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When phenotypes fail to illuminate underlying genetic processes in fish and fisheries science

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Abstract

Advances in genetic and genomic technologies have become widely available and have potential to provide novel insights into fish biology and fisheries science. In the present overview, we explore cases for which genomic analyses have proven instrumental in the rejection of hypotheses that have been well-motivated based on phenotypic and ecological properties of individuals and populations. We focus on study systems for which information derived using genomic tools contradicts conclusions drawn from traditional fisheries science methodologies and assumptions. We further illustrate the non-intuitive interplay of genomics and ecology in Atlantic salmon (*Salmo salar* L.) owing to the recently detected genetic architecture of age at maturity in this species. To this end, we explore a salmon management strategy applied in Québec, Canada and find that management measures aimed at protecting large, old individuals can lead to unexpected and undesired outcomes. Finally, we envisage ways in which genomic tools could be used more effectively in contemporary fisheries research and how their application could illuminate the ecological and evolutionary drivers of species and ecosystem dynamics.

Keywords Adaptation, Conservation, Eco-evolutionary dynamics, Fisheries management, Life-history evolution, Population genetics

Introduction

As phrased by Plato in his dialogue Phaedrus, "*Things are not always as they seem; the first appearance deceives many*." Population genetic and genomic approaches have proven this to be the case for life-history and population dynamics of several fish species, leading to misleading, if not false, conclusions about the resilience and recoverability of populations and ill-advised management. Thus, not only can genetically based investigations provide deeper knowledge about our study systems, they can also completely reverse our perception of the causal processes and mechanisms underlying observed patterns. Here, we provide an overview of situations for which genomic analyses have proven instrumental to the rejection of hypotheses that have been well-motivated based on the ecological properties of individuals and populations. To this end, we focus on study systems for which information derived using genomic tools contradicts conclusions drawn from traditional fisheries science methodologies and assumptions. In addition to reviewing recent literature, we illustrate the non-intuitive interplay of genomics and ecology through empirical model simulations. We show how an Atlantic salmon (*Salmo salar* L.) management strategy applied in Québec, Canada, aimed at protecting large reproductive individuals, can lead to unexpected and undesirable outcomes owing to the recently detected genetic architecture of the age at maturity in this species (Barson *et al.*, 2015).

The words 'evolution' and 'genetic' enter the lexicon of fisheries science

Concerns regarding the selective removal of large, old individuals by fishing date from at least the 19th Century in Newfoundland (Hutchings *et al.*, 2002) and the UK (Smith, 1994) and as a possibly general feature of fisheries in the early 20th Century (Ricker, 1981). Following the detailed work by Handford *et al.* (1977) and Ricker (1981), the evolutionary consequences of such selection gained the attention of a wider audience in the late 1980s and early 1990s. Analyses of fitness landscapes of Atlantic cod (*Gadus morhua* L.) (Grey and Law 1989; Hutchings, 1995; Heino *et al.*, 2002) and other species (Stokes *et al.*, 1993), coupled with empirical selection experiments on Atlantic silverside (*Menidia menidia*; Conover and Munch, 2002), revealed that increased mortality, especially when size-selective, can cause genetically based reductions in fish age and size at maturity over a few generations. Traces of fishing-induced evolution (hereafter FIE) have since been investigated in numerous populations of marine and freshwater species subject to intensive fishing (see reviews by Devine *et al.*, 2012; Audzijonyte *et al.*, 2013; Heino *et al.*, 2015). The emerging message was that decreasing trends in the age and size at maturity of fishes can reflect evolutionary shifts towards younger maturing, faster growing phenotypes which, in the presence of high fishing mortality, have higher individual fitness than later maturing, slower growing individuals (Dieckmann and Heino, 2007; Law, 2007; Heino *et al.*, 2015). As phrased by Richard Law (2007), in the presence of selection and heritability, some evolutionary responses in fish life histories to intensive fishing seem inevitable based on the principles of the breeder's equation, $R = h^2S$, where the response to selection, R, is a function of trait heritability, h^2, and the selection differential, S. Of course, this need not mean that phenotypic trends similar to those predicted by FIE models actually reflect selection responses to fisheries.

