the fact that, for males, we were limited to sampling post-spawning kelts, rather than pre-spawning adults on their upriver migration. For example, if larger males were more likely to die on the spawning grounds but also experienced higher *LRS* than smaller surviving males, then our male selection estimates would be biased downwards (an example of the "invisible fraction" problem *sensu* Grafen [1988]; see also Hadfield [2008]). We are unable to explore this potential source of bias as we almost always only sampled males as kelts that, by definition, survived the spawning period. This problem may be male-specific, as spawning survival rates for females are much higher (55%-80%; Anon.) – as evidenced by our much higher sample sizes for females relative to males (Table S2).

(b) Quantitative genetic parameters and observed versus expected evolutionary dynamics

Although heritability estimates are by their nature population- and environment-specific, our estimate of heritability for female body size was similar to previously published estimates for this trait in adult Atlantic salmon ($h^2 = 0.32$ in Saura et al. [2010]; $h^2 = 0.27$ in Reed et al. [2019]), and fell within the range of previous estimates for heritability of size during juvenile stages within our system (Reed et al. 2015). More generally, our estimate of body size heritability was congruent with the median estimate of 0.21 reported by Carlson and Seamons (2008) for morphological traits across 11 salmonid species. Dam effects on body size were effectively non-existent: when expressed as a percentage of the total variation, V_{dam} only explained ~0.022% (Table 2). This was unsurprising, in that maternal effects on offspring traits are expected to attenuate with offspring age in salmonids (Heath et al. 1999; Reed et al. 2015), such that by the time the offspring is an adult, there is almost no discernible maternal effect remaining. Among the remaining phenotypic variation not attributable to additive genetic or maternal effects, cohort effects accounted for ~7.2% and residual effects for ~67% (Table 2). This implies that environmentally-driven variation in growth among individuals within years is greater than between-year variation, which is largely driven by marine growth.

Our univariate animal model for *LRS* revealed a very low h^2 for this fitness trait, with a modal estimate that was close to zero. The low h^2 for *LRS* reflected very low V_A for *LRS*, with the posterior distribution of V_A similarly abutting zero and having a long right tail. There may be very little segregating genetic variation in fitness in this population, which is what one would expect theoretically at equilibrium (Fisher 1930), unless balancing selection mechanisms or a high mutational target maintain genetic variance in fitness (Houle 1998). Low h^2 for fitness does not necessarily imply low V_A, however, as various stochastic environmental and demographic processes can lead to very high environmental sources of fitness variance which can dominate in the calculation of h^2 (e.g. Kruuk et al. 2000). Our animal model for *LRS* contained a log link function, making V_A of fitness interpretable as the genetic variance of relative fitness. While our estimate of this was modest (0.003), the 95% HPD contained non-trivial values which may represent the true parameter value. If V_A in relative fitness is indeed rather low in our salmon population, this may provide a partial explanation for our observed evolutionary stasis: there can be no genetic covariance between body size and fitness, i.e. microevolution, if there is no genetic variance in fitness (Orr 2009).

Indeed, the observed lack of microevolution was consistent with the predicted rate according to the STS being effectively zero. As explained in Morrissey et al. (2010) and Morrissey et al. (2012), the STS provides a more robust, less assumption-laden guide to expected microevolution in natural populations than the BE, although it is not itself completely without problems: various ecological complications such as spatio-temporal variation in the expression of genetic variation, non-random migration, and non-constant demographic structure may render STS predictions inaccurate. Given the partial agreement between the STS prediction and our observed evolutionary stasis, we tentatively conclude that our study is not hampered by such complications.

The BE in both its univariate and multivariate forms assumes that all relevant traits have been included in the analysis (Lande and Arnold 1983). A necessary condition for the univariate BE to always produce accurate evolutionary predictions is that the focal trait must be the *sole* cause of covariation between phenotype and fitness. In the case of the multivariate BE, the key assumption is the presence of what Morrissey et al. (2010) call "joint-sole" causation; that is, the traits included in the analysis are collectively the only traits determining phenotype-fitness covariance. In practice, these assumptions can be rather restrictive in natural populations, where entire suites of traits may be under selection and inter-correlated to varying degrees. Failure to include any of these traits in a multivariate BE analysis may render the results biased. Adult body size in salmon is likely to be correlated with other traits such as return timing, sea age, or aspects of intrinsic metabolic rate, which may each experience different, potentially antagonistic, direct selection pressures. This is the reason, we believe, why our BE prediction suggested a positive directional response to selection, whereas the STS prediction was equivocal, with the potential for either a positive or a negative evolutionary change in body size. However, we are cautious not to over-interpret this comparison between STS and BE predictions, because both were associated with rather large 95% credible intervals, likely due to our relatively low sample sizes and shallow pedigree. Thus, while the posterior mode of the STS prediction was close to zero (-0.004 haldanes) the upper credible interval was higher (0.10 haldanes) than the posterior mode for the BE prediction (0.05 haldanes). It remains possible, therefore, that both approaches actually predict positive directional evolution in this system, but there is insufficient statistical power to conclude the STS prediction is different from zero. The fact that our comparison of selection at the genetic versus environmental levels provided reasonably strong support for a bias (i.e. missing traits or environments), and that there was also no evidence for any observed microevolutionary trend, points towards a scenario of true evolutionary stasis that is correctly predicted by the STS but not the BE. But the statistical power to detect relatively subtle evolutionary trends was likely low, so again we cannot outright reject a scenario of true directional evolution that would be correctly predicted in sign (but not necessarily magnitude) by both the STS and BE approaches if the sample sizes had been higher and/or the pedigree was deeper. These caveats must be born in mind in interpreting our results, and if any of our estimates are to be used in meta-analyses, we recommend that they are appropriately weighted by their large uncertainty.

(c) Quantifying bias in selection gradients

Our estimation of the probability of bias in the female phenotypic selection gradient (i.e. the probability that $\Delta\beta > 0$) for size further suggested the existence of missing traits or missing environmental factors, given that 94.2% of the posterior distribution of $\Delta\beta$, was greater than zero (Figure 4). Therefore, $\Delta\beta$ provides substantial evidence that the potential discordance between the BE and STS predictions was caused by unmeasured traits/environments (regardless of the low power of our analyses). While female body size is likely to have causal effects on fitness components such as fecundity (de Eyto et al. 2015), the weight of the posterior distribution seems to indicate that indirect selection on unmeasured correlated traits, which could include the same trait(s) measured in males, may be constraining the evolution of larger body size. Our analysis of selection on body size in males suggested a lack of overall directional selection, which may weaken overall selection at a genetic level in females if body size is positively genetically correlated across the sexes, as might be expected. We attempted to explore this using a bivariate animal model of body size in males and females, but this model suffered from convergence issues. However, the caveat of low sample size constraining our ability to estimate directional selection on males must be borne in mind here.

One potential weakness of our study is the fact that our fitness measure, by necessity of sampling constraints, is an adult-to-adult measure of *LRS*. Evolutionary genetics theory traditionally asserts that fitness should be counted from conception to death, e.g. the expected lifetime production of zygotes by a given zygote, thus avoiding complications associated with attributing offspring fitness components to parental fitness and conflating selection with inheritance (Lande and Arnold 1983; Cheverud 1984; Grafen 1988). For example, selection pressures and evolutionary potential can be over- or under-estimated when heritable maternal effects and their potential genetic covariance with direct genetic effects are not accounted for in a Breeder's Equation-type analysis (Wolf and Wade 2001; Wilson et al. 2004, 2005). In practical terms, adult-to-adult *LRS* measures are more easily obtained in salmonid populations (Seamons et al. 2007; Reed et al. 2019) than other types of individual-level fitness measures such as adult-to-fry reproductive success, or egg-to-egg fitness, since assigning zygotes or juveniles to adults is made impractical by the sheer quantities of eggs/fry involved, and by their aquatic nature. Due to these difficulties in tracking individuals throughout their lifetime, our results must be considered in light of the 'invisible fraction' *sensu* Grafen (1988) and Hadfield (2008), which refers to situations where some individuals in the population die before a trait is measured or expressed and thus are 'missing' in the accounting of overall selection pressures. For example, fast growth may be costly to survival and thus a part of the population that would otherwise express large adult body size could have died by the time adult body size is actually measured; hence true selection on genes coding for larger fish may in fact be weaker. This is an issue faced by all (to the best of our knowledge) long-term salmonid monitoring programmes that typically are limited to sampling adults on their return to freshwater. While it may also be possible to monitor smolts on their migration from freshwater to saltwater, it may not be possible, or be otherwise unadvisable, to actually handle smolts at this vulnerable life-stage, and in any case it remains extremely difficult to get data on what happens to different phenotypes at sea. Thus, unless advances are made in our ability to track individual fish across their entire life (perhaps by the genetic tagging of fertilized ova in wild redds), the expansion of quantitative genetics and selection analyses in wild fish populations will remain somewhat hampered. Simulation studies could be used to better understand how the type of fitness measure influences evolutionary inferences under different scenarios of direct and indirect effects of trait on fitness.

(d) Concluding remarks

Across three generations of our molecular pedigree, we could not demonstrate a clear pattern of change in body size for female Atlantic salmon at the phenotypic level, congruent with both the observed stasis in breeding values and the predicted evolutionary stasis according to the STS. We used the $\Delta\beta$ test to infer that missing traits correlated to female body size were likely present, and thus that using the estimated phenotypic selection gradient in the BE will likely lead to a biased microevolutionary prediction – i.e. that larger body size should evolve, when in fact no evolutionary trend was observed, nor was any predicted by the STS. Our results caution against naïve expectations of directional evolution, even when the key "ingredients" of (apparent) directional selection and heritability are present, especially in studies where power may be low. By exploring evolutionary potential in a fish species, our study complements a growing literature reviewed by Pujol et al. (2018), most of which has been on birds and mammals, showing how mismatches between predicted and observed microevolution can result from a range of biological and statistical mechanisms. Additionally, we highlight how caution must be taken when interpreting results based on data-poor systems with low power and limited sampling regimes. Many unanswered questions remain, however, such as the role of constraints due to sexual conflict and the stability of selection gradients and quantitative genetic parameters through time, or across age classes/environmental contexts, and whether a feasible solution to the invisible fraction problem will become available for highly fecund aquatic species such as Atlantic salmon. These issues are particularly important to understand/solve for body size and related traits in fish populations, given their key role in mediating eco-evolutionary responses to anthropogenic changes (Naish and Hard 2008), including climate change, harvest selection, and release or escape of captive-reared fish into wild populations.

4.6 Supplementary Material

Genotyping

In addition to the 29 microsatellite markers described in Aykanat et al. (2014), the MHCII region was used as a polymorphic marker (see Vähä et al. [2007] for primer information), which was multiplexed together with “panel 2” markers (Aykanat et al. 2014).

Sex determination

Both phenotypic sexing (i.e. identifying sex by expression of secondary sexual characteristics during sampling), and genetic assays were employed to determine the sex of an individual. The genetic sex determination is a PCR-based presence and absence assay, which targets the sex determination gene, *sdy*, in Atlantic salmon (presence of *sdy*=male, absence of *sdy*=female; Yano et al. [2013], see Aykanat et al. [2016] for primer information). The presence or absence of the *sdy* gene was determined by either agarose gel or using an ABI3130 fragment analyser. In the agarose gel method, two lab workers independently evaluated the presence/absence of *sdy* amplification in the gel, using the 18S region as the positive control. In the fragment analyser method, the normalised intensity of *sdy* amplification (log-normalized to the intensity of the microsatellite markers, “ssosl438”, “ssa124”, “sssp1605”, “ssf43”, “ssa202”, “sssp3016”, which were multiplexed with the *sdy* marker) was evaluated. The log-normalized *sdy* intensity is expected to exhibit a clear bimodal distribution where females are expected to have zero, or close to zero normalized intensity values. As such, arbitrary thresholds of 0.05 and 0.13 were used as cut-offs for sex determination (i.e. threshold < 0.05 is female and threshold > 0.13 is male). Genetic sex determination was highly concordant within and between platforms. Concordance was 95.7% (44/46) among replicate assays between agarose and fragment analyser methods. Likewise, sex determination within the fragment analyser method was highly concordant with 98.6% (145/147) of individuals accurately sexed across replicated assays.

If genetic sex and phenotypic sex were in contradiction with each other, genetic sex was prioritised over phenotypic sex. Overall, phenotypic and genotypic sex were highly concordant within the final dataset, agreeing in 93.4% of cases (1296/1387).

Identity analysis

Individual genotypes in the dataset may have identical or near identical genotypes due to contamination, or as a result of underlying biological reasons such as re-sampling of the same fish within a given year, or across subsequent years (i.e. repeat spawning fish). To detect such genotypes, identity analysis was performed using Cervus 3.0.7 (Kalinowski et al. 2007), whereby an individual pair is considered as potentially identical, if they have a maximum of three mismatches, and the difference between matches and mismatches is at least 10. The resulting list of identical pairs were further inspected by eye and, based on the concordance of secondary information (length between putative identical pairs should be less than or equal to 4 cm and capture years should be biologically plausible), a decision was made and the pair were marked as biologically identical, or as a result of contamination throughout the processing of samples. The identity analysis was performed using a larger set of individuals which included cohorts from later years as well as fish with hatchery origins (N=5152). This gave a total of 13268976 pairwise genotype comparisons, of which 168 pairs matched the initial criteria (Figure S2). Most identical genotypes were biological (153/168), either being fish trapped both upstream and downstream (most of which were hatchery fish), or previous spawning fish which were sampled in subsequent years, and 15 were marked as contaminated. Finally, there were 34 “incidental” identical pairs that exhibited low mismatch (<4) but also low match-mismatch difference (<10) due to low numbers of overlapping loci being successfully genotyped. One of these incidental pairs, i.e. the one with lower genotyping success, was removed from downstream analyses. The identity analysis modestly altered the dataset used in the study: 32 pairs marked as previously spawned salmon were excluded from the dataset, and only two individuals in two incidental pairs were removed from further analysis. Only individuals genotyped at more than nine loci were included in the identity and the subsequent parentage analyses.

Parentage analysis

A likelihood-based parentage analysis was performed using Cervus 3.0.7 (Kalinowski et al. 2007). A combination of LOD scores (logarithm of the odds of an individual being a parent compared to the average likelihood score of the population) and delta scores (the difference in the likelihood scores of being the parent between the two most likely candidate parents) were used to assign parentage. A candidate parent was assigned to an offspring if the LOD score of a link was greater than the 95% LOD score threshold, or if the LOD score was between the 80-95% threshold score but with the delta score still higher than the 95% confidence threshold.

The cohort-specific critical values for the log-likelihood statistics for LOD scores and delta values were obtained using the simulation module in Cervus 3.0.7 (Kalinowski et al. 2007). For that, a conservative number of 1000 parents for both mother and father, and 5000 for offspring were simulated for each cohort - which are conservative estimates compared to census sizes for salmon from the Burrishoole system, or compared to un-sampled parent estimates as in Aykanat et al. (2014). Cohort-specific missing individual proportions and empirical missing genotype information were implemented in the simulations. Genotype error rates (ER1) were calculated the same as Aykanat et al. (2014) by averaging all values across loci, and between paternal and offspring cohorts. For cohorts that were not included in Aykanat et al. (2014), the ER1 was estimated using the linear regression formula that models ER1 as a function of time but restrained to a minimum value of 0.01. Allele frequency distributions were obtained using all wild samples from the system. Simulations were carried out for females and males separately. The paternity analysis was carried out, first using mothers only (maternity analysis), and then feeding confidently assigned mothers to the subsequent paternity analysis. Any resulting trios (both mother and father identified) were later inspected for the confidence of the likelihood father-mother-offspring link (i.e. trio confidence).

Our parentage analysis was also robust to false positive parentage assignments. We adapted an empirical test to quantify the rate of false discovery rates (FDR) in this study. For that, we performed another parentage analysis, identical to the aforementioned described analysis, but included parental candidates with zero probability of being first order relatives to the offspring cohort tested. These "improbable parent candidates" were from the Burrishoole population (either of wild or hatchery origin). Hence, we quantified the FDR by assessing the proportion of false positives (i.e. number of false positive links divided by number of links tested) to the proportion of parental links from probable cohorts. For example, in the 1977 cohort, 63 valid maternal parents were assigned out of 20206 possible parent-offspring combinations. Among impossible mother-offspring links, 63 were assigned out of 351581 pairwise combinations tested. This provided an FDR of 0.0355778. Overall, the false discovery rate was small, with an average of 0.055 across cohorts (SE±0.025, see Table S1), further suggesting that the parentage testing was robust.

Table S1: Assessing the false discovery rate of parentage using empirically improbable parentage links as the source of false positive links for the full pedigree. Pr(probable) and Pr(improbable) refer to the probability of the assigned links in both scenarios. FDR = False Discovery Rate. Pr() = probability.

Sex	Parent spawning cohort	Assigned, probable links	Probable links	Pr(probable)	Assigned, improbable links	Improbable links	Pr(improbable)	FDR $_{\text{weighted}}$	FDR $_{\text{cohort average}}$
Females	1977	63	20206	0.003118	39	351581	0.000111	0.035578	
	1978	94	19941	0.004714	34	423821	8.02E-05	0.017018	
	1979	128	59772	0.002141	46	564110	8.15E-05	0.038079	
	1980	59	17366	0.003397	34	334043	0.000102	0.029959	
	1981	128	41804	0.003062	61	547844	0.000111	0.036365	
	1982	21	9059	0.002318	20	123600	0.000162	0.069803	
	1984	23	4773	0.004819	16	125326	0.000128	0.026494	
	1985	208	132385	0.001571	70	768231	9.11E-05	0.057994	
	1989	111	72200	0.001537	47	456109	0.000103	0.067026	
	Total	835	377506	0.002212	367	3694665	9.93E-05	**0.044908**	**0.042035**
Males	1977	11	4145	0.002654	25	204565	0.000122	0.046051	
	1978	10	6850	0.00146	29	241029	0.00012	0.082417	
	1979	41	30667	0.001337	35	318468	0.00011	0.082203	
	1980	2	2980	0.000671	36	180777	0.000199	0.296719	
	1981	30	14368	0.002088	32	291369	0.00011	0.0526	
	1982	2	2226	0.000898	16	66505	0.000241	0.267769	
	1984	8	2277	0.003513	16	66296	0.000241	0.068692	
	1985	101	99527	0.001015	51	358268	0.000142	0.140275	
	1989	63	44880	0.001404	43	232504	0.000185	0.13175	
	Total	268	207920	0.001289	283	1959781	0.000144	**0.112032**	**0.129831**

Table S1 (cont.)

All	1977	74	24351	0.003039	64	556146	0.000115	0.037868	
	1978	104	26791	0.003882	63	664850	9.48E-05	0.02441	
	1979	169	90439	0.001869	81	882578	9.18E-05	0.049114	
	1980	61	20346	0.002998	70	514820	0.000136	0.045352	
	1981	158	56172	0.002813	93	839213	0.000111	0.039398	
	1982	23	11285	0.002038	36	190105	0.000189	0.092914	
	1984	31	7050	0.004397	32	191622	0.000167	0.037978	
	1985	309	231912	0.001332	121	1126499	0.000107	0.080616	
	1989	174	117080	0.001486	90	688613	0.000131	0.087943	
	Total	1103	585426	0.001884	650	5654446	0.000115	**0.061013**	**0.055066**

Table S2: Number of wild fish enumerated in a given cohort (*Wild fish census*), sample size of fish used in these analyses (*No.fish*), mean length ($Size_{mean}$) with associated standard error ($Size_{SE}$), and mean lifetime reproductive success (LRS_{mean}) with associated standard error (LRS_{SE}) for female and male Atlantic salmon used in these analyses. Note that *Wild fish census* does not include hatchery fish that escaped up the catchment and spawned.

		Female					Male				
Cohort	*Wild fish census*	*No.fish*	$Size_{mean}$	$Size_{SE}$	LRS_{mean}	LRS_{SE}	*No.fish*	$Size_{mean}$	$Size_{SE}$	LRS_{mean}	LRS_{SE}
1977	594	128	62.29	±0.42	0.52	±0.1	20	59.25	±1.27	0.15	±0.08
1978	400	64	65.32	±0.96	1.19	±0.22	8	63.38	±2.96	0.38	±0.18
1979	854	208	60.23	±0.26	0.59	±0.08	63	58.87	±0.59	0.57	±0.13
1980	628	110	61.02	±0.61	0.47	±0.08	7	58.61	±1.40	0.29	±0.18
1981	355	124	62.73	±0.64	0.9	±0.11	22	58.4	±1.23	1.05	±0.24
1982	392	127	60.14	±0.43	0.17	±0.04	19	58.1	±0.89	0.16	±0.09
1984	345	81	59.31	±0.62	0.25	±0.06	30	56.5	±0.81	0.23	±0.08
1985	472	154	62.52	±0.36	1	±0.12	60	59.86	±0.58	0.92	±0.20
1989	501	189	61.02	±0.30	0.42	±0.1	73	60.36	±0.0.61	0.47	±0.1
Total	**4541**	**1185**					**302**				

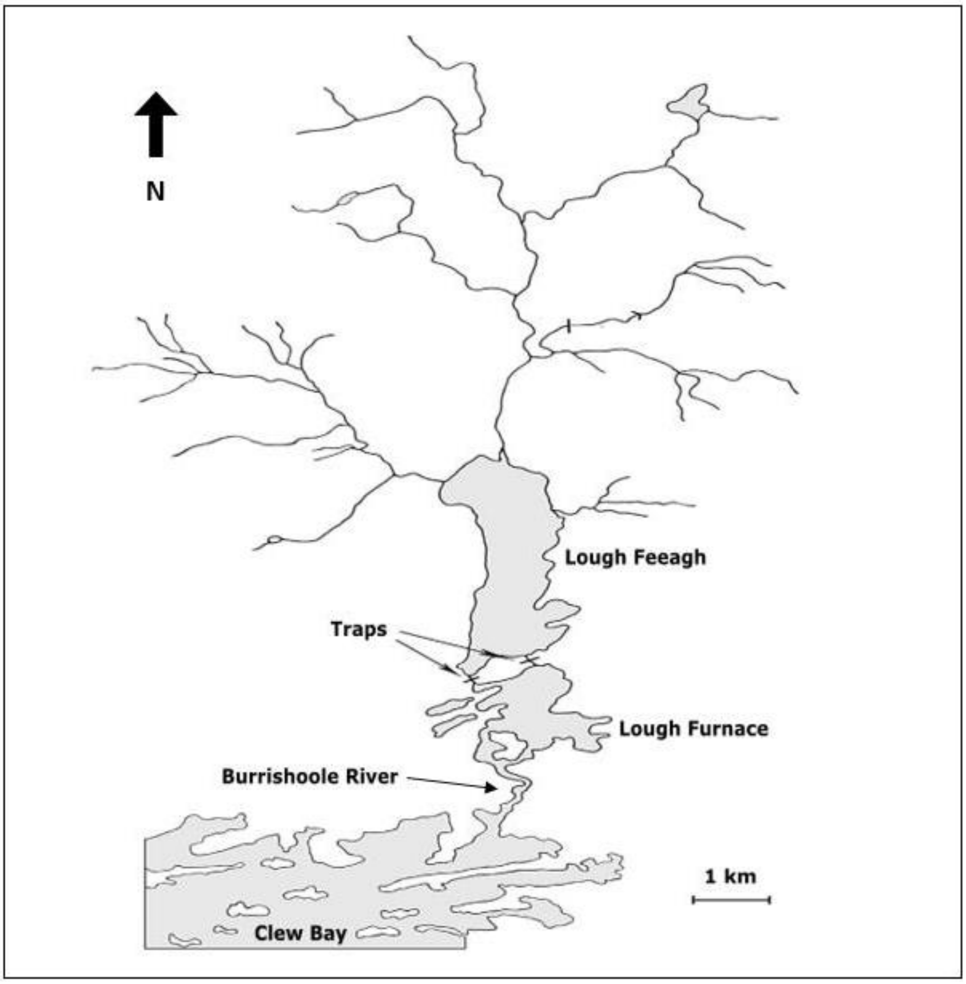

Figure S1: Map of the Burrishoole catchment, County Mayo, Ireland. Adapted from McGinnity et al. 2003.