Hypothesized FIE is instead population replacement

On the Baltic Sea coast of Estonia, in Matsalu Bay, Eurasian perch (*Perca fluviatilis* L.) age and size at maturity decreased across a 24-year period. The change in perch life-histories was coincident with a dramatic change in fishing intensity from the Soviet-regulated 1980s to the unregulated fishing period associated with the early decades of Estonian independence (Pukk *et al.*, 2013). As estimated from scale growth patterns, the trend in perch life-histories looked very similar to trends claimed to be reflective of FIE in other fish species across the North Sea and the Atlantic; indeed, the most dramatic phenotypic shifts matched the years when fishing intensity dramatically increased.

Pukk *et al.* (2013), however, went further by expanding the phenotypic investigation with population genetic analyses. Fish were genotyped at 11 microsatellite loci, which revealed a clear genetic clustering between young and late maturing phenotypes. The trend reflected by the phenotypic data mirrored, in fact, the change in the relative frequencies of two genetically distinctive groups of perch. In the early part of the period, the early and small maturing group in Matsalu Bay occurred infrequently but their incidence rapidly increased during 1990s. At the same time, the population had experienced a bottleneck but retained its diversity, suggesting that the causal mechanism behind the change in the age and size at maturity could be attributed to local population collapse and replacement (immigration) by a genetically and phenotypically distinct perch population in the region. The study by Pukk *et al.* (2013) demonstrates how relatively simple genetic analyses can completely reverse a well-motivated hypothesis of FIE; demonstration of evolution requires genetic evidence to support phenotypic trends (Kuparinen and Merilä, 2007).

What constitutes the evidence for FIE – academic side-tracks

Debate about the adequateness of phenotypic observations to test for FIE, as opposed to the necessity of obtaining supportive genetic evidence, has gained unduly much attention in fisheries biology. At its core, the debate stems from the impossibility of conclusively demonstrating that detectable temporal trends in fish phenotypes reflect life-history evolution caused by fishing. Even common-garden experiments have failed in this respect. The selection experiment conducted on silverside by Conover and Munch (2002) is in many ways a cornerstone study of FIE, as it demonstrated how rapidly life-history traits can change under highly intense size-selective harvesting. But as soon as harvesting was relaxed and populations were allowed to recover, phenotypic traits in one of the selected lines rapidly shifted towards their original values (Conover *et al.,* 2009). Either stabilizing selection in the absence of ‘fishing’ was very strong or a large component of the original phenotypic shifts were related to plastic changes in growth and maturity, possibly in response to changes in population density.

Probabilistic maturation reaction norms (hereafter PMRNs) offered a potentially informative analytical tool to disentangle genetic change from plastic change in age and size at maturity arising from changes in individual fish growth. Their utility has been intensively discussed elsewhere (*e.g*., Marshall and Browman, 2007) and will not be repeated here. Despite the potential of PMRNs as a tool to understand components of phenotypic changes in fish, their role in merging evolution and genetic thinking to fisheries science has been relatively minor. At its core, the use of PMRNs to detect FIE incorporates the implicit assumption that changes to bivariate reaction norms between age and size at maturity represent genetic rather than non-genetic change(s). Uusi-Heikkilä *et al*. (2010) explored the veracity of this assumption in their common-garden selection experiment on zebrafish (*Danio rerio*). They found that genetically similar zebrafish reared under different feeding regimes exhibited shifts in PMRNs among the feeding regimes; after five generations of selection, when fish were both phenotypically and genetically differentiated, PMRNs did not show any differences among selection lines (Uusi-Heikkilä *et al*., 2010).

From a science-communication perspective, the outburst of studies on FIE and the debate surrounding the efficacy of various methodologies to detect FIE have undoubtedly increased the evolutionary awareness of fisheries scientists and managers. On the other hand, the debate surrounding the evidence of evolution distanced many from the core objectives of fisheries science: (i) sustainable harvesting; (ii) provision of science advice to decision-makers over managerially meaningful time frames (usually less than 10 years); and (iii) maintenance of the diversity, stability, and functioning of aquatic ecosystems (but see Law and Plank, 2018). Thus, the question of whether phenotypic changes in fishes reflect evolution is somewhat irrelevant; what matters is the degree to which FIE affects things such as species resilience, recovery following depletion, and population sustainability under exploitation (*e.g.*, Hutchings and Fraser 2008).