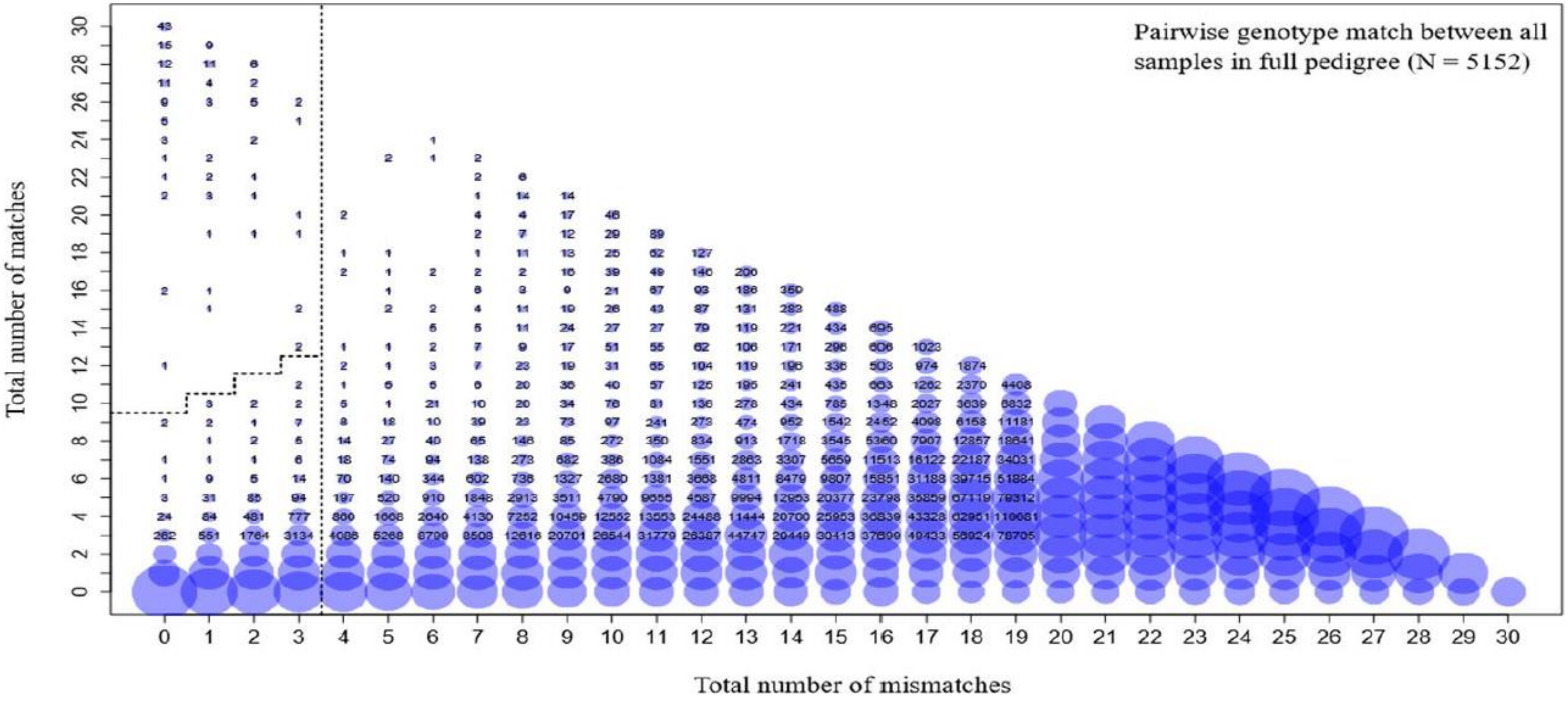

Figure S2: Identity analysis showing the total number of all pairwise genotype matches and mismatches.

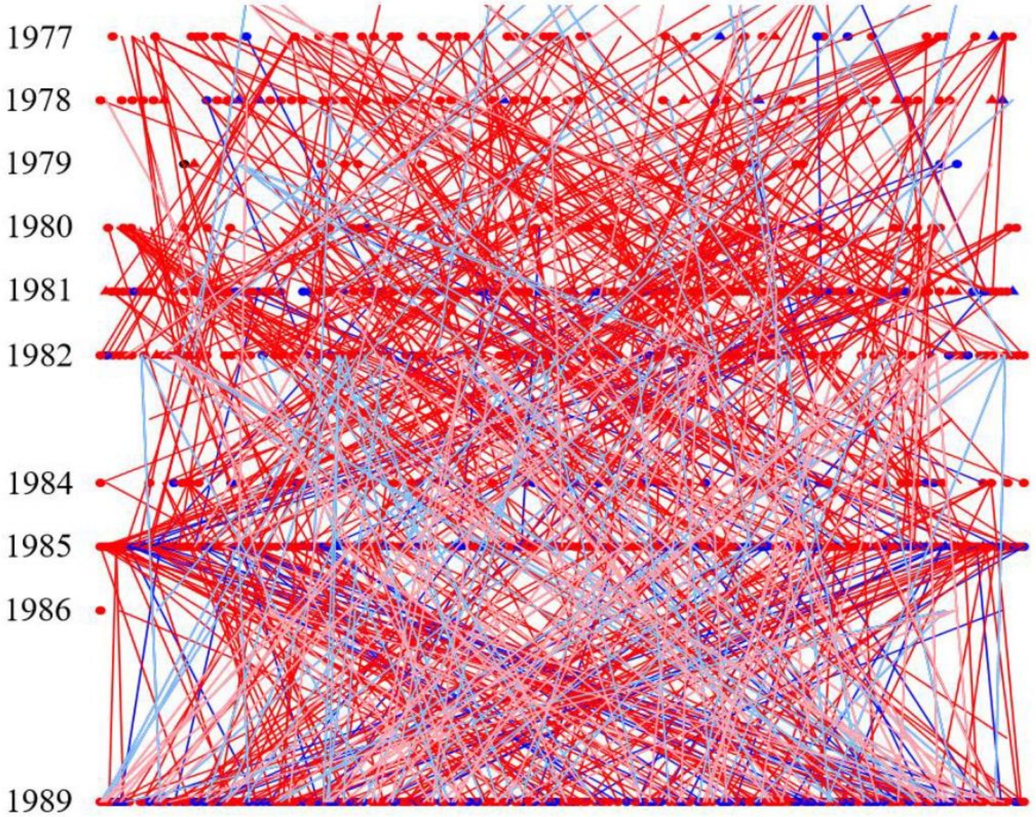

Figure S3: Pedigree of Atlantic salmon, *Salmo salar*, from the Burrishoole catchment, Ireland. Red lines represent maternities and blue lines represent paternities. Hatchery maternal/paternal links are represented with lighter shading. Hatchery and wild parents are represented with triangles and circles, respectively. Years on the y-axis represent the spawning cohort to which an individual belonged. The unrooted individuals at the top of the pedigree represent dams and sires whose offspring spawned in one of the study cohorts.

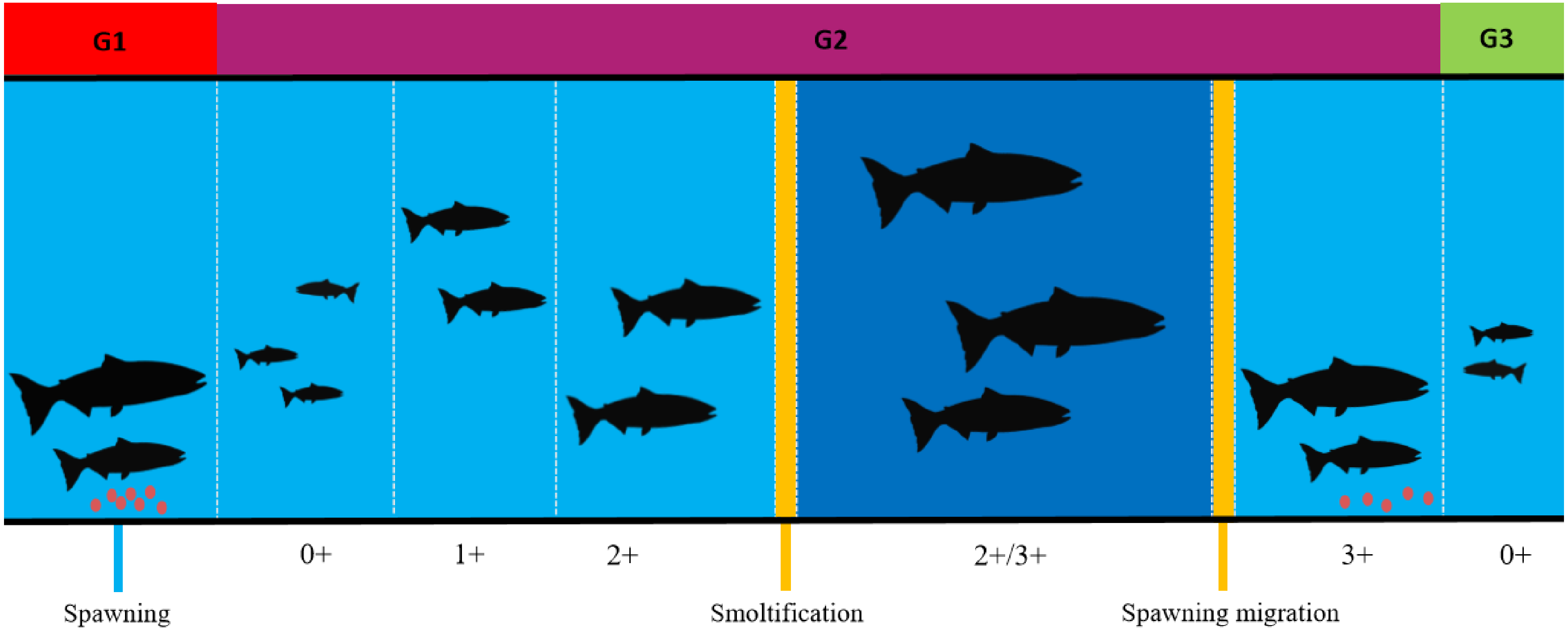

Figure S4: Stylized four-year lifecycle of Burrishoole Atlantic salmon. Adult fish spawn in freshwater, G1. G1's offspring, G2, typically spend 3 years in freshwater (0+, 1+, 2+) before leaving the river (smoltification) during their third year of life and undergoing an oceanic feeding stage (2+/3+). G2 typically return to freshwater to spawn during their fourth year of life (3+), giving rise to the next generation, G3.

Chapter 4

A synthetic review of genetically-explicit eco-evolutionary models in fisheries science

This chapter is in preparation for submission to the journal Fish and Fisheries and is, therefore, written in the style of that journal, except for minor stylistic changes.

A synthetic review of genetically-explicit eco-evolutionary models in fisheries science

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Authorship: **RJOS** had the initial idea for reviewing this topic, carried out the literature review, performed the synthetic analysis, stared into the face of the fish gods, and wrote the first draft. All authors helped in further idea conceptualisation as well as contributing to subsequent drafts.

4.1 Abstract

Since the early 2010s, there has been an increase in the application of eco-evolutionary modelling to address various policy-relevant research topics in fisheries science and stock management. Given this increased interest, we review the use of genetically-explicit eco-evolutionary modelling in finfish, discuss key assumptions/decisions made when designing models, and synthesise the literature on the taxa studied, research topics explored, evolvable traits investigated, genetic architectures used to control inheritance, and the predictive ability of models. Out of 91 reviewed studies, the most common topic of research was fisheries-induced evolution (44.0%) and the most common taxa studied were salmonids (44.0%). 59.3% of studies explored the evolution of a life history trait; 61.5% of studies controlled inheritance via explicit loci; and 90.1% of all studies made anticipatory predictions about the future of a fish population or specific stock. On the basis of our synthesis, we proffer the opinion that future applications of genetically-explicit eco-evolutionary models in fisheries science should aim to: (1) broaden the range of studied taxa, topics, and traits; (2) explore interactions among multiple stressors, e.g. fisheries-induced evolution and climate change; (3) develop more corroborative models to explicitly test theory and enhance knowledge of key eco-evolutionary mechanisms; and (4) more rigorously report and explore the sources of uncertainty in such models so that results can be interpreted with appropriate caution.

4.2 Introduction

The last three decades have coincided with renewed interest in the study of contemporary interactions and feedbacks between ecological and evolutionary processes - so-called ‘eco-evolutionary dynamics’ (Pelletier et al. 2009; Post and Palkovacs 2009; Govaert et al. 2019; Hendry 2017; Hendry 2019). The primary motivating factor behind this renewed interest has been the realisation that evolutionary dynamics can occur on human-observable timescales (Thompson 1998; Hendry and Kinnison 1999; Hairston Jr et al. 2005; Salamin 2010) and are, thus, relevant to applied biology (Stockwell et al. 2003; Kinnison and Hairston Jr. 2007; Hendry et al. 2011; Carroll et al. 2014). Contemporary evolution is particularly likely in response to anthropogenic pressures that drive ‘unnatural selection’ on natural phenotypes (Allendorf and Hard 2009; Dairmont et al. 2009) or natural selection on ‘unnatural phenotypes’ (Bailey et al. 2010).

Modelling studies help us to understand how the world works. They generate theoretically-informed predictions that can be compared against empirical observations, or to anticipate possible futures (Jenouvrier and Visser 2011; Sutherland and Freckleton 2012; Maris et al. 2018). Within ecology, fisheries science has a particularly strong quantitative tradition (Hilborn and Walters 1992), with modelling contributing to our understanding and management of aquatic resources (Schnute 2008; Keyl and Wolff 2008; Barange et al. 2010; Koenigstein et al. 2016). The incorporation of eco-evolutionary modelling into fisheries science has been particularly rapid (Figure 1), fuelled by an appreciation that anthropogenic factors such as harvesting, stocking, aquaculture, hydropower, pollution, habitat loss/fragmentation, and climate change can drive inter-dependent genetic and demographic responses (McClure et al. 2008; Waples et al. 2008; Fraser 2013; Crozier and Hutchings 2014; Heino et al. 2015). This uptake has been further facilitated by the availability of extensive pre-existing datasets for many fish stocks that allow for robust model parameterisation/validation, in addition to increases in computing power over the last two decades which has enabled the exploration of questions previously deemed analytically impossible.

In an early application, Hutchings (1991) modelled interbreeding between wild and cultured Atlantic salmon, *Salmo salar* L. 1758, showing that interbreeding can threaten the persistence and genetic integrity of wild populations. A key assumption of this model – reduced fitness of cultured relative to wild fish under natural conditions – was subsequently validated experimentally in the context of farm escapes (McGinnity et al. 1997, 2003; Skaala et al. 2012, 2019) and hatchery releases (Araki et al. 2007a, 2009). This empirical work raised new questions, in turn motivating the development of increasingly sophisticated eco-evolutionary models over time (Hindar et al. 2006; Castellani et al. 2015, 2018; Sylvester et al. 2019; Yang et al. 2019; Bradbury et al. 2020). Eco-evolutionary modelling has also been used to explore, *inter alia*, the effects of climate change on life-history traits (Ayllón et al. 2016, 2019a; Reed et al. 2011), pesticide resistance (Christie et al. 2019), the maintenance of breeding strategies (Kokko and Heubel 2011), the robustness of meta-populations (Yeakel et al. 2018), and evolution's role in the dynamics and economics of harvested fish stocks (Ernande et al. 2004; Kuparinen et al. 2012; Heino et al. 2015; Mollet et al. 2016; Eikeset et al. 2013, 2016).

Here we present the state of the art for genetically-explicit eco-evolutionary modelling in fisheries. Specifically, we synthesize the relevant literature on finfishes, as very little work has been done on non-finfish species of commercial or ecological interest. Given the increase in studies published on this topic since the early 2010s (Figure 1), we believe a review is warranted in order to take stock, synthesise current knowledge, and suggest future research directions. This review has four primary aims: (1) to provide a clear definition of the term 'genetically-explicit eco-evolutionary model' (hereafter, GE-EE model); (2) to discuss two key decisions/assumptions (predictive capacity and genetic architecture) that are made when designing a GE-EE model; (3) to summarise the taxonomic breadth of studies, topics explored, evolvable traits considered, genetic architectures assumed, and nature of predictions generated; and (4) to suggest research directions whose investigation, we believe, will help to advance the field.

4.3 What are genetically-explicit eco-evolutionary models?

We define GE-EE models as those in which there is explicit exchange of genetic material between parents and offspring (genetically-explicit) and co-occurring evolutionary and ecological dynamics (eco-evolutionary) occur which might influence evolution. The exchange of genetic material can be via sexual or asexual reproduction and in the form of either quantitative genetic parameters or explicit loci. For example, a change in an ecological variable such as temperature could drive selection on a heritable trait (e.g. body size, age at maturity) such that evolution occurs, which in turn influences some aspect of a population's ecology such as intrinsic growth rate, demographic structure, or species interactions. Additional processes such as non-adaptive genetic change (Lowe et al. 2017), phenotypic plasticity (Dunlop et al. 2009), and age-structure can be incorporated. We use the term 'eco-evolutionary' (as supposed to 'eco-genetic' or 'demo-genetic'; see Dunlop et al. [2009]; Frank and Baret [2013]) as it encompasses any two-way interaction between ecology and evolution (Hendry 2017, 2019; de Meester et al. 2019).

Adaptive dynamic models (Dieckmann 1997; Waxman and Gavrilets 2005), in which evolution proceeds solely via *de novo* mutations, are also "eco-evolutionary", but the evolution is assumed to act slowly relative to ecological dynamics, and hence is less immediately relevant to contemporary conservation/stock management. Additionally, genetic mechanisms are not explicit, with evolution modelled through the introduction of new phenotypes, not genotypes, into focal populations (Barton and Polechová 2005). Therefore, we do not review adaptive dynamics models here but acknowledge their important contribution to major questions in fisheries science (Heino et al. 2015) and recognise that both approaches have merits and drawbacks. Similarly, we do not consider studies where models employ the simple copying of a trait value from parent to offspring if the trait value is not underpinned by some genetic mechanism. To illustrate this point, consider Mullon et al. (2002). In that study, the authors developed an evolutionary individual-based model of *Engraulis capensis* larval dispersal and coupled it to an ocean circulation model to predict how spawning strategies (time and place of spawning) might evolve given differential survival between simulated larvae with different strategies. Those larvae that survived to recruitment were used as the parents for the next generation. These second generation *E. capensis* larvae 'inherited' the spawning strategy of their parents, that is, a spawning time and a spawning location. By our definition, the model of Mullon et al. (2002) is not a GE-EE model as the model's spawning strategy is merely copied with no exchange of genetic material. The argument could be made that the two elements of the spawning strategy are analogous to two loci in full linkage disequilibrium. However, this argument ignores the fact that such an 'inheritance' mechanism would not allow for mutation, recombination, crossing over, epistasis, pleiotropy, or individual locus effects (i.e. large-effect loci). Therefore, we believe our exclusion of such studies to be justified.

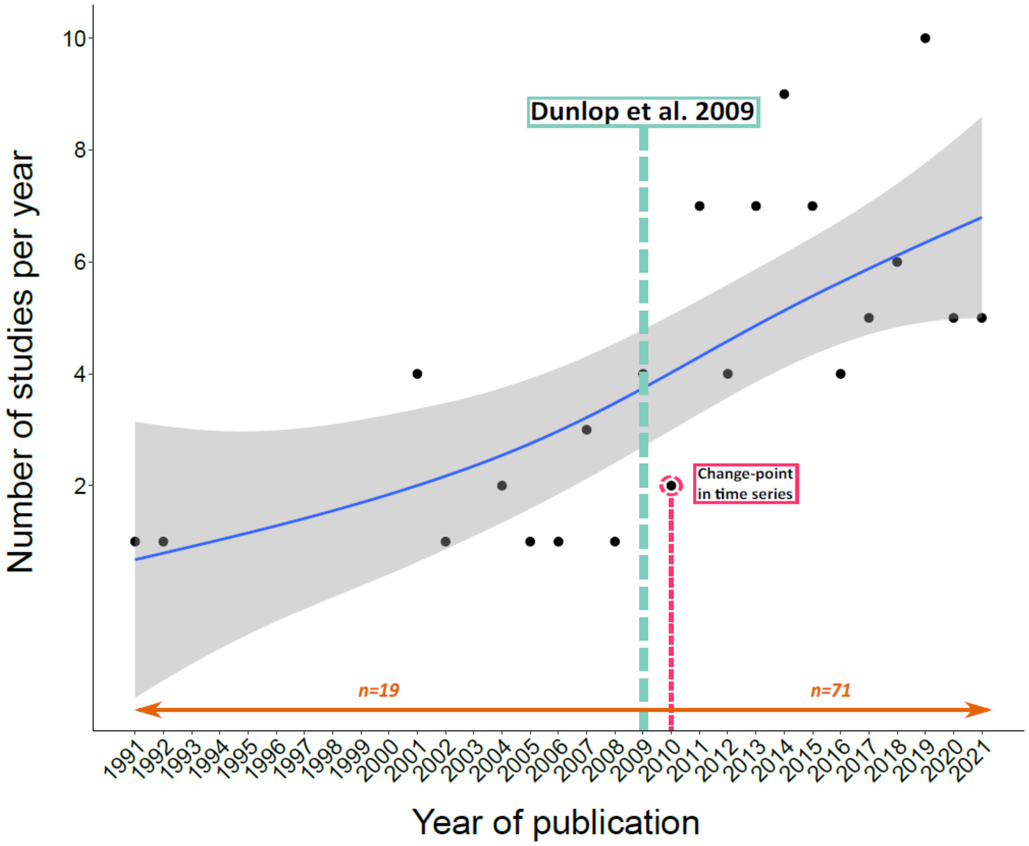


Figure 1: Number of studies in fisheries science published since 1991 that use a genetically-explicit eco-evolutionary (GE-EE) model. Turquoise highlight marks the year of publication of Dunlop et al. (2009) which was seminal in providing an accessible overview of the development and use of eco-genetic models. Trend analysis revealed a significantly increasing slope in the number of studies published over time, with 2010 (pink highlight) being the statistical 'change point' after which the trend manifested itself. The blue line and grey shading represent the line-of-best-fit and 95% confidence interval from a generalised additive model (GAM) fit with a loess smoothing term but are shown here for purely illustrative purposes. The number of studies published pre- and post-change point is highlighted above the orange arrow. See Text S1 of the Supplementary Material for further information on the trend analysis.

4.4 Decisions and assumptions of GE-EE models

(a) What ‘models’ are and the nature of prediction

Models are simply ″idealized versions of the real world’’ (Kokko 2007). Whatever form they take, be they mathematical, statistical, or agent-based, models cannot, nor should they, strive to perfectly describe reality (Caswell, 1988). Too simple, and a model will tell us little of the biological phenomena it aims to describe. Too complex and a model will, at best, sacrifice generality for (potentially) increased realism and precision (Levins 1966) and, at worst, become intractable (Kokko 2005).

GE-EE modelling studies should clearly state their goals and the nature of any resulting predictions. Maris et al. (2018) propose that predictions can be either corroborative or anticipatory. The former involves the generation of hypothesis-derived predictions, and then confronting these predictions with data in order to test the validity of theories about how the world might work. Corroboratory models are time-neutral, meaning their predictions can be applied to past observations or future experimental results. In contrast, anticipatory models have an explicit temporal dimension and aim to explore possible futures, given predetermined assumptions about how the world works and how it might change (Maris et al. 2018). Their predictive nature allows anticipatory models to be used as one of many tools in a responsive, adaptive management framework that can help managers, conservation practitioners, and policy-makers to appreciate the range of possible trajectories that complex systems might follow, given the many layers of uncertainty (Schindler and Hilborn 2015).

Both corroborative and anticipatory GE-EE models are used in fisheries science, although it is not always obvious which of the two philosophies is adopted. Additionally, a small number of studies use models that are capable of both corroboratory and anticipatory prediction (Figure 3d). For corroboratory models, a good match between model-generated and empirical data suggests that the processes operating in the model might be those same processes that occur in nature. An obvious concern is that the same observed patterns can often be generated by simulations based on very different mechanisms (Oreskes et al. 1994; Needle 2001). Additionally, using the same data to both parameterise and validate a model potentially confounds the model's predictions, with cross-validation being an imperfect solution to this. Thus, corroboratory GE-EE models are best viewed as heuristic tools, and studies employing such models should explicitly acknowledge their limitations and be open to alternative mechanistic explanations for the patterns observed.

GE-EE models are most commonly used for anticipatory prediction (Figure 3d; Chapter 5). Anticipatory GE-EE models are powerful tools for those with an interest in, *inter alia*, mitigation, risk assessment, and policy (e.g. Baskett et al. 2005; Dunlop et al. 2009; Eikeset et al. 2013; Eldridge et al. 2010; Jusufovski and Kuparinen 2014, 2020; Castellani et al. 2018; Christie et al. 2019; Bradbury et al. 2020; see Table S1 for a comprehensive list). A major limitation of anticipatory prediction is that observed past relationships amongst variables might not persist into the future, and thus should not be used to forecast what will actually happen, but rather simply to explore what might happen (Schindler and Hilborn 2015). Anticipatory GE-EE models can still lay out hypotheses and predictions, but the key difference compared to corroboratory prediction is that they are tested using model-generated, rather than empirical data. Often, model results simply confirm one's initial expectations, but sometimes results can be non-intuitive and deviate from hypothesis-driven predictions (Chapter 5). Such deviation helps to refine hypotheses and suggest empirical work to test whether similar outcomes would occur in the real world (see Chapter 6, section 6.4).

(b) Genetic architecture

GE-EE models can assume monogenic inheritance, where a trait is determined by a single gene, oligogenic inheritance (trait influenced by a few genes), or polygenic inheritance (trait influenced by many genes). In the monogenic and oligogenic cases, one or more loci are explicitly modelled ("explicit loci"), whereas in the polygenic case it is often more convenient and computationally efficient to use quantitative genetics to model heritable phenotypes at the individual- or population-level. The explicit loci approach makes strong assumptions regarding the number of genes and gene effect sizes, but quantitative genetics also makes simplifying assumptions that may or may not be appropriate to the questions being asked, or timescales considered.

Quantitative genetics (Fisher 1919; Barton et al. 2017) assumes that an effectively infinite number of loci, each of very small effect, influence traits which allows inheritance to be statistically derived using variance components. Therefore, evolution results in changes in the mean (or higher moments) of phenotype distributions across generations (Lynch and Walsh 1998). The quantitative genetic "gambit" is that one does not need knowledge of the actual underlying allele/genotype frequencies in order to understand and model phenotypic evolution. This gambit can pay off in some situations, but not others, as we discuss further below.

With population-based quantitative genetic models, individuals are not explicit and one simply tracks the evolutionary responses of mean phenotype(s) or entire phenotypic distributions to selection using either the univariate or multivariate Breeder's equation, or extensions thereof (see Lynch and Walsh [1998] and Baskett and Waples [2013]). With the individual-based approach, the phenotype of an individual is modelled as the sum of normally-distributed genetic and environmental values, with full distributions of each tracked at the population level. While more computationally demanding, this facilitates more realistic/complex population dynamics including demographic and genetic stochasticity due to finite population size. One must decide whether to fix additive genetic (co)variances at initial input values, or to allow these parameters to themselves evolve over time, e.g. as a function of effective population size.

With explicit loci models, two or more alleles per locus can be coded (e.g. as 0 or 1 in the biallelic case) and genotypic values (per-locus contributions to phenotype) summed across loci to give individual breeding values, to which environmental noise can be added (Roff 2010). Alleles are inherited via Mendelian segregation or asexual reproduction and allele/genotype frequencies and phenotype distributions are tracked across generations. Such models are more computationally intensive than individual-based quantitative genetic models but have the advantage that different types of genetic architecture, including genes of large effect (Kuparinen and Hutchings 2017, 2019; Christie et al. 2019; Oomen et al. 2020), or more complicated phenomena such as dominance (Christie et al. 2019), epistasis (Marty et al. 2015), crossing over (Ivan and Höök 2015) and pleiotropy (Jager 2005) can be modelled. Moreover, genetic drift occurs "naturally" in these models, while mutation can be directly incorporated at the allele level, rather than indirectly as in quantitative genetics (Roff 2010).

Kuparinen and Hutchings (2017) demonstrated how the inclusion of a large-effect locus can influence the predictive capacity of GE-EE models. They compared a single locus model based on *VGLL3* – a locus known to explain 39% of phenotypic variation in *S. salar* sea age-at-maturity (Barson et al. 2015) – to a model that assumed a polygenic basis (the quantitative genetic gambit) for age-at-maturity. They found that single locus simulations produced more variable results – that is, model predictions became less precise (see also Kuparinen and Hutchings [2019] and Oomen et al. [2020]). This has implications for the use of GE-EE models in risk assessment and fisheries management, since the dynamics generated by models that ignore potential large-effect loci might not encompass the full breadth of possible eco-evolutionary outcomes.

4.5 Synthetic review of GE-EE modelling studies

(a) Study selection and descriptive synthesis

This review takes a '*sensu lato*' approach in its definition of fisheries science and considers the discipline to encompass any research that employs a model to examine some aspect of finfish eco-evolutionary dynamics, thus, not restricting to scrutiny only those studies that examined eco-evolutionary dynamics in exploited (be it commercial, recreational, or subsistence) fishes. The terms ((eco-genetic OR eco-evolutionary OR demo-genetic OR "seascape genetics" OR "landscape genetics" OR individual-based OR genetically-explicit) AND (model OR simulation OR framework) AND fish*) were searched for in the TOPIC field across all databases on Web of Science, returning 1101 results. Reviewing the literature revealed references to studies that had not appeared in the initial Web of Science search. For example, Hutchings (1991) while clearly being, by our definition, a GE-EE model did not appear in the results of the final literature search as much of the terminology of GE-EE modelling (e.g. eco-genetic, demogenetic, individual-based model) had not entered the vernacular of ecology and evolutionary biology at the time of the study's publication. This is a common feature of many of the older studies included in this review. Additional studies were suggested by those with expert knowledge (Daniel Ayllón, pers. comm., Thomas E. Reed, pers. obs.). The number of papers returned by the Web of Science search and through the aforementioned process of secondary reading was 51 and 40, respectively.

Studies had their titles, abstracts, and methods scanned to determine whether they applied a GE-EE model to some aspect of fisheries science. The following information was extracted from each study: taxa (Family, lowest taxonomic level); focus of the study; genetic architecture (Quantitative genetic, Explicit loci); migration strategy (Table 1) and trait type (Table 2). Furthermore, studies were categorised under eight headings (Table 2). Studies that could be placed in more than one category were also grouped under an Overlap heading, with a breakdown of the other categories under which they were placed. Trait type definitions as well as definitions and justifications for category headings can be found in Table 2.

The percentage representation of each taxa, taxonomic family, genetic architecture, trait type, migration strategy, prediction type, and category was calculated. The refined Web of Science results and a full table of reviewed studies can be found in the Supplementary Material (Text S2, Table S1). All percentages were calculated in R (R Core Team 2021).

Table 1: Definitions of migration strategies expressed by taxa from the 91 reviewed GE-EE modelling studies.

Strategy[*]	**Definition**
Anadromous	Adults spawn in freshwater (lake or river), juveniles hatch and rear for some period (weeks to years) in the freshwater environment, juveniles then migrate to the ocean for some portion (months to years) of their lives, fish mature when at sea and undertake a migration back to freshwater so as to spawn and complete the lifecycle.
Fluvial potamodromous	The entire lifecycle takes place within rivers with any migration being between river stems in a catchment.
Lacustrine-adfluvial	Adults spawn in a river, juveniles hatch and rear for some period (usually weeks to months) in the river, juveniles then migrate to a lake for some portion (months to years) of their lives, fish mature in the lake and undertake a migration back to riverine habitat so as to spawn and complete the lifecycle.
Oceanodromous	The entire lifecycle takes place in the ocean.
Amphidromous	Both adult and juvenile fish move between freshwater and saline environments at various points throughout their lifecycle.
Resident	The entire lifecycle takes place within a single river or lake.

[*] Some taxa such as Yellowstone cutthroat trout consist of individuals from the same population that display different migratory strategies within a catchment i.e. fluvial potamodromous and lacustrine-adfluvial. In such cases, both migratory strategies were recorded. If a given taxon was mentioned but no migratory strategy explicitly stated within the text of the study, then the strategy of that taxon was taken from Fishbase.se. If neither a taxon nor a migratory strategy were mentioned, then the migratory strategy was recorded as “NA”.

Table 2: Definitions of trait types allowed to evolve, and definitions and justifications for categories into which each of the 91 reviewed GE-EE modelling studies was grouped.

Trait type	**Definition**
Behavioural	Traits characterised by a response to stimuli such as colour preference in a mate, preferred thermal conditions, group size preference
Morphological	Traits such as gross body size, secondary sexual characteristics
Physiological	Traits such as metabolic rate, energy storage capacity
Life history	Age- or size-at-maturity, asymptotic length, and threshold traits such as migration tactic, age/size at sex change in sequential hermaphrodites
Generic	Traits where the explicit purpose of the trait is not stated but the trait is assumed to affect some aspect of survival/reproductive rate. Often designated by the letter '*z*'
Phenotype-free	Studies where no phenotypic traits were considered explicitly, and the focus was rather on evolving genetic characteristics, e.g. some haplotypic feature of the genome such as allele frequency or sex karyotype
Categories	Studies were classified under eight categories: Fisheries-induced evolution, Alien species, Captive-wild interactions, Divergence/Niche evolution, Climate change, Barriers, Movement ecology, and Miscellaneous. When studies could be grouped into more than one category, they were additionally categorised under an Overlap heading. We acknowledge that the classification of a study into a given category carries with it a degree of subjectivity which could generate disagreement between individual scientists. Thus, our categories should be viewed only as a useful guide and not as the 'last word' on the topic .
Fisheries-induced evolution	Studies where a fishing-generated selection pressure or related ecological change leads to the evolution of a trait/gene frequency in a population
Alien species	Studies where the eco-evolutionary impact of alien species on a native species/ecosystem is assessed, or where the extirpation of an alien species is considered
Captive-wild interactions	Studies where the release and potential introgression of captively-reared fish (be it from a farm or hatchery) leads to the evolution of a trait/gene frequency in a population
Divergence/Niche evolution	Studies that explore the eco-evolutionary conditions that either influence ecological/evolutionary divergence, speciation events, or the degree of adaptation to a particular set of conditions that a population might display
Climate change	Studies that explicitly examine the effects of changing climatic regimes on the evolution of some trait/gene frequency in a population
Miscellaneous	Studies that could not logically be classified into any of the other seven categories
Barriers	Studies that examine the eco-evolutionary effects of the addition or removal of a physical barrier
Movement ecology	Studies that explore the evolution of some movement-related trait (e.g. facultative anadromy)

4.6 Results of synthesis and interpretation

(a) Taxonomic breadth and research focus

41 taxa were identified across 91 studies (Figure 2a). The most common taxa studied were *S. salar* and Atlantic cod, *Gadus morhua* L. 1758 (*n* =13, 14.3% for both; Figure 2a), while 23 taxa featured only once (25.3% in total). The most common taxonomic family was the Salmonidae (*n* = 40, 44.0%) with the next most common being the Gadidae (*n* = 13, 14.3%). Nine families were recorded only once (9.9% in total; Figure 2a). There were seven non-specific models (i.e. that apply in theory to any taxa), accounting for 7.7% of all studies. 40 studies were categorised under Fisheries-induced evolution (44.0%), with Captive-wild interactions being the next most common (*n* = 15, 16.5%). Divergence/Niche evolution and Alien species accounted for 14 studies (15.4%) and 13 studies (14.3%) respectively, with the remaining studies grouping under Climate change (*n* = 8, 8.8%), Miscellaneous (*n* = 4, 4.4%), Barriers (*n* = 3, 3.3%), and Movement ecology (*n* = 2, 2.2%). There were eight incidences of overlap between categories (two between Alien species and Divergence/Niche evolution; two between Fisheries-induced evolution and Climate change; and one each between Captive-wild interactions and Barriers, Alien species and Captive-wild interactions, Fisheries-induced evolution and Alien species, and Movement ecology and Fisheries-induced evolution (Figure 2b).

The standout observation from the synthesis of taxonomic breadth and research focus is that the majority of studies examined salmonid taxa and questions in fisheries-induced evolution (Figure 2a,b). There are likely myriad reasons as to why salmonids feature so prominently. These range from the less tangible (e.g. cultural significance, individual researcher interest, ease of study), to more easily quantified rationale such as, *inter alia*, the sensitivity of salmonid populations to fishing, hatcheries, and climate and, thus, their applicability to investigating environmental change. The interest in fisheries-induced evolution likely stems from the collapse of many fish stocks in the 20th century and a desire to better understand how fisheries-induced evolution might affect stock recovery (Eikeset et al. 2016; Kuparinen and Hutchings 2012, 2014; Kuparinen et al. 2014a,b; Mollet et al. 2016), and fishery yields (Gobin et al. 2018). However, this research effort must be put into context given Hutchings and Kuparinen (2020) who, reviewing empirical and modelling studies, found little evidence for fisheries-induced evolution affecting stock recovery, with background mortality and overfishing being of greater importance. In light of this, we propose that future GE-EE modelling efforts should focus on research topics where there is more substantial evidence for eco-evolutionary impacts on fish i.e. aquaculture escapes, alien species, climate change. To illustrate, consider that captive-wild interactions was the second-most common categorisation after fisheries-induced evolution, consisting of 15 studies of which seven had *S. salar* as a focal taxon. Given the now substantial empirical evidence (Araki et al. 2007a, 2009; Berejikian et al. 2009; Bolstad et al. 2017; Karlsson et al. 2016; Koch and Narum 2021; McGinnity et al. 1997, 2003; O'Sullivan et al. 2020; Skaala et al. 2012,2019; Sylvester et al. 2019; Thériault et al. 2011) for the negative effects of captive-wild interactions on fish populations, we suggest that more GE-EE modelling of this topic is justifiable based on a need to better understand how to safeguard wild fishes whilst safely expanding global aquaculture (Bradbury et al. 2020).

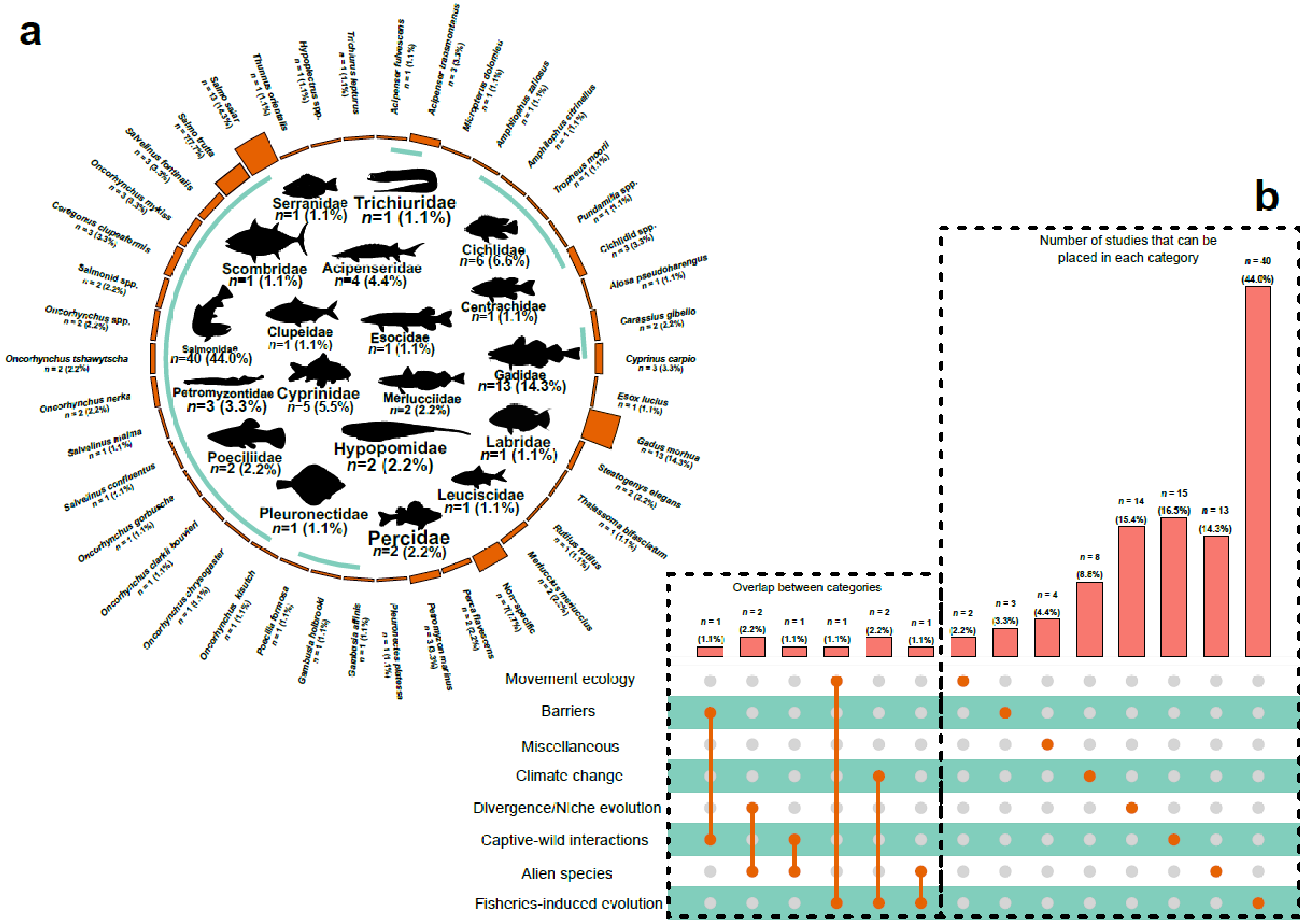
Only 26 studies (28.2%) were categorised under either alien species, climate change, barriers, or movement ecology (Figure 2b). This relatively small percentage was surprising given recently increased awareness of alien species, anthropogenically-mediated climate change, the impact of barriers on riverine fish populations, and the supposition that many fish populations will need to evolve different movement strategies in order to cope with climate change. Of the 13 alien species studies, five examined the effects of invasive cyprinines (Common carp, *Cyrpinus carpio* L. 1758 - McCormick et al. 2021; Mintram et al. 2021; Thresher et al. 2014: Prussian carp, *Carassius gibelio*, Bloch 1782 – Barbuti et al. 2011, 2012). This prevalence can be explained by the negative effects cyprinines have on recipient ecosystems (*C. carpio* digs up vegetation, *C. gibelio* is a sperm parasite on various taxa) which is further reflected in the focus of these studies being on control/extirpation of introduced carps. The control/extirpation theme is found across many of the other studies in the alien species category (effect of Sea lamprey, *Petromyzon marinus* L. 1758, on commercial fisheries – Christie et al. 2019; Thresher et al. 2019; Dunlop et al. 2021: Trojan Y chromosomes to control Brook trout, *Salvelinus fontinalis*, Mitchill 1814 – Day et al. 2020, and two *Gambusia*, Poey 1854, species - McNair Senior et al. 2013). There has been a near continuous increase over the past 200 years in the rate of species introductions, many of which can become invasive in their new environment (Seebens et al. 2017), with the problem likely escalating as the volume of international travel and trade increases.

Of the 91 studies, only eight explored the eco-evolutionary consequences of climate change, such as the effects of increased water temperature and changes in flow rate (Ayllón et al. 2016, 2019b, 2021; Nathan et al. 2019; Piou and Prévost 2013; Piou et al. 2015; Reed et al. 2011). A noteworthy study in this category is that of Vincenzi (2014) who explicitly modelled the eco-evolutionary consequences of highly stochastic, extreme weather events on freshwater fishes such as deluge-induced floods and landslides. Despite the prediction that such phenomena will increase in frequency due to climate change (Prein et al. 2017), this was the only study to explore such high energy events.

A small number of GE-EE models explicitly considered the eco-evolutionary effects of barriers (Jager 2001; Jager et al. 2001, Frank and Baret 2013) and movement ecology (Kane et al. *Submitted.*; Thériault et al. 2008). Given the vast number of barriers (>1,000,000 in Europe, Belletti et al. 2020) and other factors (e.g. parasitism, Volsett 2019; Finstad et al. 2021) that alter fish movement, we believe further GE-EE modelling of these topics is required to better understand how to rehabilitate adversely affected populations and stocks.

The 14 studies in the Divergence/Niche evolution category and the four studies in the Miscellaneous category typically deal with more esoteric questions than the other categories (but see Barbuti et al. 2012 for an applied perspective). Examples include sexual selection (Arnegard and Kondrashov 2004; Kawata et al. 2007; Matsumoto et al. 2014; Puebla et al. 2012), how speciation is affected by landscape/environmental change (Aguilée et al. 2013; Cooke et al. 2014; Beheregary et al. 2015), to the ecology and evolution of sex changes (Hurley et al. 2004; Rogers and Koch 2011), and the maintenance of an all-female taxon of sperm parasites (Kokko and Heubel 2011).

Figure 2 (Overleaf): (a) The percentage representation and number of each taxa and family across the 91 reviewed GE-EE modelling studies. Bar heights correspond to the percentage share of each taxa. Internal turquoise lines span taxa belonging to the same family and are shown in order to highlight the number of studies exploring questions related to salmonids. See the Extended Acknowledgements in the Supplementary Materials for sources of fish silhouettes; (b) the percentage representation and number of GE-EE modelling studies in each category, as well as the percentage representation and number of studies that displayed overlap between categories. Overlap between categories represented using vertical orange bars. For example, 40 studies in total modelled some aspect of fisheries-induced evolution. Of these 40 studies, one modelled the effects of fisheries-induced evolution and an alien species, two modelled the effects of fisheries-induced evolution and climate change, and one modelled the effects of fisheries-induced evolution and movement ecology. See Text S3 of Supplementary Materials for details of R packages used in making of figures and for acknowledgement of those who made the fish silhouettes or took the photographs used to make the silhouettes.


a
Salmo salar n = 13 (14.3%)
Thunnus orientalis n = 1 (1.1%)
Hypoplectrus spp. n = 1 (1.1%)
Trichiurus lepturus n = 1 (1.1%)
Acipenser fulvescens n = 1 (1.1%)
Acipenser transmontanus n = 3 (3.3%)
Micropterus dolomieu n = 1 (1.1%)
Amphilophus zaliosus n = 1 (1.1%)
Amphilophus citrinellus n = 1 (1.1%)
Tropheus moorii n = 1 (1.1%)
Pundamilia spp. n = 1 (1.1%)
Cichlidid spp. n = 3 (3.3%)
Alosa pseudoharengus n = 1 (1.1%)
Carassius gibelio n = 2 (2.2%)
Cyprinus carpio n = 3 (3.3%)
Esox lucius n = 1 (1.1%)
Gadus morhua n = 13 (14.3%)
Steatogenys elegans n = 2 (2.2%)
Thalassoma bifasciatum n = 1 (1.1%)
Rutilus rutilus n = 1 (1.1%)
Merluccius merluccius n = 2 (2.2%)
Non-specific n = 7 (7.7%)
Perca flavescens n = 2 (2.2%)
Petromyzon marinus n = 3 (3.3%)
Pleuronectes platessa n = 1 (1.1%)
Gambusia affinis n = 1 (1.1%)
Gambusia holbrooki n = 1 (1.1%)
Poecilia formosa n = 1 (1.1%)
Oncorhynchus kisutch n = 1 (1.1%)
Oncorhynchus chrysogaster n = 1 (1.1%)
Oncorhynchus clarkii bouvieri n = 1 (1.1%)
Oncorhynchus gorbuscha n = 1 (1.1%)
Salvelinus confluentus n = 1 (1.1%)
Salvelinus malma n = 1 (1.1%)
Oncorhynchus nerka n = 2 (2.2%)
Oncorhynchus tshawytscha n = 2 (2.2%)
Oncorhynchus spp. n = 2 (2.2%)
Salmonid spp. n = 2 (2.2%)
Coregonus clupeaformis n = 3 (3.3%)
Oncorhynchus mykiss n = 3 (3.3%)
Salvelinus fontinalis n = 3 (3.3%)
Salmo trutta n = 7 (7.7%)
Serranidae n=1 (1.1%)
Trichiuridae n=1 (1.1%)
Cichlidae n=6 (6.6%)
Scombridae n=1 (1.1%)
Acipenseridae n=4 (4.4%)
Centrachidae n=1 (1.1%)
Salmonidae n=40 (44.0%)
Clupeidae n=1 (1.1%)
Esocidae n=1 (1.1%)
Gadidae n=13 (14.3%)
Petromyzontidae n=3 (3.3%)
Cyprinidae n=5 (5.5%)
Merlucciidae n=2 (2.2%)
Poeciliidae n=2 (2.2%)
Hypopomidae n=2 (2.2%)
Labridae n=1 (1.1%)
Leuciscidae n=1 (1.1%)
Pleuronectidae n=1 (1.1%)
Percidae n=2 (2.2%)
b
Overlap between categories
Number of studies that can be placed in each category
n = 1 (1.1%)
n = 2 (2.2%)
n = 1 (1.1%)
n = 1 (1.1%)
n = 2 (2.2%)
n = 1 (1.1%)
n = 2 (2.2%)
n = 3 (3.3%)
n = 4 (4.4%)
n = 8 (8.8%)
n = 14 (15.4%)
n = 15 (16.5%)
n = 13 (14.3%)
n = 40 (44.0%)
Movement ecology
Barriers
Miscellaneous
Climate change
Divergence/Niche evolution
Captive-wild interactions
Alien species
Fisheries-induced evolution

(b) Evolving traits and migration strategies

54 studies tracked the evolution of life history traits (59.3%), 14 tracked genetic variables only (phenotype-free, 15.4%), 13 tracked generic traits (14.3%), nine tracked morphological traits (9.9%), eight tracked behavioural traits (8.8%), and five tracked physiological traits (5.5%). See Figure 3a. This focus on life history traits related to maturation schedule and reproduction likely reflects the fact that such traits tend to display a greater effect on fitness or fitness components (e.g. fecundity, survival) compared to 'lower-level' physiological, behavioural, or gross morphological traits.

31 modelled taxa were Resident (34.1%), 25 were anadromous (27.5%), 16 were oceanodromous (17.6%), 15 were fluvial potamodromous (16.5%), four were lacustrine-adfluvial (4.4%), and one was amphidromous (1.1%). Nine studies could not be assigned a migration strategy (9.9%). See Figure 3b.

(c) Genetic architecture

56 studies employed an explicit loci genetic architecture (61.5%), 34 employed quantitative genetics (37.4%), while one study (Frank and Baret 2013) combined quantitative genetics and explicit loci (12 neutral biallelic loci) to model the inheritance of length and to track genetic diversity, respectively. See Figure 3c. The high percentage of GE-EE models employing explicit loci architectures is likely due (as mentioned in Section 3.2) to them being more flexible in terms of genetic architecture, whilst also allowing changes in genetic variation to emerge "naturally" as selection and demographic stochasticity play out, rather than being forced by arbitrary rules.

The anticipatory predictions generated by GE-EE models were considerably influenced by the inclusion of large-effect loci into their genetic architectures. The results of Kuparinen and Hutchings (2017,2019) and Oomen et al. (2020) demonstrate how the precision of models decreases when such loci are included, resulting in a greater range of potential outcomes. Therefore, studies that assume, by default, that evolvable traits display polygenic inheritance may lead to predictions being interpreted with an unrealistic level of confidence. Erosion of genetic variation can also occur unrealistically slowly in polygenic models, which affects adaptation rates, predictability, and population viability (Kardos and Luikart 2021). Accounting for large-effect loci and other chromosomal structures that disproportionately influence phenotype (collectively known as 'supergenes' [Thompson and Jiggins 2014]) in the genetic architectures of GE-EE models should become standard practise as the number of polymorphisms in fishes known to be controlled by large-effect loci/supergenes increases (e.g. Miller et al. 2012; Pearse et al. 2014; Barson et al. 2015; Sodeland et al. 2016; Barth et al. 2017; Berg et al. 2017; Leitwein et al. 2017; Micheletti et al. 2018; Sinclair-Waters et al. 2018). Beyond the academic, this has obvious implications for when conservation or fisheries policy is based on anticipatory model predictions - possible future outcomes cannot be planned for nor mitigated against if they are not anticipated.

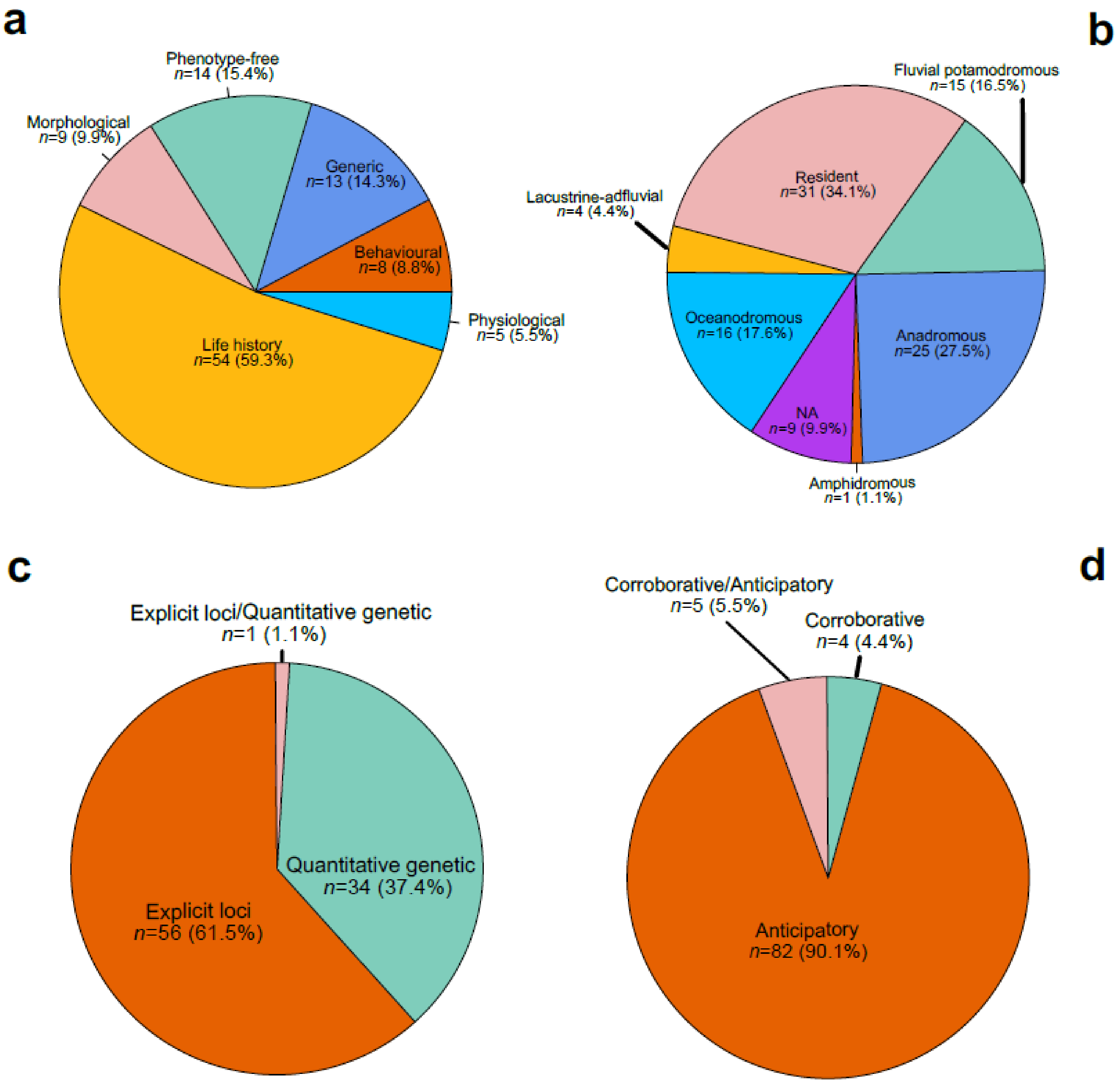


Figure 3: (a) Percentage representation and number of evolving trait types across the 91 reviewed studies; (b) percentage representation and number of each migration strategy across the 91 reviewed studies; (c) percentage representation and number of each genetic architecture across the 91 reviewed studies; (d) percentage representation and number of studies where GE-EE models made either anticipatory or corroborative predictions.

(d) Nature of predictions

82 studies made anticipatory predictions (90.1%), four made corroboratory predictions (4.4%), and five made both anticipatory and corroboratory predictions (5.5%). See Figure 3d. This disparity in prediction types is striking considering the role corroborative studies have in helping researchers devise sound theory and formulate generalizations regarding system dynamics. For example, Mollet et al. (2016), assuming specific demographic and fishing processes, were able to recreate (corroborate) the observed trends in biomass, abundance, and adult population proportion for European plaice, *Pleuronectes platessa* L. 1758. This gave the authors reasonable confidence that the anticipatory predictions of future *P. platessa* demographics also produced by their model could arise, assuming the underlying mechanisms regulating *P. platessa* populations were unchanging. Despite the caveats associated with corroborative modelling (Section 3.1), a philosophy of careful study design and conservative interpretation such as that by Mollet et al. (2016) could greatly benefit the field of fisheries-related GE-EE modelling and provide a more nuanced understanding of how fish populations and stocks responded to changes in the past and, thus, how they might respond to changes in the future.

Given the prevalence of models that make anticipatory predictions, we believe it necessary to stress two overlooked and rarely commented-on aspects of anticipatory modelling. As stated in Section 3.1, anticipatory predictions assume that present system mechanisms can be projected into the future (i.e. are constant over time [Schindler and Hilborn 2015]). Therefore, assumed mechanisms or parameters inputted into anticipatory GE-EE models should be meticulously scrutinised and any inferences or applications arising from such predictions should consider the potential sensitivity of model outputs to changes in model inputs. Another overlooked aspect of anticipatory modelling relevant to climate change studies is that the climatic scenarios that modelled fish are subjected to are themselves anticipatory predictions (Jenouvrier and Visser 2011). These climatic model predictions come with all the same caveats and inherent uncertainties as the predictions from fisheries GE-EE models. This can be generalised to any GE-EE model that uses future-orientated predictions as input. Therefore, GE-EE models using future-orientated predictions to anticipate future fish population dynamics contain two separate, but potentially multiplicative, sources of uncertainty – the (non-) stationarity of system mechanisms and the use of predictions to make further predictions.

4.7 Future research directions

This review of the literature involving GE-EE models in fisheries science is novel in its overarching scope across multiple categories, with previous reviews being limited to a single research topic (e.g. fisheries-induced evolution, Kuparinen and Merilä 2007; Audzijonyte et al. 2013; Perälä and Kuparinen 2020). A synthesis of the field is timely given the rapid increase in the number of GE-EE modelling studies that have been published in the past decade (Figure 1, see trend analysis in Text S1). Overall, the field is rich in studies but dominated by models exploring fisheries-induced evolution and by studies on salmonids. Models exploring climate change, alien species, and barriers to fish movement were not as common as expected *a priori*. The realisation that genetic architectures involving large-effect loci or supergenes lead to less precise model predictions should give pause with regard to how the inheritance component of GE-EE models is designed, as well as how much confidence can be put in previously published studies that modelled the evolution of traits now known to be controlled by large-effect loci/supergenes. This should not be seen as a criticism of GE-EE modelling in fisheries science but as a call for increased research on understudied topics and greater exploration of how different population mechanisms and inheritance structures affect model output. Coupled with the ever-accelerating pace of computation speed, we believe the field to be well placed to explore an increasingly rich range of modelling scenarios involving hitherto little-considered mechanisms. To help guide future research efforts, we proffer four suggestions that we believe will help to advance the field:

(1) broaden the range of taxa studied and research topics explored. We are not suggesting that no future GE-EE modelling studies investigate fisheries-induced evolution or salmonid biology. Indeed, as the review of Hutchings and Kuparinen (2020) makes clear, there is still much we do not understand concerning fisheries-induced evolution. 'Casting a broader net' and exploring other highly pertinent issues such as climate change and the effects of alien species across a variety of taxa will allow for generalisations and commonalities on eco-evolutionary dynamics in finfish populations to be made.

(2) integrate across various spheres of research simultaneously (e.g. fisheries-induced evolution *and* climate change, captive-wild interactions *and* climate change; see McGinnity et al. 2009) as this will allow for GE-EE models to contribute insights relevant to a broader range of interlinked policy issues or act as flexible tools that managers might be guided by when trying to determine the best course of action in the face of multiple interacting stressors. Our review found very few studies that explicitly modelled the effects of more than one stressor on a population/stock (Figure 2b). The development of more comprehensive 'Overlap' GE-EE models will likely be facilitated by increased computation speeds and the implementation of more efficient modelling techniques (e.g. Hamiltonian mechanics [Stan Development Team 2021]).

(3) develop more corroborative models to facilitate the explicit testing of theory. The large number of published models that make anticipatory predictions is likely a consequence of a desire to understand how fish populations *might* respond in the future to over-fishing, aquaculture escape events, climate change, and alien species. However, there is also a need to understand what *does* happen in current populations. This will foster increased mechanistic understanding of how fish populations respond in eco-evolutionary terms to anthropogenic pressures and allow for more targeted prevention/mitigation strategies to be implemented.

(4) more systematically explore the various sources of uncertainty that models contain and be explicit about assumptions and limitations of a given modelling

approach. The use of models in biology helps to focus thought and provides useful abstractions of complicated systems and processes. However, models are still only abstractions based upon educated assumptions about how the world works. The increased variability of anticipatory predictions from models with large-effect loci/supergenes in their genetic architectures relative to models assuming polygenic inheritance highlights the need for sensitivity testing of model parameters to be expanded to include more fundamental model processes such as inheritance mechanisms. Additionally, the potentially multiplicative uncertainty structure found in model predictions (see Section 4.2.4) must be explicitly acknowledged and, if possible, explored. Complete acknowledgement of sources of uncertainty in such models, sensitivity testing to explore the effects of such uncertainty on prediction, coupled with cautious inference will allow for model output to be safely interpreted. This will ensure that if model results are used to influence policy, then those making policy will have available to them knowledge of the strengths and weaknesses of a given set of predictions.

4.8 Supplementary Material

Text S1: Trend analysis

To explore any temporal trend in the number of studies utilizing GE-EE models, we collated the number of publications per year and performed a trend analysis using the *trend* R package (Pohlert 2020; R Core Team 2021). Initial exploration of the data demonstrated that the number of studies per year displayed a positively skewed distribution. As such, we performed a non-parametric Mann-Kendall Test to determine if there was either an increasing or a decreasing monotonic trend across years in the number of published studies. We detected a positive trend ($S = 125$, $z = 3.56$, $n = 22$, $p < 0.001$), with an average slope of 0.27 ($Sen's\ slope = 0.27$ 95%CI [0.14-0.43], $n = 22$, $p < 0.001$). Finally, we used the Pettitt Test to determine if the trend displayed a 'change point', that is, a datum in the time series where data either side of this point displayed different distributions. Determining this point helps to identify where in a time series a trend, if any, begins to manifest. Identifying the change point is of use when considering potential causal drivers behind a trend. The Pettitt Test found evidence for a change point at the eleventh time series datum, corresponding to the year 2010 in the time series ($U^* = 117, p < 0.01$).

Text S2: Refined Web of Science search parameters

On the 02/04/2021

Results: 1,101

(from All Databases)

You searched for: TOPIC: ((eco-genetic OR eco-evolutionary OR demo-genetic OR "seascape genetics" OR "landscape genetics" OR individual-based OR genetically-explicit) AND (model OR simulation OR framework) AND fish*)

Refined by: [excluding] RESEARCH AREAS: (NUTRITION DIETETICS OR BIOCHEMISTRY MOLECULAR BIOLOGY OR AGRICULTURE OR ENTOMOLOGY OR ENGINEERING OR PSYCHOLOGY OR PLANT SCIENCES OR ENDOCRINOLOGY METABOLISM OR GEOLOGY OR CELL BIOLOGY OR CHEMISTRY OR ANTHROPOLOGY OR PHARMACOLOGY PHARMACY OR FORESTRY OR GEOCHEMISTRY GEOPHYSICS OR INFORMATION SCIENCE LIBRARY SCIENCE OR SPORT SCIENCES OR AUTOMATION CONTROL SYSTEMS OR ENERGY FUELS OR GOVERNMENT LAW OR INSTRUMENTS INSTRUMENTATION OR PALEONTOLOGY OR GERIATRICS GERONTOLOGY OR MECHANICS OR BIOTECHNOLOGY APPLIED MICROBIOLOGY OR GENERAL INTERNAL MEDICINE OR ROBOTICS OR MICROBIOLOGY OR DERMATOLOGY OR HISTORY OR OPERATIONS RESEARCH MANAGEMENT SCIENCE OR RADIOLOGY NUCLEAR MEDICINE MEDICAL IMAGING OR GASTROENTEROLOGY HEPATOLOGY OR HEALTH CARE SCIENCES SERVICES OR HISTORY PHILOSOPHY OF SCIENCE OR MEDICAL INFORMATICS OR OPHTHALMOLOGY OR RESPIRATORY SYSTEM OR

IMAGING SCIENCE PHOTOGRAPHIC TECHNOLOGY OR INTERNATIONAL RELATIONS OR ARTS HUMANITIES OTHER TOPICS OR MATERIALS SCIENCE OR MEDICAL LABORATORY TECHNOLOGY OR NUCLEAR SCIENCE TECHNOLOGY OR ONCOLOGY OR PEDIATRICS OR PHILOSOPHY OR RESEARCH EXPERIMENTAL MEDICINE OR ACOUSTICS OR ANESTHESIOLOGY OR CONSTRUCTION BUILDING TECHNOLOGY OR CRIMINOLOGY PENOLOGY OR EDUCATION EDUCATIONAL RESEARCH OR HEMATOLOGY OR MICROSCOPY OR MINING MINERAL PROCESSING OR ORTHOPEDICS OR OTORHINOLARYNGOLOGY OR RHEUMATOLOGY OR SPECTROSCOPY OR THERMODYNAMICS)

Timespan: All years. Databases: WOS, BCI, BIOSIS, CCC, DRCI, DIIDW, KJD, MEDLINE, RSCI, SCIELO, ZOOREC.

Search language=Auto

NOTICE: Your organization does not receive data updates to the following database(s): BIOSIS Previews.

Text S3: Acknowledgements

S3.1 Silhouette and image credits

All silhouettes for Figure 2a downloaded from Phylopic.org, except for the Serranidae, Hypopomidae, and the Trichiuridae. Use of a silhouette or image does not represent endorsement of this work by those credited with the silhouette or image. Credit for the silhouettes and images are as follows: Acipenseridae – Duane Raver/USFWS; Centrachidae - Sherman Foote Denton (illustration, 1897) and Timothy J. Bartley (silhouette)(Creative Commons Attribution-ShareAlike 3.0 Unported license); Cichlidae – Milton Tan (Creative Commons Attribution-NonCommercial-ShareAlike 3.0 Unported license); Clupeidae – Felix Vaux; Cyprinidae – Carlos Cano-Barbacil; Esocidae - Timothy Knepp (vectorized by T. Michael Keesey); Gadidae – Milton Tan; Labridae – Kent Sorgon (Creative

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S3.2 R package citations

1. Wickham H, Hester J. (2020). readr: Read Rectangular Text Data. R package version 1.4.0. https://CRAN.R-project.org/package=readr

2. Wickham H. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, 2016. https://ggplot2.tidyverse.org

3. Wickham H, Seidel D. (2020). scales: Scale Functions for Visualization. R package version 1.1.1. https://CRAN.R-project.org/package=scales

4. Wickham H, François R, Henry L, Müller K. (2021). dplyr: A Grammar of Data Manipulation. R package version 1.0.6.

https://CRAN.R-project.org/package=dplyr

5. Pohlert T. (2020). trend: Non-Parametric Trend Tests and Change-Point Detection. R package version. 1.1.4. https://CRAN.R-project.org/package=trend
6. Gehlenborg N. (2019). UpSetR: A More Scalable Alternative to Venn and Euler Diagrams for Visualizing Intersecting Sets. R package version 1.4.0. https://CRAN.R-project.org/package=UpSetR

Table S1: Citations for the 91 reviewed genetically-explicit eco-evolutionary modelling studies. Where DOIs are not available, a link to the journal or Google Scholar is provided.

Publication	Category	Citation
Ayllón et al. 2018	Fisheries-induced evolution	Eco-evolutionary responses to recreational fishing under different harvest regulations. *Ecology and Evolution*, 8, 9600–9613. https://doi.org/10.1002/ece3.4270
Ayllón et al. 2019a	Fisheries-induced evolution	Optimal harvest regulations under conflicting tradeoffs between conservation and recreational fishery objectives. *Fisheries Research*, 216, 47–58. https://doi.org/10.1016/j.fishres.2019.03.021
Bromaghin et al. 2011	Fisheries-induced evolution	A model of chinook salmon population dynamics incorporating size-selective exploitation and inheritance of polygenic correlated traits. *Natural Resource Modeling*, 24, 1–47. https://doi.org/10.1111/j.1939-7445.2010.00077.x
de Roos et al. 2006	Fisheries-induced evolution	Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1873–1880. https://doi.org/10.1098/rspb.2006.3518
Dercole and Della Rossa 2017	Fisheries-induced evolution	A deterministic eco-genetic model for the short-term evolution of exploited fish stocks. *Ecological Modelling*, 343, 80–100. https://doi.org/10.1016/j.ecolmodel.2016.10.016
Dunlop et al. 2007	Fisheries-induced evolution	Demographic and evolutionary consequences of selective mortality: predictions from an eco-genetic model for smallmouth bass. *Transactions of the American Fisheries Society*, 136, 749–765. https://doi.org/10.1577/T06-126.1
Dunlop et al. 2009	Fisheries-induced evolution	Eco-genetic modeling of contemporary life-history evolution. *Ecological Applications*, 19, 1815–1834. https://doi.org/10.1890/08-1404.1
Dunlop et al. 2015	Fisheries-induced evolution	From genes to populations: How fisheries-induced evolution alters stock productivity. *Ecological Applications*, 25, 1860–1868. https://doi.org/10.1890/14-1862.1
Eikeset et al. 2013	Fisheries-induced evolution	Economic repercussions of fisheries-induced evolution. *Proceedings of the National Academy of Sciences*, 110, 12259. https://doi.org/10.1073/pnas.1212593110
Eikeset et al. 2016	Fisheries-induced evolution	Roles of density-dependent growth and life history evolution in accounting for fisheries-induced trait changes. *Proceedings of the National Academy of Sciences*, 113, 15030. https://doi.org/10.1073/pnas.1525749113
Eldridge et al. 2010	Fisheries-induced evolution	Simulating fishery-induced evolution in chinook salmon: The role of gear, location, and genetic correlation among traits. *Ecological Applications*, 20, 1936–1948. https://www.jstor.org/stable/25741359.
Enberg et al. 2009	Fisheries-induced evolution	Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evolutionary Applications*, 2, 394–414. https://doi.org/10.1111/j.1752-4571.2009.00077.x
Enberg et al. 2010	Fisheries-induced evolution	Fishing-induced evolution and changing reproductive ecology of fish: The evolution of steepness. *Canadian Journal of Fisheries and Aquatic Sciences*, 67, 1708–1719. https://doi.org/10.1139/F10-090
Gobin et al. 2021	Fisheries-induced evolution	Maturation reaction norm evolution under varying conditions of eco-evolutionary change. *Canadian Journal of Fisheries and Aquatic Sciences*. Just In. https://doi.org/10.1139/cjfas-2020-0274
Jusufovski and Kuparinen 2014	Fisheries-induced evolution	Estimating the relative fitness of escaped farmed salmon offspring in the wild and modelling the consequences of invasion for wild populations. *Evolutionary Ecology Research*, 12, 705–717. http://www.evolutionary-ecology.com/abstracts/v16/n02/2897.html
Jusufovski and Kuparinen 2020	Fisheries-induced evolution	Exploring individual and population eco-evolutionary feedbacks under the coupled effects of fishing and predation. *Fisheries Research*, 231, 105713. https://doi.org/10.1016/j.fishres.2020.105713
Kuparinen and Hutchings 2012	Fisheries-induced evolution	Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proceedings of the Royal Society B: Biological Sciences*, 279, 2571–2579. https://doi.org/10.1098/rspb.2012.0120
Kuparinen and Hutchings 2014	Fisheries-induced evolution	Increased natural mortality at low abundance can generate an Allee effect in a marine fish. *Royal Society Open Science*, 1, 140075. https://doi.org/10.1098/rsos.140075
Kuparinen and Hutchings 2017	Fisheries-induced evolution	Genetic architecture of age at maturity can generate divergent and disruptive harvest-induced evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160035. https://doi.org/10.1098/rstb.2016.0035
Kuparinen and Hutchings 2019	Fisheries-induced evolution	When phenotypes fail to illuminate underlying genetic processes in fish and fisheries science. *ICES Journal of Marine Science*, 76, 999–1006. https://doi.org/10.1093/icesjms/fsz002

Table S1 (cont.)

Kuparinen and Uusi-Heikkilä 2020	Fisheries-induced evolution	Atlantic cod recovery from the Allee effect zone: Contrasting ecological and evolutionary rescue. *Fish and Fisheries*, 21, 916–926. https://doi.org/10.1111/faf.12470
Kuparinen et al. 2014a	Fisheries-induced evolution	Allee effect and the uncertainty of population recovery. *Conservation Biology*, 28, 790–798. https://doi.org/10.1111/cobi.12216
Kuparinen et al. 2014b	Fisheries-induced evolution	Fundamental population–productivity relationships can be modified through density-dependent feedbacks of life-history evolution. *Evolutionary Applications*, 7, 1218–1225. https://doi.org/10.1111/eva.12217
Kuparinen et al. 2016	Fisheries-induced evolution	Harvest-induced evolution and effective population size. *Evolutionary Applications*, 9, 658–672. https://doi.org/10.1111/eva.12373
Lin et al. 2017	Fisheries-induced evolution	Modeling local adaptation and gene flow in sockeye salmon. *Ecosphere*, 8, e02039. https://doi.org/10.1002/ecs2.2039
Marty et al. 2015	Fisheries-induced evolution	Fisheries-induced neutral and adaptive evolution in exploited fish populations and consequences for their adaptive potential. *Evolutionary Applications*, 8, 47–63. https://doi.org/10.1111/eva.12220
Matsumura et al. 2011	Fisheries-induced evolution	Assessing evolutionary consequences of size-selective recreational fishing on multiple life-history traits, with an application to northern pike (*Esox lucius*). *Evolutionary Ecology*, 25, 711–735. https://doi.org/10.1007/s10682-010-9444-8
Matthias et al. 2019	Fisheries-induced evolution	Evolutionary and demographic impacts of sex change rules and size-selective exploitation on sequential hermaphrodites. *ICES Journal of Marine Science*, fsz137. https://doi.org/10.1093/icesjms/fsz137
Mollet et al. 2016	Fisheries-induced evolution	Reconstructing the effects of fishing on life-history evolution in North Sea plaice *Pleuronectes platessa*. *Marine Ecology Progress Series*, 542, 195–208. 10.3354/meps11441
Okamoto et al. 2009	Fisheries-induced evolution	Mitigating fisheries-induced evolution in lacustrine brook charr (*Salvelinus fontinalis*) in southern Quebec, Canada. *Evolutionary Applications*, 2, 415–437. https://doi.org/10.1111/j.1752-4571.2009.00095.x
Oomen et al. 2020	Fisheries-induced evolution	Consequences of single-locus and tightly linked genomic architectures for evolutionary responses to environmental change. *Journal of Heredity*, 111, 319–332. https://doi.org/10.1093/jhered/esaa020
Ratner and Lande 2001	Fisheries-induced evolution	Demographic and evolutionary responses to selective harvesting in populations with discrete generations. *Ecology*, 82, 3093–3104. https://doi.org/10.1890/0012-9658(2001)082[3093:DAERTS]2.0.CO;2
Sun et al. 2015	Fisheries-induced evolution	Trawl selectivity-induced evolution effects on age structure and size-at-age of largehead hairtail (*Trichiurus lepturus*) Linnaeus, 1758 in the East China Sea, China. *Journal of Applied Ichthyology*, 31, 657–664. https://doi.org/10.1111/jai.12774
Wang and Höök 2009	Fisheries-induced evolution	Eco-genetic model to explore fishing-induced ecological and evolutionary effects on growth and maturation schedules. *Evolutionary Applications*, 2, 438–455. https://onlinelibrary.wiley.com/doi/10.1111/j.1752-4571.2009.00088.x
Wang et al. 2017	Fisheries-induced evolution	Fishing-induced changes in adult length are mediated by skipped-spawning. *Ecological Applications*, 27, 274–284. https://doi.org/10.1002/eap.1441
Wood et al. 2018	Fisheries-induced evolution	Eco-evolutionary feedbacks from non-target species influence harvest yield and sustainability. *Scientific Reports*, 8, 6389. https://doi.org/10.1038/s41598-018-24555-0
Aguilée et al. 2013	Divergence/Niche evolution	Adaptive radiation driven by the interplay of eco-evolutionary and landscape dynamics. *Evolution*, 67, 1291-1306. https://doi.org/10.1111/evo.12008
Arnegard and Kondrashov 2004	Divergence/Niche evolution	Sympatric speciation by sexual selection alone is unlikely. *Evolution*, 58, 222–237. https://doi.org/10.1111/j.0014-3820.2004.tb01640.x
Beheregaray et al. 2015	Divergence/Niche evolution	Ecological speciation in the tropics: insights from comparative genetic studies in Amazonia. *Frontiers in Genetics*, 5. https://doi.org/10.3389/fgene.2014.00477
Cooke et al. 2014	Divergence/Niche evolution	Riverscape genetics identifies replicated ecological divergence across an Amazonian ecotone. *Evolution*, 68, 1947–1960. https://doi.org/10.1111/evo.12410
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Kang and Thibert-Plante 2017	Divergence/Niche evolution	Eco-evolution in size-structured ecosystems: simulation case study of rapid morphological changes in alewife. *BMC Evolutionary Biology*, 17, 58. https://doi.org/10.1186/s12862-017-0912-4

Table S1 (cont.)

Kawata et al. 2007	Divergence/Niche evolution	A genetically explicit model of speciation by sensory drive within a continuous population in aquatic environments. *BMC Evolutionary Biology*, 7, 99. https://doi.org/10.1186/1471-2148-7-99
Matsumoto et al. 2014	Divergence/Niche evolution	Sensory drive speciation and patterns of variation at selectively neutral genes. *Evolutionary Ecology*, 28, 591–609. https://doi.org/10.1007/s10682-014-9697-8
Puebla et al. 2012	Divergence/Niche evolution	Pairing dynamics and the origin of species. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1085–1092. https://doi.org/10.1098/rspb.2011.1549
Rogers and Koch 2011	Divergence/Niche evolution	The evolution of sex-change timing under environmental uncertainty: a test by simulation. *Evolutionary Ecology Research*, 13, 387–399.
Schueller and Hayes 2011	Divergence/Niche evolution	Minimum viable population size for lake sturgeon (*Acipenser fulvescens*) using an individual-based model of demographics and genetics. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 62–73. https://doi.org/10.1139/F10-129
Yeakel et al. 2018	Divergence/Niche evolution	Eco-Evolutionary Dynamics, Density-Dependent Dispersal And Collective Behaviour: Implications For Salmon Metapopulation Robustness. *Philosophical Transactions Of The Royal Society B: Biological Sciences*, 373, 20170018. Https://Doi.Org/10.1098/Rstb.2017.0018
Baskett and Waples 2013	Captive-wild interactions	Evaluating alternative strategies for minimizing unintended fitness consequences of cultured individuals on wild populations. *Conservation Biology*, 27, 83–94. https://doi.org/10.1111/j.1523-1739.2012.01949.x
Baskett et al. 2013	Captive-wild interactions	Assessing strategies to minimize unintended fitness consequences of aquaculture on wild populations. *Evolutionary Applications*, 6, 1090–1108. https://doi.org/10.1111/eva.12089
Byrne et al. 1992	Captive-wild interactions	Modeling the response of native steelhead to hatchery supplementation programs in an Idaho river. *North American Journal of Fisheries Management*, 12, 62–78. https://doi.org/10.1577/1548-8675(1992)012<0062:MTRONS>2.3.CO;2
Bradbury et al. 2020	Captive-wild interactions	Model-based evaluation of the genetic impacts of farm-escaped Atlantic salmon on wild populations. *Aquaculture Environment Interactions*, 12, 45–59. https://doi.org/10.3354/aei00346
Castellani et al. 2015	Captive-wild interactions	IBSEM: An Individual-Based Atlantic Salmon Population Model. *PLoS ONE*, 10(9), e0138444. https://doi.org/10.1371/journal.pone.0138444
Castellani et al. 2018	Captive-wild interactions	Modeling fitness changes in wild Atlantic salmon populations faced by spawning intrusion of domesticated escapees. *Evolutionary Applications*, 11, 1010–1025. https://doi.org/10.1111/eva.12615
Ford 2002	Captive-wild interactions	Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology*, 16, 815–825. https://www.jstor.org/stable/3061228
Hutchings 1991	Captive-wild interactions	The threat of extinction to native populations experiencing spawning intrusions by cultured Atlantic salmon. *Aquaculture* 98, 119–132. https://doi.org/10.1016/0044-8486(91)90377-J
Jager 2005	Captive-wild interactions	Genetic and demographic implications of aquaculture in white sturgeon (*Acipenser transmontanus*) conservation. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 1733–1745. https://doi.org/10.1139/f05-106
Sylvester et al. 2019	Captive-wild interactions	Estimating the relative fitness of escaped farmed salmon offspring in the wild and modelling the consequences of invasion for wild populations. *Evolutionary Applications*, 12, 705–717. https://doi.org/10.1111/eva.12746
Tufto 2001	Captive-wild interactions	Effects of releasing maladapted individuals: a demographic-evolutionary model. *The American Naturalist*, 158, 331–340. https://doi.org/10.1086/321987
Willoughby and Christie 2019	Captive-wild interactions	Long-term demographic and genetic effects of releasing captive-born individuals into the wild. *Conservation Biology*, 33, 377–388. https://doi.org/10.1111/cobi.13217
Yang et al. 2019	Captive-wild interactions	Life history and temporal variability of escape events interactively determine the fitness consequences of aquaculture escapees on wild populations. *Theoretical Population Biology*, 129, 93–102. https://doi.org/10.1016/j.tpb.2018.12.006
Christie et al. 2019	Alien species	Rapid resistance to pesticide control is predicted to evolve in an invasive fish. *Scientific Reports*, 9, 18157. https://doi.org/10.1038/s41598-019-54260-5
Day et al. 2020	Alien species	Simulating effects of fitness and dispersal on the use of Trojan sex chromosomes for the management of invasive species. *Journal of Applied Ecology*, 57, 1413–1425. https://doi.org/10.1111/1365-2664.13616
Della Croce et al. 2014	Alien species	Simulating the effects of stream network topology on the spread of introgressive hybridization across fish populations. *Ecological Modelling*, 279, 68–77. https://doi.org/10.1016/j.ecolmodel.2014.02.014

Table S1 (cont.)

Dunlop et al. 2021	Alien species	Life history evolution of sea lamprey is predicted to reduce the effectiveness of pesticide control. *Journal of Great Lakes Research*, S0380133021000812. https://doi.org/10.1016/j.jglr.2021.03.021
McCormick et al. 2021	Alien species	Simulated use of YY male stocking and suppression for eradicating common carp populations. *North American Journal of Fisheries Management*, 41, 366–382. https://doi.org/10.1002/nafm.10525
McNair Senior et al. 2013	Alien species	The practicality of Trojan sex chromosomes as a biological control: an agent based model of two highly invasive *Gambusia* species. *Biological Invasions*, 15, 1765–1782. https://doi.org/10.1007/s10530-013-0407-1
Mintram et al. 2021	Alien species	Genetic variation in resistance and high fecundity impede viral biocontrol of invasive fish. *Journal of Applied Ecology*, 58, 148–157. https://doi.org/10.1111/1365-2664.13762
Thresher et al. 2014	Alien species	Sex-ratio-biasing constructs for the control of invasive lower vertebrates. *Nature Biotechnology*, 32, 424–427. https://doi.org/10.1038/nbt.2903
Thresher et al. 2019	Alien species	Evaluating active genetic options for the control of sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 76, 1186–1202. https://doi.org/10.1139/cjfas-2018-0153
Ayllón et al. 2016	Climate change	InSTREAM-Gen: Modelling eco-evolutionary dynamics of trout populations under anthropogenic environmental change. *Ecological Modelling*, 326, 36–53. https://doi.org/10.1016/j.ecolmodel.2015.07.026
Ayllón et al. 2019b	Climate change	Mechanistic simulations predict that thermal and hydrological effects of climate change on Mediterranean trout cannot be offset by adaptive behaviour, evolution, and increased food production. *Science of The Total Environment*, 693, 133648. https://doi.org/10.1016/j.scitotenv.2019.133648
Nathan et al. 2019	Climate change	A spatially-explicit, individual-based demogenetic simulation framework for evaluating hybridization dynamics. *Ecological Modelling*, 401, 40–51. https://doi.org/10.1016/j.ecolmodel.2019.03.002
Piou and Prévost 2013	Climate change	Contrasting effects of climate change in continental vs. oceanic environments on population persistence and microevolution of Atlantic salmon. *Global Change Biology*, 19, 711–723. https://doi.org/10.1111/gcb.12085
Reed et al. 2011	Climate change	Time to evolve? Potential evolutionary responses of Fraser River sockeye salmon to climate change and effects on persistence. *PLoS ONE*, 6(6), e20380. https://doi.org/10.1371/journal.pone.0020380
Vincenzi 2014	Climate change	Extinction risk and eco-evolutionary dynamics in a variable environment with increasing frequency of extreme events. *Journal of The Royal Society Interface*, 11, 20140441. https://doi.org/10.1098/rsif.2014.0441
Hurley et al. 2004	Miscellaneous	A model for environmental sex reversal in fish. *Journal of Theoretical Biology*, 227, 159–165. https://doi.org/10.1016/j.jtbi.2003.10.010
Ivan and Höök 2015	Miscellaneous	Energy allocation strategies of young temperate fish: an eco-genetic modeling approach. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 1243–1258. https://doi.org/10.1139/cjfas-2014-0197
Kokko and Heubel 2011	Miscellaneous	Prudent males, group adaptation, and the tragedy of the commons. *Oikos*, 120, 641–656. https://doi.org/10.1111/j.1600-0706.2011.19544.x
Piou and Prévost 2012	Miscellaneous	A demo-genetic individual-based model for Atlantic salmon populations: model structure, parameterization and sensitivity. *Ecological Modelling*, 231, 37–52. https://doi.org/10.1016/j.ecolmodel.2012.01.025
Jager 2001	Barriers	Individual variation in life history characteristics can influence extinction risk. *Ecological Modelling*, 144, 61–76. https://doi.org/10.1016/S0304-3800(01)00362-3
Jager et al. 2001	Barriers	A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. *Environmental Biology of Fishes*, 60, 347–361. https://doi.org/10.1023/A:1011036127663
Kane et al. *Submitted*	Movement ecology	Escalating the conflict? Inter-sex genetic correlations influence adaptation to environmental change in facultatively migratory populations
Ayllón et al. 2021	Fisheries-induced evolution, Climate change	Climate change will render size-selective harvest of cold-water fish species unsustainable in Mediterranean freshwaters. *Journal of Applied Ecology*, 58, 562–575. https://doi.org/10.1111/1365-2664.13805
Barbuti et al. 2011	Divergence/Niche evolution, Alien species	Computational models for population dynamics: two case studies. *Atti Della Società Toscana Di Scienze Naturali Residente in Pisa Memorie Serie B*, 118, 103–110. https://doi.org/10.2424/ASTSN.M.2011.29

Table S1 (cont.)

Barbuti et al. 2012	Divergence/Niche evolution, Alien species	Population dynamics with a mixed type of sexual and asexual reproduction in a fluctuating environment. *BMC Evolutionary Biology*, 12, 49. https://doi.org/10.1186/1471-2148-12-49
Escalante et al. 2018	Captive-wild interactions, Alien species	The interplay of riverscape features and exotic introgression on the genetic structure of the Mexican golden trout (*Oncorhynchus chrysogaster*), a simulation approach. *Journal of Biogeography*, 45, 1500–1514. https://doi.org/10.1111/jbi.13246
Frank and Baret 2013	Captive-wild interactions, Barriers	Simulating brown trout demogenetics in a river/nursery brook system: the individual-based model DemGenTrout. *Ecological Modelling*, 248, 184–202. https://doi.org/10.1016/j.ecolmodel.2012.09.017
Gobin et al. 2018	Fisheries-induced evolution, Alien species	Ecological change alters the evolutionary response to harvest in a freshwater fish. *Ecological Applications*, 28, 2175–2186. https://doi.org/10.1002/eap.1805
Piou et al. 2015	Fisheries-induced evolution, Climate change	Modelling the interactive effects of selective fishing and environmental change on Atlantic salmon demogenetics. *Journal of Applied Ecology*, 52, 1629–1637. https://doi.org/10.1111/1365-2664.12512
Thériault et al. 2008	Fisheries-induced evolution, Movement ecology	The impact of fishing-induced mortality on the evolution of alternative life-history tactics in brook charr. *Evolutionary Applications*, 1, 409–423. https://doi.org/10.1111/j.1752-4571.2008.00022.x

Chapter 5

Interactions between soft and hard selection influence evolutionary and population dynamics in salmonine populations experiencing intrusion from non-local stock.

This chapter is in preparation for submission to the journal Evolutionary Applications and is, therefore, written in the style of that journal, except for minor stylistic changes.

Interactions between soft and hard selection influence evolutionary and population dynamics in salmonine populations experiencing intrusion from non-local stock.

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Authorship: **RJOS** and TER conceived the study. **RJOS** built the NetLogo model, ran model simulations, and created the summary output. AK provided advice with regard to NetLogo coding. **RJOS** wrote the initial draft of the paper with all co-authors contributing to subsequent drafts. Fish silhouette vectorised by RJOS from a photograph taken by Mikkel René Anderson.

5.1 Abstract

The introduction or escape of non-local individuals into the wild has a range of consequences for the genetics and demography of recipient populations. Selection against non-local genotypes can limit the rate of introgression of foreign alleles into wild populations, while purging can occur in subsequent generations if admixed individuals display lower fitness than wild-types. These processes are accompanied by a demographic cost to the wild population if selection is 'hard' i.e. selection not only influences which, but also how many, individuals survive/reproduce. However, if selection is soft (influencing only which, but not how many, individuals survive/reproduce), then the demographic penalties of introgression and purging might be minimal. Soft selection could even influence demography positively if it indirectly weakens the strength of hard selection. We developed a genetically-explicit eco-evolutionary model to explore these issues in a hypothetical salmonine population that experienced intrusion from non-local stock. Soft selection was modelled as phenotype-dependent competition amongst females for limited spawning sites where competitive ability was controlled by a single biallelic locus and local genotypes were competitively superior to non-local genotypes. Hard selection was modelled as phenotype-dependent survival during the migratory stage of the life cycle, mediated by a polygenic trait assumed to differ in mean value between local and non-local fish, the former being closer to an environmental optimum (i.e. locally adapted). The rate of purging of non-local alleles at the competitive locus was faster when soft selection was stronger, which occurred under higher population densities. By reducing the number of non-locals or their hybrid offspring that could breed in the first few generations post-intrusion, soft selection also decreased the strength of hard selection and its associated demographic cost, since the mean of the polygenic trait (for the overall admixed population) was now closer to the environmental optimum. These results imply an indirect role for soft selection in buffering populations against catastrophic declines following introgression from non-local sources. Better understanding of the ecological causes and consequences of soft and hard selection should illuminate conservation biology in general, as well as specific fisheries

management issues relating to stocking, farm escapes, and interspecific hybridisation with invasive congeners.

5.2 Introduction

Being able to understand the dynamics that mediate introgression of non-local and potentially maladapted alleles into wild populations is of particular interest in conservation biology as many populations that require protection are supported by the introduction of genetically divergent captive-bred individuals (Cross et al. 2007). Additionally, invasion by either escaped, domesticated conspecifics (Diserud et al 2020) or sexually compatible heterospecifics (McFarlane and Pemberton 2019; Quilodrán et al. 2020) can also cause the breakdown of local adaptation, stymieing conservation efforts (Lynch and O'Hely 2001). Despite the widespread occurrence of introgression between genetically divergent lineages and extensive knowledge of the negative effects such intrusion has on local populations, why introgression occurs in some incidences but not others remains unclear, as do the circumstances under which introgression causes demographic decline (White et al. 2018; Lehnert et al. 2020).

Salmonine populations are often intruded by genetically divergent genotypes since many of their populations are stocked with captive-bred hatchery fish (Morán et al. 1991; Araki et al. 2008; Berejikian et al. 2009; Theriáult et al. 2011; Jonsson et al. 2019; O'Sullivan et al. 2020; King et al. 2021), invaded by escaped farmed Atlantic salmon, *Salmo salar* L. 1758 (Glover et al. 2017), or exposed to non-native, closely related heterospecific taxa with which they can potentially interbreed (Sato 2007; Muhlfeld et al. 2009). Maladaptive introgression has the potential to reduce wild population abundance and, in worst-case scenarios, lead to the population's extinction through demographic decline (Araki et al. 2009). A more thorough understanding of how ecological processes and genetics interact to shape evolution and demography in intruded populations is required in order to better understand maladaptive introgression between fish of different genetic provenances.

Differences between local and non-local genetic lineages can arise through various mechanisms. For wild versus captive-bred fish, examples include the maintenance of 'closed' hatchery lineages i.e. no new genetic material introduced from the wild (Baskett and Waples 2013; Baskett et al. 2013; Waters et al. 2015; Klütsch et al. 2021), establishment of stocking populations with individuals derived from non-local broodstock (McGinnity et al. 2007; O'Toole et al. 2015), inadvertent selection within the hatchery (Ford 2002), or in the case of farmed Atlantic salmon, deliberate selection for commercially desirable traits (Gjedrem 2010). For local wild fish and non-local, invasive heterospecifics, genetic differences exist as a result of speciation and distinct evolutionary trajectories for the respective lineages. Muhlfeld et al. (2009) demonstrated that when rivers with native populations of westslope cutthroat trout, *Oncorhynchus clarkii lewisi* Suckley 1856, were stocked with congeneric rainbow trout, *Oncorhynchus mykiss* Walbaum 1792, the taxa interbred to the extent that the local westslope genome was mostly lost and replaced with non-local rainbow trout genes.

In tandem with genetics, the ecological context under which introgression might occur must be considered (Hansen and Youngson 1998). It is the interaction between genetics and ecology – an 'eco-evo' pathway (Hendry 2017) – that determines whether non-local alleles introgress and persist in the wild population, and whether any associated purging pressure negatively affects population viability and persistence. The prevailing hypothesis is that the release of non-local individuals (be they hatchery-bred or domesticated conspecifics, or invasive heterospecifics) causes declines in the mean absolute fitness of wild-living populations following interbreeding between locals and non-locals, with the magnitude of such demographic costs scaling with the degree of divergence between the two genetic lineages (Lynch and O'Hely 2001). Even wild fish from neighbouring populations often display lower fitness when transplanted between catchments (McGinnity et al. 2004; de Eyto et al. 2007, 2011). This presupposes that the phenotypes of fish of non-local provenance are to some extent mismatched to the local 'external' environment, e.g. abiotic conditions, predators, parasites, etc., such that fish carrying foreign alleles (first generation stocked/escaped/invading fish, or future generations of hybrids and backcrosses) would always display lower fitness in the home environment of locals than fish carrying fewer foreign alleles. This is the idea of 'hard selection'.

Hard selection occurs when the absolute fitness of an individual is independent of the phenotypes of other individuals in the population but dependent on the match between an individual's trait value and the theoretical trait optimum for that environment (Figure 1). The greater this mismatch, the less fit that individual is (Wallace 1975). For example, a fish of a given size might have a fixed survival probability in a given abiotic or heterospecific environment, which does not depend on the sizes of other conspecifics with which it interacts. Due to hard selection reducing mean absolute fitness, it causes population declines when the mean phenotype is far from the theoretical optimum. Populations that are unable to evolve towards such optima, or which evolve too slowly, risk extinction due to the depressed demographic risks associated with hard selection (Burger and Lynch 1995; Gomulkiewicz and Holt 1995; Garcia de Leaniz et al. 2007; Almodóvar et al. 2012).

However, another possibility is that the relative fitness of the different provenances/genotypes is determined purely by their success in competition for limited ecological vacancies, e.g. spawning sites, fry territories. In this scenario, the fitness of a pure non-local fish, or a first generation non-local-wild hybrid, is now dependent on the number and phenotypic composition of conspecific competitors. Fish with non-local genotypes might survive and reproduce perfectly well in the wild environment in the absence of wild competitors but be outcompeted in their presence (or vice versa). This is the idea of soft selection, where absolute individual fitness is dependent on the phenotypic composition of the population, and not on a theoretical trait optimum (Wallace 1968; Bell et al. 2021; Figure 1). For example, a fish of a given size might be a strong competitor if it is larger than most interacting conspecifics but be a weak competitor if most other conspecifics are larger. Importantly, the mean absolute fitness of the whole population, that is all provenances/genotypes taken together, is invariant with respect to genotypic composition in a pure soft selection scenario, because the environment only provides a fixed number of ecological vacancies. Some genotypes are more likely to fill these slots than others, and hence fish with those genotypes will display higher relative fitness, but all slots will be filled regardless, so long as there are more individuals than slots.

Key to understanding soft selection is the idea of ‘reproductive excess’. Consider a population consisting of N individuals that is regulated by the availability of some resource (e.g. breeding or feeding territories), where K represents the carrying capacity (number of ecological vacancies/territory slots). Competition for these vacancies is mediated by a heritable trait. Only those individuals that gain access to one of the K resources survive and breed. If individuals with a certain trait value (e.g. relatively larger individuals) have preferential access to the resource, then individuals with different trait values (e.g. relatively smaller individuals) will lose out on access to the resource. The strength of soft selection, and whether or not it operates in a population, depends on the ratio N/K. The logic of soft selection applies equally to quantitative (continuous) traits as it does to discrete traits (Bell et al. 2021), but for simplicity let us consider a discrete trait where individuals fall into either a preferred class (better competitors) or a disfavoured class (worse competitors). If $N \leq K$, then all individuals survive and breed i.e. there is no reproductive excess and no selection occurs (Figure 1:Case 1). If $N > K$ and the number of individuals with the preferred trait value also exceeds K, then $N - K$ individuals represent the reproductive excess of the population that die without reproducing (Grafen 1988), while only those with the preferred trait value survive and breed (Figure 1:Case 2). Soft selection against the less competitive class of individuals is thus very strong. Finally, if $N > K$ but the number of individuals with the preferred trait value is less than K, then soft selection occurs but of weaker strength than in Case 2. Those individuals with the preferred trait value gain access to the ecological vacancies first and the remaining number of vacancies are then filled by individuals with the 'non-preferred' trait value (Figure 1:Case 3). Notice how in both Case 2 and Case 3, K individuals survive in total, regardless of the phenotypic composition of the N individuals competing for the limited ecological vacancies. Thus, for a given N, the mean fitness is constant at K/N regardless of the strength of soft selection. Similarly, if $N >$ K but all individuals are of the same phenotype, no selection occurs but mean fitness is still K/N. Therefore, pure soft selection has no demographic cost to the population.

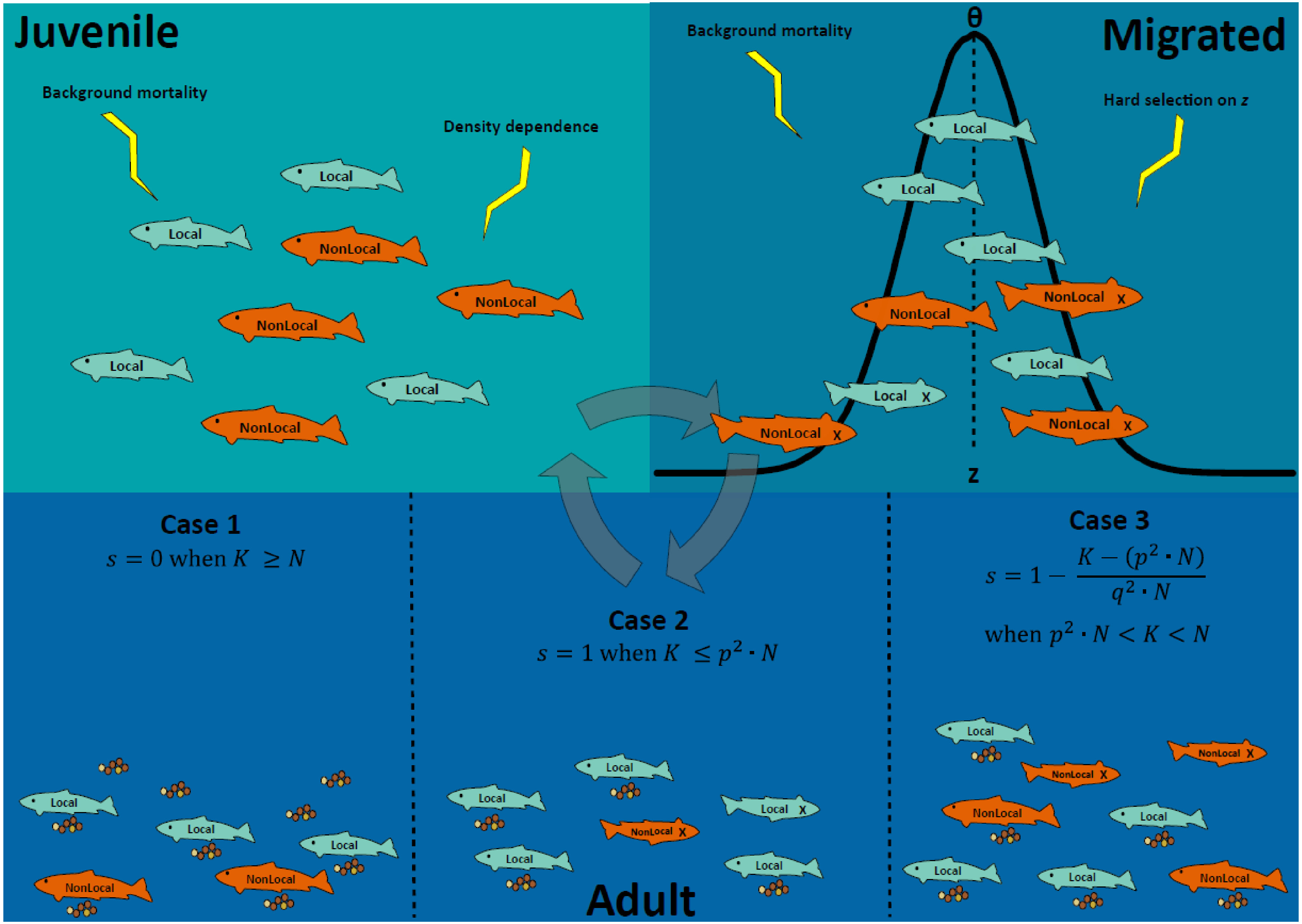
Many studies of salmonines have documented reduced fitness of non-local relative to local genotypes (Araki and Schmid 2010; Fleming and Petersson 2001; McGinnity et al. 1997, 2003, 2007; O'Sullivan et al. 2020; Sylvester et al. 2019), but this observation alone is insufficient to distinguish hard selection from soft selection scenarios, because both predict differences in relative fitness between provenances. The key difference is that hard selection predicts reduced mean absolute fitness (lower population growth rate) of an admixed population relative to a pure wild population, whereas soft selection predicts equal mean absolute fitness (i.e. no effect of genotypic composition on population growth rate). Both can operate in a single population, acting at the same time on the same trait, or on different traits, which may or may not be genetically correlated. Thus, hard and soft selection can interact in interesting ways, potentially leading to unexpected and context-specific changes in demography. To explore these issues, we developed a genetically-explicit eco-evolutionary model in which soft selection occurs on a trait mediating success in competition for limited spawning sites, while hard selection occurs on another unlinked trait mediating survival during the migratory life stage. The overarching goal was to investigate how changes in the strengths of soft and hard selection, and interactions between them, affected the dynamics of purging/introgression of non-local alleles and how such evolutionary dynamics affected mean absolute fitness and population dynamics.

5.3 Materials and Methods

(a) Basic model details

We developed a genetically-explicit eco-evolutionary model (hereafter, simply ‘model’) using the individual-based modelling software NetLogo 6.2 (Wilensky 1999). In the NetLogo environment, individuals with pre-assigned characteristics are allowed to interact with other such individuals as well as with a spatially-explicit environment over the course of a specified life cycle. The model described herein includes components of code from the model of Kane et al. *Submitted* and from various models in NetLogo’s model library. What follows is a summary of the lifecycle, ecological processes, and genetic architecture employed in the model.

Figure 1 (Overleaf): Lifecycle of the generic salmonine taxon simulated in the genetically-explicit eco-evolutionary model described herein. Fish in the Juvenile life stage (top left) are subject to a background mortality rate as well as density-dependent population regulation. At age 123 weeks, fish migrate to a new habitat and are considered to be in the Migrated stage of the lifecycle (top right). Again, fish are subject to a constant background mortality rate. In this new habitat, fish also experience a selective episode where the quantitative trait z is subject to hard selection. z can be thought of as mediating survival in the new habitat. Initially, fish with locally adaptive values for z will more likely survive hard selection than non-local fish who display maladaptive trait values. If a fish survives to age 185 weeks, they enter the Adult life stage and breeding females are potentially subject to soft selection at the *comp* locus that mediates competitive ability at gaining a redd (bottom row). Females compete for a set number of redds, K. If there are more redds than the total number of potentially spawning females, N, then soft selection does not occur ($s = 0$, Case 1). If there are more females with the competitively superior L allele (which is completely dominant over the competitively inferior F allele) than there are redds, then the strength of soft selection is 1 since only K females with a copy of the L allele gain access to a redd ($s = 1$, Case 2). When there are fewer redds than the total number of potentially spawning females but not enough females with the genotypes *LL, LF,* or *FL* to monopolize all of the redds, then redds are filled by females with the *LL, LF,* or *FL* genotypes first, and the remaining redds are then filled by the competitively-inferior females with the non-local *FF* genotype at the *comp* locus (Case 3). Allele frequencies of the L and F alleles are represented by p^2 and q^2, respectively.


Juvenile
Background mortality
Density dependence
Local
Local
NonLocal
NonLocal
NonLocal
Local
Local
NonLocal
Background mortality
θ
Migrated
Hard selection on *z*
Local
Local
Local
NonLocal X
NonLocal
Local
Local X
NonLocal X
NonLocal X
z
Case 1
$s = 0$ when $K \geq N$
Local
Local
Local
NonLocal
NonLocal
Case 2
$s = 1$ when $K \leq p^2 \cdot N$
Local
Local
Local X
NonLocal X
Local
Local
Adult
Case 3
$s = 1 - \frac{K - (p^2 \cdot N)}{q^2 \cdot N}$
when $p^2 \cdot N < K < N$
Local
NonLocal X
NonLocal X
NonLocal
Local
Local
Local
NonLocal

(b) Lifecycle, ecology, and genetics

The model simulates the lifecycle of a migratory salmonine taxon that displays semelparity (only spawns once). As such, the model reflects to a large degree the lifecycle of many Atlantic salmon populations (Verspoor et al. 2007) or the semelparous Pacific salmon and trout taxa, *Oncorhynchus* spp., Suckley 1861 (Quinn 2005). The lifecycle is divided into three life stages; Juvenile, Migrated, and Adult. Simulations are initialised by seeding the model with a user-specified number of two distinct kinds of ova – local ($N_{initial\ L}$) and non-local ($N_{initial\ F}$). Individual fish are tracked at time steps throughout each model run. Each time step is equivalent to one week in their lifecycle.

Ova hatch instantly and display four distinct traits/loci: (1) a biallelic locus that mediates female competitive ability at spawning time, where L and F are the local and non-local (foreign) alleles with L assumed to be completely dominant over F. Therefore, individuals can be either homozygote dominant ($comp_{LL}$), homozygote recessive ($comp_{FF}$), or heterozygotic ($comp_{LF}$ or $comp_{FL}$); (2) a quantitative trait z that mediates survival during the Migrated life stage; (3) a selectively-neutral quantitative trait used to monitor genetic drift; and (4) a selectively-neutral biallelic diagnostic marker, *diag*, used to track the persistence of local and non-local alleles that are not directly exposed to selection (with the model initially seeded with just $diag_{LL}$ and $diag_{FF}$ homozygotes). For the quantitative trait z, breeding values were drawn from a normal distribution with a mean equal to $\bar{z}$ and a standard deviation equal to σ. z was under stabilizing selection defined by a Gaussian survival function of width ω and a mean equal to the theoretical trait optimum, Θ (see Eqn.2). At the start of each model run, local fish were assumed to be more adapted for z than non-local fish, with $\bar{z}$ for local fish being close to the optimum in the first generation. $\bar{z}$ for non-local fish was equal to Θ - x, x representing the maladaptation of non-local fish to the local environment. Breeding values for the selectively-neutral quantitative trait were drawn from a normal distribution of width ω, mean Θ, and standard deviation σ (Table 1). Genotypes are assumed to be completely heritable i.e. no environmental noise affects the expressed traits.

Since local and non-local fish differ in their mean trait values, there is an initial non-random association between provenance-specific breeding values at the z trait and genotypes/breeding values at the other loci at the start of each model run. However, the four traits/loci are assumed to be unlinked (on different chromosomes) and, hence, random assortment at segregation breaks down this non-random association, such that after a number of generations there is no expected difference in the z trait between genotypes at the $comp$ or $diag$ loci, nor any linkage disequilibrium between the $comp$ and $diag$ loci.

The various juvenile life stages exhibited by salmonines are not explicitly modelled in our simulations. Instead, newly-hatched juveniles are immediately subject to density-dependent regulation through the imposition of a carrying capacity. If the number of juvenile fish exceeds the carrying capacity, then fish are randomly chosen with a probability of p to die. p is calculated as

(Eqn.1) $$p = \frac{N_{juveniles} - K_{demographic}}{N_{juveniles}},$$

where $N_{juveniles}$ is the number of juvenile fish that are alive at the current time step and $K_{demographic}$ is the juvenile carrying capacity of the system. We deviate from convention by representing the demographic carrying capacity with the affixed subscript $_{demographic}$. This is done to distinguish demographic carrying capacity from K in the soft selection equations where K represents the number of ecological vacancies that mediate soft selection. Individual fish that survive this initial bottleneck are then subject to an overall juvenile-specific freshwater mortality rate, $Mortality_{Juvenile}$, at each time step of the model.

Once juvenile fish reach age 123 weeks, they undergo a migration to a new habitat. They are now considered to be in the 'Migrated' life stage. In reality, the habitat into which they migrate could represent either a marine or lake environment (Ferguson et al. 2019). Again, fish experience background mortality, $Mortality_{Migrated}$, for every time step that they are in the new environment. Background mortality during the Migrated life stage occurs at a higher rate than background mortality at the Juvenile stage. At age 125 weeks, all surviving fish are subject to hard selection acting on z. The expected fitness of a fish with a given z value is estimated from a survival function of the form

(Eqn.2) $$W_i\,(z_i) = e^{-\frac{(z_i-\theta)^2}{(2\omega^2)}},$$

where $W_i\,(z_i)$ is the estimated expected survival for the i^{th} individual with trait value z_i, e is Euler's constant, Θ is the theoretical phenotypic optimum for z, and ω is the width of the Gaussian survival function (Estes and Arnold 2007). The value of $W_i\,(z_i)$ is then compared to a random draw from a uniform distribution bounded by zero and one. If $W_i\,(z_i)$ is less than the random draw, the individual fish dies i.e. hard selection has 'acted' against that fish. The further an individual's trait value from the theoretical trait optimum, the more likely it will die during the hard selection episode. Such a selection landscape imposes stabilizing selection, culling fish with extreme trait values and maintaining the population-level mean trait value for z at its adaptive optimum (Wright 1932; Lande 1975). Initially, local fish will have values for z that are closer to the trait optimum than non-local fish and, thus, will be better adapted. This is done to replicate the negative effects that non-local fish would experience having undergone a migration to which they are potentially maladapted. The Gaussian survival function could also have been imposed during the freshwater phase of the life cycle (post density dependence), which would not have made a qualitative difference to our conclusions.

At age 184 weeks, fish enter the Adult stage of the lifecycle by returning to their natal river environment. Adult fish experience no additional background mortality. At age 207 weeks, female salmon 'compete' for access to randomly placed nest sites called 'redds'. In our model, this competition is effectively a hierarchical filling of the available redds based on the *comp* genotypes of the female spawners. Females with the $comp_{LL}$ and $comp_{LF/FL}$ genotypes are moved to redds first (one female per redd) and if there are any redds left unoccupied, then females with the $comp_{FF}$ genotype are moved to these redds. This situation corresponds to competitive dominance of individuals with the L allele over individuals with the FF genotype at this locus, such that heterozygotic females display equal competitive ability to homozygotes. The occurrence and strength of soft selection is then dependent on the ratio of N/K and the allele frequencies, p^2 and q^2 for the L and F alleles, respectively. If a female does not gain a redd during the soft selection episode, they die without breeding. Females that gain a redd are assigned two random mates from the available pool of male spawners. For simplicity, males do not express any competitive ability related to the *comp* locus. Male fish are, however, carriers of the L and F alleles at the locus.

Sexual reproduction occurs at age 209 weeks. All females produce 200 ova. In reality, many salmonine taxa can produce far more than 200 ova, but this number was chosen to decrease computation time (which scales exponentially with the number of individuals). For each ova, the female chooses one of the two available male spawners. For z, genetic inheritance is assumed to follow a quantitative genetic model where the z value of offspring is taken as a random draw from a Gaussian distribution with a mean equal to the mid-parental trait value and a standard deviation equal to half the initial population-level additive genetic variance for the trait (Lynch and Walsh 1998). For the *comp* locus, genetic inheritance is modelled using a simple model of explicit Mendelian segregation. The ova inherits one allele from their mother and one allele from their father. The selectively-neutral quantitative trait and diagnostic marker are inherited via the same mechanisms as the selected-for quantitative and competitive traits, respectively. During sexual reproduction, the ancestry of each ovum as well as its genotypes, life stage, age, and generation, are recorded. Following the reproductive event, the parental generation dies and the lifecycle of the next generation begins. The age, generation, and life stage of each fish is updated at every time step. A full list of parameter values is found in Table 1.

Table 1: Descriptions and values for parameters used in the genetically-explicit eco-evolutionary model described herein. See Methods for further details.

Parameter	Description	Value
$N_{initial\,L}$	Initial seed number of ova with the *LL* genotype at the competitive locus	10000
$N_{initial\,F}$	Initial seed number of ova with the *FF* genotype at the competitive locus	10000
$Mortality_{Juvenile}$	Background mortality at the Juvenile life stage	0.01
$Mortality_{Migrated}$	Background mortality at the Migrated life stage	0.047
$K_{demographic}$	Demographic carrying capacity at the Juvenile life stage	15000
K	Number of redds available at spawning	35, 50, 65, 100, 150
Θ	Theoretical trait optimum for z and mean of normal distributions	0
σ	Standard deviation of normal distributions	1
ω	Width of Gaussian survival functions	5
x	Initial level of maladaptation for non-local fish	-5

(d) Modelled scenarios and predictions

In each model run, all parameters were kept constant except for the number of redds, *K*, available to females at spawning (Table 1) and whether soft selection was ‘turned’ on or off in a particular model run. Soft selection was turned on and off by a TRUE/FALSE logical operator in the Netlogo code. When TRUE, soft selection could take place at spawning time. When FALSE, a random subset of *K* spawners would get a redd, regardless of their genotype at the *comp* locus. Hard selection occurred in all models. Comparison of model results when both soft and hard selection occurred with the results from models where only hard selection occurred was used to examine the effects of soft selection on the evolutionary dynamics and demography of the population. In total, there were ten sets of results (five levels of *K* varied under two selection scenarios each). Regardless of provenance (hatchery, domesticated, heterospecific) of the non-local fish, we made the following set of predictions:

(1) Soft selection would purge the non-local *F* allele at the *comp* locus from the population faster when *K*, the number of ecological vacancies, was smaller since fewer females with the *FF* genotype at the *comp* locus would have the opportunity to breed. Furthermore, we predicted that no purging of the *F* allele would occur when soft selection was not operating since access to redds would

no longer be genotype-dependent and a random set of K females would get to breed;

(2) Unlike hard selection, soft selection is presumed to impose no demographic cost on a population since it doesn't limit the number of breeding individuals but rather determines the genotypic/phenotypic composition of those individuals that do breed (Wallace 1968; Bell et al. 2021). However, if soft selection operates to exclude individuals with non-local genotypes from breeding (and, therefore, stymie or prevent the introgression of maladapted genes at the z locus), then a demographic buffering effect should be observed in initial generations post-intrusion, compared to situations with no soft selection where the demographic declines associated with hard selection are more severe;

(3) Due to each of the four traits/genotypes being able to freely assort during segregation, alleles for non-local fish at the selectively-neutral diagnostic marker should persist in the population despite originally being associated with the non-local provenance.

During each simulation, the following global variables were tracked: replication number, time step, generation, age, population-level mean z trait value, population-level mean neutral trait value, total number of homozygote*,* heterozygote, and recessive genotypes at the *comp* locus, total number of homozygote*,* heterozygote, and recessive genotypes at the *comp* locus among smolts, total number of females with the homozygote*,* heterozygote, and recessive genotypes at the *comp* locus among smolts, total number of potential spawners, total number of females with the homozygote*,* heterozygote, and recessive genotypes at the *comp* locus among potential spawners, and the total number of each genotype at the diagnostic marker. All model runs were replicated 100 times using the BehaviourSpace tool in Netlogo and terminated when the simulation reached the 75th generation. Θ was set to zero and σ set to one in all simulations, allowing for evolutionary change of the quantitative traits to be expressed in haldanes. Model output was saved in plain text files and analysed using R version 4.1.1 (R Core Team 2021).

5.4 Results

As the number of redds available to potential female spawners increased, the rate at which soft selection purged the uncompetitive F allele from the *comp* locus decreased. When the number of redds equalled 150, no purging took place as all females (N ≤ K), regardless of their genotype at the *comp* locus, were able to spawn (Figure 2 top line). Similarly, when no soft selection was imposed on females at breeding time, no purging took place (Figure 2 bottom line).

As the number of redds increased and more non-local fish and their feral or backcrossed descendants were afforded the opportunity to breed, the degree of maladaptation displayed by $\bar{z}$ was larger. This led to very strong hard selection on z causing rapid evolution back towards the optimum. Under scenarios with soft selection and $K = 35$, 50, or 65, there was a sharp initial increase in average z that wasn't seen when $K = 100$ or 150 or in scenarios where only hard selection was operating (Figure 3a). This is evidence of soft selection having an indirect effect on the evolution of z by weakening the strength of hard selection. The concomitant indirect effect soft selection had on demography is seen by comparing the number of potentially spawning females at each value of K when both soft and hard selection operate, and when only hard selection acts. When $K = 35$, 50, or 60 (soft selection operating, being stronger when K is lower), the initial demographic declines caused by the introgression of maladapted breeding values for z are not as severe compared to when only hard selection is imposed (Figure 3b).

Figure 4a demonstrates that the selectively-neutral diagnostic F allele for non-local genotypes persisted in the population despite the purging of the associated F allele at the *comp* locus (see $K = 35$, 50, 65, and 100 in the top rows of Figures 2 and 4a). Finally, Figure 4b demonstrates that genetic drift had a negligible impact on evolution when averaged across all model runs.

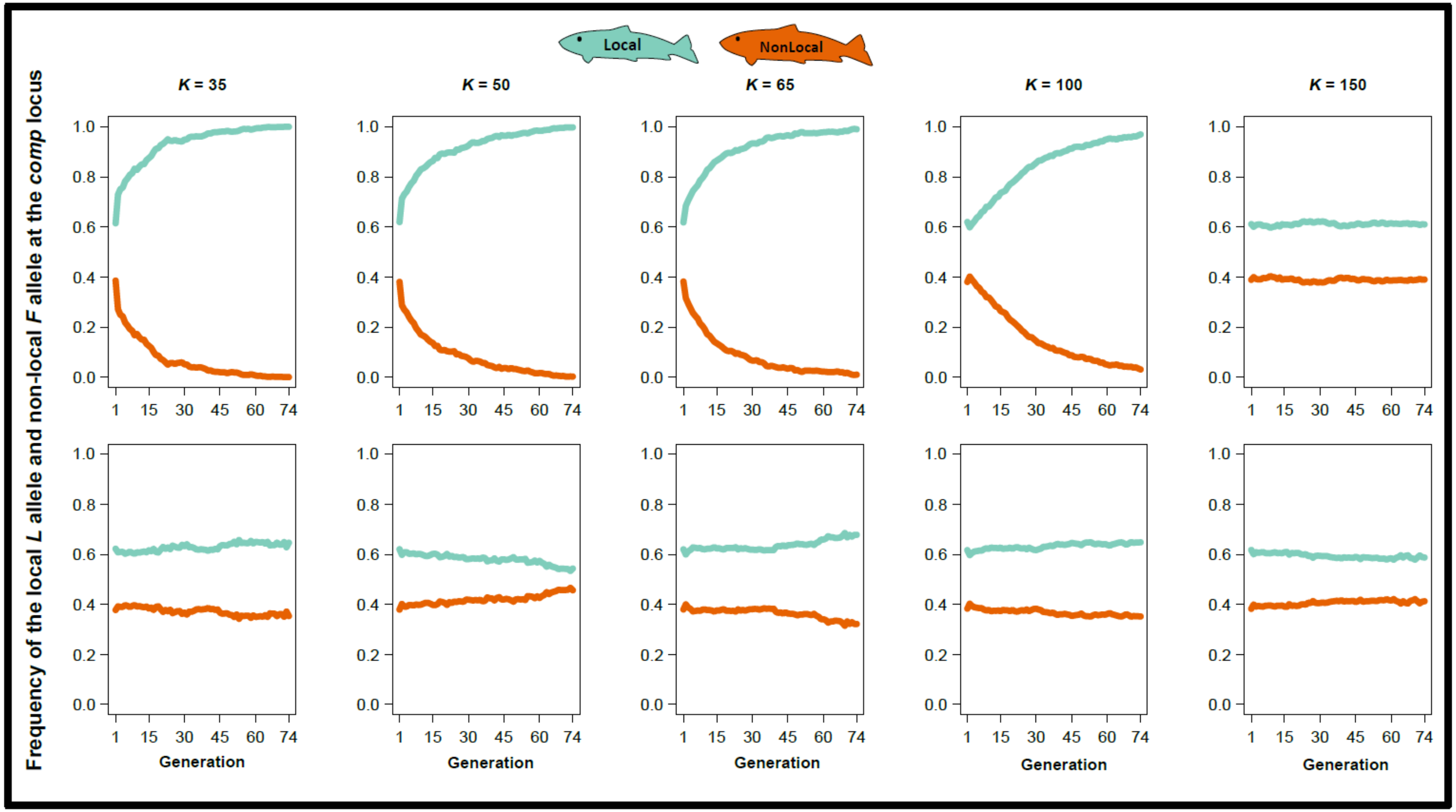


Figure 2: Evolution of the frequency of the *L* allele and the *F* allele at the *comp* locus which mediates competitive ability in redd acquisition among potentially spawning females. K = number of redds available to females during a given simulation. Top line – soft selection and hard selection. Bottom line – only hard selection.

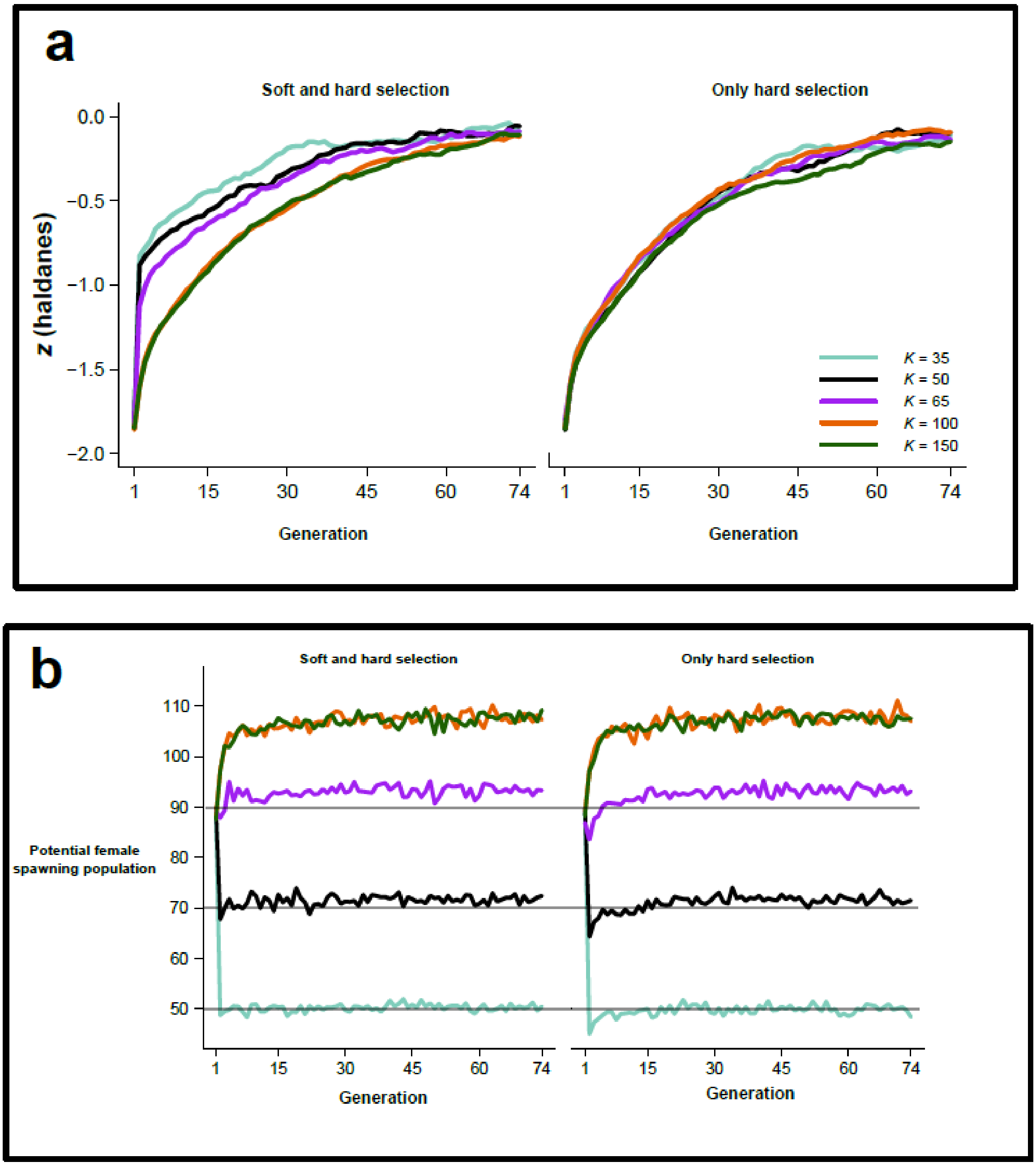


Figure 3: (a) Evolution of the quantitative trait *z* that mediates survival of fish during the Migrated stage of the lifecycle when different numbers of redds, *K*, were available to potentially spawning female fish. Changes in *z* are measured in haldanes. Evolution was tracked under scenarios where fish experienced both soft and hard selection, and where fish experienced hard selection only. (b) Changes in the number of potentially spawning females when different numbers of redds, *K*, were available to potentially spawning female fish. Horizontal grey lines used to highlight the increased demographic cost under scenarios where fish experienced only hard selection, compared to scenarios with both soft and hard selection.

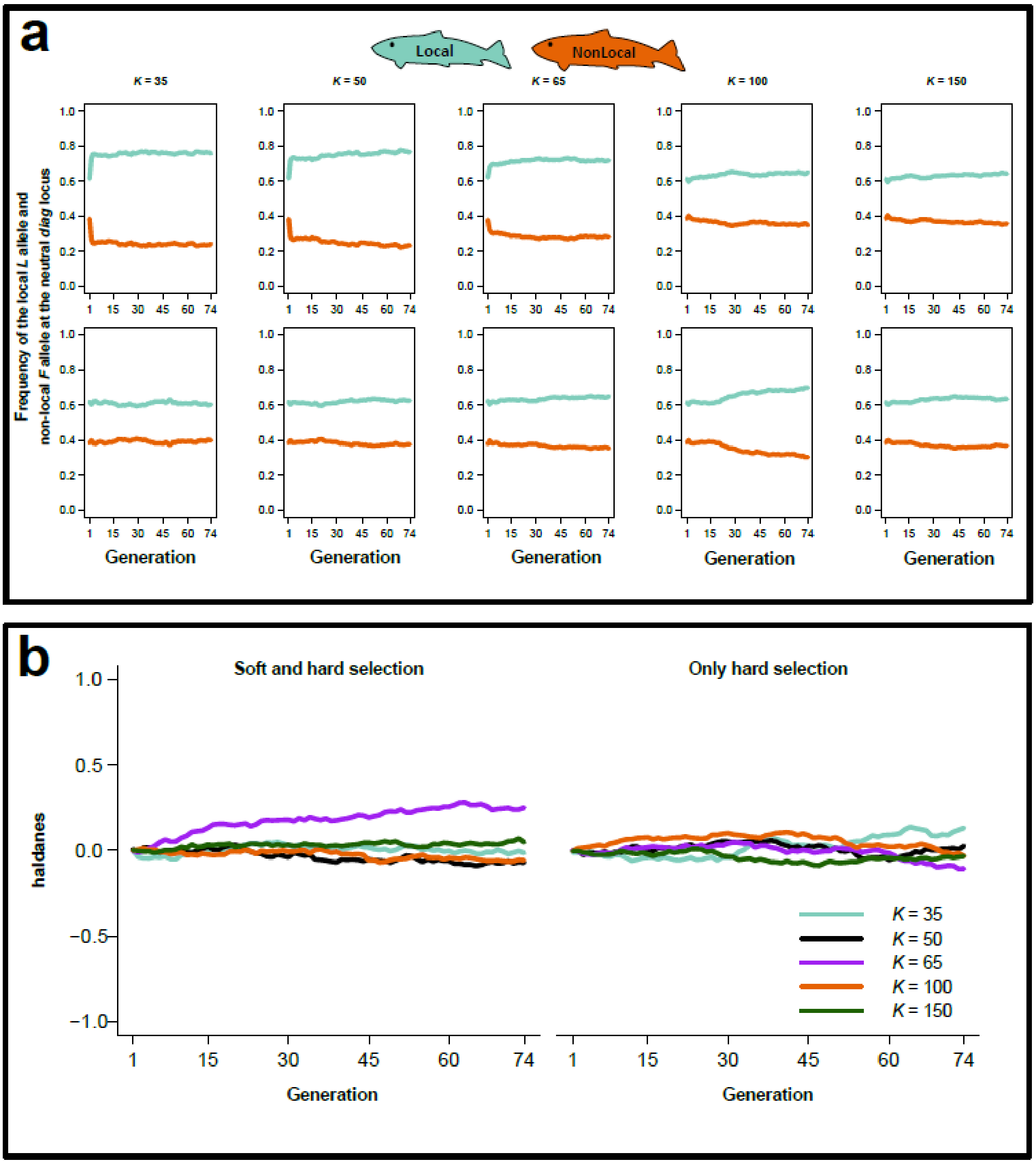


Figure 4: (a) Evolution of the frequency of the L allele and the F allele at the selectively-neutral *diag* locus. $K =$ number of redds available to females during a given simulation. Top line – soft selection and hard selection. Bottom line – only hard selection. (b) Change in haldanes in the selectively-neutral quantitative trait when the number of redds available to females, K, is varied. Regardless of whether both soft and hard selection occur, or only hard selection occurs, there is minimal effect of genetic drift on evolution in the simulations.

5.5 Discussion

Using a genetically-explicit eco-evolutionary model, we demonstrated how the ecological processes of soft and hard selection affected evolution and demography in a wild salmonine population. On average, stronger soft selection led to a purging of deleterious non-local alleles at the female competitive locus while hard selection removed individuals with maladapted trait values for z. Soft selection interacted with hard selection, such that stronger soft selection caused a weakening of the latter, which indirectly reduced the demographic impact of hard selection on the population. This indirect effect of soft selection on the evolutionary dynamics of a hard-selected trait and the associated demographic penalties may provide a mechanism to help understand why certain introgressed populations experience population declines while others remain much less impacted.

(a) Interactions between soft and hard selection

The most interesting result arising from our simulations was the indirect effect soft selection had on hard selection and by extension, the initial level of maladaptation and subsequent rate of evolution of the trait z under hard selection. The strength of soft selection scaled negatively with K (because initial N was fixed), and when soft selection was on average stronger ($K = 35$, 50, 65), fewer individuals with non-local (less competitive) genotypes at the *comp* locus had the opportunity to breed. This prevented maladaptive breeding values for z introgressing into the local population's gene pool which meant that the initial drop in mean z was much less pronounced. With weaker soft selection (higher K), the number of maladapted individuals that bred increased, resulting in more admixture and a much greater initial drop in mean z (Figure 3a). This was associated with a greater initial drop in the number of spawners N in the first few generations, owing to the demographic cost of stronger hard selection (Figure 3b). The subsequent rate of evolution of z back towards the optimum was also faster, owing to stronger directional selection – the latter scaling with the distance between mean z and the optimum.

Apart from selection, fish were only exposed to the limiting factors of background mortality and a juvenile carrying capacity. Therefore, for each value of K there was an equilibrium population size. In a given generation, the more individuals with maladaptive trait values for z, the more intensely that population would be subject to hard selection. Since hard selection comes with a demographic cost, population abundance should decrease as the proportion of maladapted individuals within the population increases. Through its indirect effect on the evolution of z, soft selection acted as a demographic buffer in populations that experienced introgression from maladapted individuals. By limiting the number of non-local females that got to breed, soft selection limited the introgression of maladaptive breeding values for z. Similar to Tufto (2001), this reduced the demographic cost of hard selection as fewer maladapted offspring hatched with z genotypes that were highly divergent from the trait's optimum. However, our model and the model of Tufto (2001) came about this reduced demographic cost via different mechanisms – theirs by limiting the rate of immigration from non-local fish and the initial degree of maladaptation, ours via the indirect effect of soft selection on hard selection. The reduced effect on demography can be seen in the less severe initial reduction in the number of potential female spawners under scenarios with both soft and hard selection compared to scenarios without soft selection (Figure 3b).

(b) Purging effects

As K decreases, the greater efficiency with which soft selection purges the F allele from the local population's gene pool is an obvious result arising from our model. If a certain genotype is favoured relative to another, *ceteris paribus*, the unfavoured genotype will have less of an opportunity to breed, with the probability of breeding decreasing as the number of breeding sites is reduced.

What was unexpected was the lack of effect soft selection had on the dynamics of z and female population size when $K = 100$ (Figure 3). It was expected given that soft selection was still operating when $K = 100$ (Figure 2 top line), that the dynamics of z and population size would be intermediate between the dynamics observed when $K = 65$ and 150. However, the dynamics were essentially the same as when $K = 150$ while also being similar to the dynamics observed under hard selection only scenarios (Figure 3). This pattern is likely due to a decoupling of the indirect effect soft selection has on hard selection due to the high number of hybrids that would arise after the first generation when the number of redds equalled 100 or 150. Such numbers of redds would allow a large relative number of females with the $comp_{FF}$ genotype to breed, thus, producing hybrids who would be carriers of the F allele ($comp_{LF}$ or $comp_{FL}$) but shielded from soft selection due to complete dominance of the L allele over the F allele, hence the weakening seen in Figure 2 when $K = 100$. Since they are not selected against when it comes to redd acquisition, first generation hybrid females transmit maladapted breeding values for z to their offspring. This pulled the mean of z further away from the optimum in the initial generations. The production of F_1 hybrids between local and non-local fish coupled with the availability or lack thereof of breeding sites might explain why some intruded populations experience introgression (Muhlfeld et al. 2009; Kovach et al. 2015) while others do not (White et al. 2018; Lehnert et al. 2020; King et al. 2021). Another pathway to introgression is where non-local individuals are positively selected for by soft selection and gain access to ecological vacancies at the expense of local fish. Farmed Atlantic salmon fry are competitively superior to local wild fry and displace them from feeding territories under high densities (McGinnity et al. 2003). Assuming the farmed fish survive to spawning, they will likely interbreed with local wild fish, resulting in introgression between the provenances. Therefore, soft selection in the parental generation might limit introgression but depending on the ecological context that young fish hatch into, soft selection in the offspring's generation might actually promote introgression.

Environmental changes are also known to affect the occurrence of hybridisation. Marie et al. (2012) found that increasing lake surface area displayed a negative relationship with hybridisation. In reality, the number of redds available to competing females will vary depending on water depth and substrate type and, thus, be dependent on prevailing climatic conditions. Imagine the salmonine population presented in our model. In years where heavy rainfall has extended the width of the river channel, the increased availability of habitat should promote introgression as the number of females who get to breed will not be limited by the availability of redds. However, a drying up of much of the river channel under drought conditions will decrease the availability of suitable spawning sites, thus, increasing the strength of soft selection. As such, any conservation or management plans should also account for ongoing and possible future environmental change when designing hatchery stocking programmes or considering translocations since the evolutionary landscape of a population will likely change as the project progresses.

The selectively-neutral, non-local F allele at the *diag* locus persisted despite the purging of the associated F allele at the *comp* locus ($K = 35$, 50, 65, and 100 in the top rows of Figures 2 and 4a). Coupled with the return of the mean z value back to its optimum, this demonstrates how admixed populations that appear similar to 'pure' fish at one genotype might not be so across their entire genome. In other words, there is likely to be variation across genomic regions in rates of introgression, depending on whether those regions are under purging selection or not, or physically linked to/in linkage disequilibrium with other such regions. This persistence was possible in our model due to the four genotypes/traits being free to randomly assort at segregation. However, an initial increase and decrease in L and F alleles respectively at the *diag* locus across the first few generations when soft selection was operating ($K = 35$, 50, or 65, Figure 4a, top line) reveals that the initial non-random association between genotypes for each of the provenances led to a hitchhiking effect where the frequency of the diagnostic alleles changed due to being associated with the positively selected $comp_{LL}$ and negatively selected $comp_{FF}$ genotypes, respectively (Barton 2000). As mating was random and the competitive and diagnostic loci were not physically linked, the association broke down and the hitchhiking effect disappeared.

(c) Evolutionary rescue

The reduced demographic impact observed when an intruded population experienced both soft and hard selection, compared to just hard selection (Figure 3b), is a form of evolutionary rescue i.e. when evolution reduces the probability of a population going extinct compared to situations without evolution (Gomulkiewicz and Holt 1995). While the reduction in the total number of spawning females observed was not severe, it did temporarily lower productivity, thus, increasing the susceptibility of the population to extinction from sudden stochastic change. It is important to note that this reduction in extinction risk is merely suggested since we did not conduct model runs where the population could actually go extinct. Rather, the reduction in risk is inferred from the difference in the dynamics of N under scenarios with and without soft selection. Vincenzi (2014) demonstrated that extinction risk increased as the strength of hard selection and environmental stochasticity increased.

(d) Where to next? Applications to conservation and management

By simulating a salmonine population that experienced intrusion from non-local genetic stock, we were able to demonstrate the direct impact soft selection had on the purging of maladaptive genotypes as well as its indirect impacts on the evolution of z and on demographics. The results from this model highlight how variation in the strength of ecological processes and interactions between individuals with different genotypes can lead to unexpected eco-evolutionary dynamics (Kinnison et al. 2015). Salmonine populations will likely face increasingly variable climatic conditions in the future (IPCC 2021) as well as continued invasions from both domestic stock as the aquaculture industry grows

(FAO 2020) and introductions of exotic taxa continue (O'Toole et al. 2021; Seebens et al. 2021). Therefore, knowledge of how ecology, genetics, and emergent eco-evolutionary dynamics might change in the future is important for those seeking to protect the remaining 'wild' populations of given taxa and mitigate against the effects of invasion and genetic introgression. This will involve expanding the knowledge base of individual at-risk populations i.e. carrying capacities, changes in availability of breeding habitat. Knowing what processes might increase or decrease a population's ability to resist intrusion from maladapted individuals would allow for bespoke conservation measures designed to target such processes.

Chapter 6 General Discussion

6.1 Overview of data chapters

Chapter 2 examined the consequences of captive-bred Atlantic salmon from an ocean ranching programme spawning alongside wild salmon. Individual-level estimates of lifetime reproductive success were extracted from a multi-generational molecular pedigree, demonstrating that the relative fitness of the captive-bred salmon was only 36% that of wild-spawned fish (Figure 1a, Chapter 2). A deleterious transgenerational effect of the hatchery environment on the survival of the wild-bred offspring of captive-bred fish was found, where wild-bred fish that had two captive-bred parents displayed lower egg-to-adult survival than those wild-bred fish who themselves had two wild-bred parents. Using population census data collected at fish traps, coupled with estimates of population-level fecundity, I demonstrated that as the proportion of captive-bred salmon in an entire cohort of potential spawners increased, the productivity of the whole mixed population decreased (Figure 1b, Chapter 2). The results from this chapter complement the already extensive published literature demonstrating the negative effects captive-bred fish have when allowed to intrude on self-sustaining populations (Araki et al. 2007a,b,c; Fraser et al. 2010; Bacon et al. 2015; Le Cam et al. 2015; Sylvester et al. 2019). Variation in the number of potential spawners that were captive-bred was most likely due to (1) variable numbers of captive-bred fish being allowed through the fish traps and into the catchment, and (2) the potential that in years of low density for wild salmon, captive-bred females, who are known to perform poorly at spawning at high densities of wild fish (Fleming and Gross 1993), were afforded the opportunity to spawn. That is to say, soft selection against maladapted females could have been weaker which led to harder selection against maladapted feral and hybrid offspring (Chapter 5).

Chapter 3 used the same molecular pedigree as Chapter 2 to explore the evolutionary dynamics of the fitness-related trait body size at spawning in female

Atlantic salmon. Using the animal model (Lynch and Walsh 1998), both female body size and lifetime reproductive success were found to be genetically heritable (Table 2, Chapter 3). Female body size was under positive directional selection (Figure 1, Chapter 3). The application of the Breeder's Equation to the heritability estimate for length and the trait's univariate selection gradient predicted that body size should evolve at a rate of 0.05 haldanes (phenotypic standard deviations) per generation, yet no trends in either phenotypic measurements of body size nor in breeding values were apparent for the trait (Figure 2, Chapter 3). This paradox of stasis (Pujol et al. 2018) was likely due to the univariate selection gradient used in the Breeder's Equation being biased by an unknown trait that is correlated with body size. A bivariate animal model was implemented to provide an unbiased estimate of evolution using the Secondary Theorem of Selection, as well as to quantify the probability that the erroneous Breeder's Equation prediction was due to an unmeasured trait. This yielded an estimate of evolution of 0.002 haldanes with credible intervals overlapping zero (Figure 3, Chapter 3). This was consistent with the observed lack of phenotypic and genetic trends for body size. The results of the bivariate animal model were then used to estimate that there was a 94.2% probability that an unmeasured trait had biased the univariate selection gradient through a correlation with body size. The estimate of heritability for body size presented here (0.23) is very similar to the median heritability for other life history traits of salmonids (Carlson and Seamons 2008). The exploration of evolutionary dynamics in Atlantic salmon using quantitative genetics expands the realm of wild populations where a paradox of stasis has been observed (Pujol et al. 2018). Accurate measures of evolution are critical in conservation as they can be used to detect if a population is evolving in response to some genetic or environmental insult. The use of genomic methods (relying on actual genetic relatedness rather than statistically-expected relatedness estimated from pedigrees) would allow for evolutionary change to be estimated using the same predictive equations while only requiring two generations of data (Jensen et al. 2014).

My review of genetically-explicit evo-evolutionary models in Chapter 4 revealed that 44% of the 91 published studies explored some aspect of fisheries-induced evolution. The most commonly studied taxa were the salmonids (salmon, trout, charr, whitefish, and grayling) with 44% of all models concerning some aspect of their biology. Models that explicitly simulated evolution in scenarios where captive-bred fish were introduced into a wild population comprised 16.5% of studies and of these, all bar one were parameterised for salmonid species (Jager 2005 modelling the stocking of white sturgeon, *Acipenser transmontanus* Richardson 1836). The small number of studies that modelled captive-wild interactions was surprising given the known impacts of such interactions on wild populations. However, it was revealing that all bar one of those studies were on salmonids - a taxon under immense pressure from the growth of the fish farming industry (Bradbury et al. 2020) and poorly designed stocking programmes (Naish et al. 2007; Fraser 2008; Araki and Schmid 2010). A further three studies modelled scenarios involving an invasive alien taxon and a salmonid fish. Day et al. (2020) explored how Trojan Y chromosomes might be used to eliminate the invasive brook trout, *Salvelinus fontinalis* Mitchill 1814, in an area naturally populated with westslope cutthroat trout, Della Croce et al. (2014) examined how river topology influenced hybridisation between rainbow trout and native cutthroat trout, and Gobin et al. (2018) found that the evolution of lake whitefish, *Coregonus clupeafomis* Mitchill 1818, in response to fishing was influenced by the invasion of dreissenid bivalves into their habitat. Overall, this review revealed a smaller than expected number of studies exploring the effect of intrusion by non-local stock on wild salmonine populations.

Chapter 5 expanded on the insight gained in Chapters 3 and 4 by developing a novel genetically-explicit eco-evolutionary model to explore how soft and hard selection affected the evolutionary and population dynamics of a salmonine population that had experienced intrusion from non-local genetic stock. The ability of a female to acquire a redd was determined by her genotype at a biallelic locus where having at least one copy of the local, wild-type allele, made a female competitively superior over females who were homozygous at that locus for the non-local allele. As the number of redds increased relative to a fixed initial population size, soft selection weakened (Figure 2, Chapter 5). Soft selection at the female competitive locus had an indirect effect on the strength of hard selection acting on a different trait. This indirect effect influenced the degree of initial maladaptation and, thus, the rate of subsequent evolutionary adaptation, displayed by the second trait, as well as reducing the demographic impact of hard selection on the population (Figure 3, Chapter 5). Finally, a selectively-neutral diagnostic allele for fish of non-local provenance was found to persist in the gene pool of the wild, local population even after both soft and hard selection had purged individuals that expressed maladaptive genotypes. Due to the initial association between genotypes and provenance, a genetic hitchhiking effect was observed, with the frequencies of local and non-local alleles at the diagnostic marker tracking evolution of local and non-local alleles at the selected-for competitive locus (Figure 4, Chapter 5). As stated above, the results from our model provide a possible mechanism as to why some populations that experience intrusion from maladapted individuals are negatively impacted in demographic terms, while others are not, and how the effects of intrusion vary depending on the ecological conditions and, therefore, the strength of selection against non-local genotypes (Chapter 2; Bell et al. 2021). The total population density and the relative frequency of local fish compared to non-local fish appear to be two important regulating factors controlling if and how fast population change occurs under intrusion. Sægrov et al. (1997) report how a wild population of Atlantic salmon was replaced by wild-spawning farmed salmon and their feral offspring. This likely happened due to a low density of wild salmon in the system and a high relative number of escaped farmed fish (Youngson et al. 1998). Competitive displacement of the remaining wild parr by feral offspring (McGinnity et al. 2003) coupled with the production of hybrids displaying depressed fitness (McGinnity et al. 2003, 2007; Muhlfeld et al. 2009) likely drove the extirpation of the local wild individuals. This could have occurred due to soft selection being too weak to stymie introgression and the large number of offspring produced by farmed fish (Glover et al. 2017) ensured enough feral offspring survived to cause the genetic replacement of the wild genotype.

6.2 Limitations

Like all research, the work presented in this thesis has its limitations. While these are discussed in more depth in the data chapters, highlighting the most pertinent issues will hopefully inform future experimental design and monitoring regimes.

The molecular pedigree used in Chapters 2 and 3 lacked sufficient generational depth and, therefore, statistical power, to conduct more in-depth quantitative genetic analyses. The analyses in Chapter 3 were based on only three generations despite there being nine breeding cohorts of data. This was unavoidable due to the lifecycle of salmon from the pedigreed population (Burrishoole, Co. Mayo, Ireland) taking an average of four years. Furthermore, the pedigree comprised of only anadromous individuals since the vast majority of sampling occurred at a downstream fish trap. This meant the effect of mature male parr on any evolutionary dynamics was not accounted for. Different male life history types are known to impact fitness in salmonine populations (Garant et al. 2003; Thériault et al. 2011) so their absence likely influenced the evolutionary dynamics observed.

The unusual structure of the pedigree data affected analyses in Chapter 2. Captive-bred fish were sampled before spawning as they returned from sea and entered the catchment. In contrast, wild-bred fish were not sampled until after they had spawned and were captured as they left the catchment. This sampling regime introduced bias into estimates of relative lifetime reproductive success by underestimating the fitness of captive-bred fish. While this is discussed extensively in Text S1 of Chapter 2, I believe it important to highlight again here. This data structure was an unexpected complication arising from analysing a historical data set comprised of observations collected under various sampling regimes. While it did not prove insurmountable, it did lead to more extensive consideration as to how best to analyse the data. Given the importance of long-term data sets such as ours (Clutton-Brock and Sheldon 2010; Hughes et al. 2017), appreciation of data structure and knowledge of collection regimes is vital for appropriate analysis and interpretation.

The genetically-explicit eco-evolutionary model described in Chapter 5 suffers from the same issues as do all other predictive models. Its design and parameterisation represent trade-offs between biological reality, generality, and computational efficiency. The effects of hard and soft selection on evolutionary dynamics conformed to theoretical predictions, as well as providing a plausible mechanism for decreased productivity following intrusion in a real-world example (Chapter 2). However, these observed dynamics are only model predictions. Such mechanisms would need to be demonstrated experimentally as well as with targeted observational studies of wild populations before more general conclusions can be drawn on the role of soft selection in intruded populations.

6.3 The future of captive breeding programmes

To generalise, there appears to be no single answer to the question of how well captive-bred fish perform in the wild, whether introgression of hatchery genes into wild gene pools will occur, and if either of these phenomena will affect population productivity. This thesis highlights how variable the performance of captive-bred fish relative to wild individuals can be (Chapter 2; Araki et al. 2007a, 2009; White et al. 2018; Lehnert et al. 2020). Additionally, it emphasises how the rate of intrusion/introgression is affected by the selective landscape into which fish are released (e.g. carrying capacity, density dependence, degree of maladaptation; see Chapter 2, Chapter 5, Baskett and Waples 2013, and King et al. 2021). While the escape of domesticated individuals from fish farms should be prevented outright (given the known negative impacts such escapees have on wild populations [McGinnity et al. 1997; Sylvester et al. 2019; Diserud et al.

2020], coupled with salmon farming being a purely profit-based enterprise), the release of captive-bred fish for conservation purposes or to supplement existing fisheries is likely to continue into the future. As such, two questions can be posed: (1) where should captive breeding programmes be implemented and (2) how can such programmes be improved?

6.3 (a) Where should captive breeding programmes be implemented?

Given the potential for deleterious effects arising from the release/escape of captive-bred individuals into wild salmonine populations (Araki et al. 2007a, 2009; O'Sullivan et al. 2020), hatcheries should only be operated on those rivers or catchments where, without human intervention, populations would be extirpated. Stocking should not be used as a 'panacea' for the underlying environmental reasons behind such demographic declines i.e. climate change, habitat destruction (Jonsson and Jonsson 2009; Belletti et al. 2020) and once a self-sustaining population is established, stocking should cease. A captive breeding programme might also perform a societal role, providing employment and allowing local people to engage with the river and its wildlife (Kurlansky 2021). Such societal roles should also be considered when assessing hatchery projects.

Both proposed and ongoing captive breeding programmes should complete regular demographic monitoring of the river into which stocking occurs so as to ensure that density dependent regulation is not a limiting factor in the recipient population. As demonstrated in Chapter 5, the availability of habitat/resources can limit the number of fish that survive through a given life stage. In severely depleted populations, competition between all fish (both wild and captive-bred) is reduced due to the availability of ecological 'space' for the stocked fish to occupy. If the captive breeding programme succeeds and the wild-spawning population becomes self-sustaining, such demographic monitoring regimes should allow for the early detection of the new population equilibrium and, as such, an appropriately-timed cessation to stocking.

6.3 (b) How can captive breeding programmes be improved?

Traditional breeding practises are known to inadvertently promote divergence, both genetically (Ryman and Laikre 1991; Klütsch et al. 2021) and epigenetically (Le Luyer et al. 2017; Wellband et al 2021) between wild fish and those bred in hatcheries. Continued use of captive breeding programmes for conservation or supplemental stocking must be accompanied by increased application of modern hatchery practises that are known to minimise the differences between captive-bred and wild individuals. The annual renewal of broodstock used in propagating hatchery fish (Klütsch et al. 2021), more natural water conditions in rearing tanks (Hyvärinen and Rodewald 2013; Harbicht et al. 2020), and providing shelter (Hyvärinen and Rodewald 2013) have been shown to increase the wild performance of captive-bred fish. Such improved performance has been shown to positively impact the survival of any wild-spawned descendants of hatchery fish through a transgenerational effect (Evans et al. 2014).

6.4 Future research

Interactions between local and non-local salmonines are likely to increase in frequency as aquaculture expands, conservation stocking is used to support a growing number of populations threatened by climate change (Jonsson and Jonsson 2009), and the number of invasions by exotic taxa with which local fish can interbreed increases (Seebens et al. 2021). A better understanding of how natural selection and ecological context shape eco-evolutionary dynamics is required in order to prevent or limit the negative consequences of such insults on wild populations. This thesis has provided evidence of how the proportion of non-local, captive-bred fish affects productivity but also how this impact on productivity may be driven by variation in the type and strength of natural selection – variation itself caused by changes in the availability of ecological resources such as breeding territories. Given the directional trends and increased stochasticity of weather patterns predicted under climate change (IPCC 2021), more research is required to better understand how natural selection will vary as a result, and how changing ecological conditions will further influence variation in the strength and form of selection and its demographic consequences. Such variation could either enable or hinder maladaptive introgression from non-local alleles into local salmonine populations.

A framework to investigate such eco-evolutionary dynamics would ideally consist of experimental field studies coupled with genomic monitoring of the population. Such studies should allow for changes in resource availability to be imposed as well as the controlled introduction of fish from non-local stock. Changes in the availability of resources (such as the extent of spawning habitat) could be managed by controlled flooding or drying of stream channels. The managed intrusion of non-local stock through fish traps could be used to vary the extent of potential introgression from chronic and acute intrusion events (Baskett and Waples 2013). Phenotypes and genetic samples could be taken during routine electrofishing census work with genomics used to estimate evolutionary change without the need for a multi-generational pedigree. This combination of fieldwork, experimental manipulation of the environment of the fish, and genomics would allow for the effects of sudden changes in the evolutionary landscape (through climatic stochasticity, intrusion, or both) to be quantified within a single generation. Knowledge of how variation in ecological conditions and variation in the genetic composition of populations influences evolutionary and demographic outcomes would benefit the design of conservation strategies and stock management in an increasingly variable world.

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