What can genetic diversity tell about population structure?

Census (N_c) and effective population (N_e) sizes are fundamental components of conservation biology. One key manifestation is the ‘50/500 rule’ (Franklin *et al.*, 2014a) which has been used to guide threatened species assessments. Carved in the minds of several generations of biologists, the rule states that N_e must exceed 50 individuals to avoid inbreeding depression and 500 individuals to maintain evolutionary potential (Franklin *et al.*, 2014a). This guidance underpins the population-size thresholds for the IUCN’s Criterion C of < 250 mature individuals for Critically Endangered species, < 2500 for Endangered species, and < 25,000 for Vulnerable species (IUCN 2017).

Despite its popularity in the management of natural populations and the assessment of species extinction probabilities, the rule has never been conclusively validated (*e.g.*, Jamieson and Allendorf, 2012; Franklin *et al.*, 2014a,b). Strikingly, in contrast to expectations, there are numerous examples of naturally small but ecologically and genetically stable fish populations whose estimated values of N_e and N_c fall well below those specified by the 50/500 rule, and even further below the 100/1000 rule recommended by Frankham *et al.* (2014a).

One such set of brook trout (*Salvelinus fontinalis*) populations is located on Cape Race, Newfoundland. These trout are isolated (gene flow is unable to supply genetic variation), not currently subjected to human interference (including fishing) and likely never have been, and exhibit adaptive variability in life history (Hutchings, 1993). The effective number of breeders (N_b) has been estimated for several of the populations (Wood *et al.*, 2014). The median N_b for the 19 populations is 46; for 11 of the populations, N_b is less than 50. Waples *et al.* (2013) have estimated the ratio of N_b / N_e for vertebrates with overlapping generations to be 1.06. If one applies this ratio to the estimates of N_b for the trout populations, the median effective population size is 49 and the range in N_e for all 19 populations is 16 to 264. In another set of brook trout populations, almost all estimates of N_e for 14 naturally small riverine populations were less than 500, and several were less than 50 (Ruzzante *et al.*, 2016). Whiteley *et al.* (2010) estimated contemporary N_e to be less than 100 in several isolated populations of cutthroat trout (*Oncorhynchus clarkii*) in southeastern Alaska.

As noted by Fraser (2017), and experimentally explored in *Drosophila melanogaster* by Schou *et al*. (2017), there are likely to be numerous different factors responsible for shaping, maintaining or removing genetic diversity in populations that have small N_e, rendering application of the 50/500 rule increasingly problematic. That said, one could make the argument that those populations that persist despite low N_e are able to do so because they were able to purge genetic loads. Thus, the 50/500 rule may be useful in cases where data are sparse and rules must be relied upon (Franklin *et al*., 2014b).

Many population genetic studies have suggested that N_e is typically large for exploited marine fish (Cano *et al*., 2008), although this hypothesis has been questioned (*e.g.*, Hauser and Carvalho, 2008). Lack of spatial differentiation in neutral markers has been interpreted to signal large amounts of gene flow and lack of population structuring, leading to coarse (and non-biologically based) management-unit structuring. For example, neutral genetic diversity of Atlantic cod (*Gadus morhua*) in the Gulf of St. Lawrence does not show any temporal change across an 80-year period covering the time before fishing intensified up to the point the population was severely overfished (Therkieldsen *et al*., 2010). These findings suggest that neutral genetic markers might not be useful to resolve the ecological state and functioning of some populations. Indeed, comparisons of neutral (F_{ST}) with quantitative trait (Q_{ST}) differentiation show systematically high levels of Q_{ST}, even in the absence of neutral differentiation (Cano *et al*., 2008). While isolation-by-distance should generate neutral differentiation, at least to some degree, large N_e can also simply buffer against the drift causing neutral differentiation and, thus, mask finer structuring of local populations (Cano *et al*., 2018).

Spatial mismatches between management and biological units: co-existing ecotypes

A fundamental challenge to successful management and threat mitigation is to correctly match the spatial scale of marine fish management units with a spatial scale that appropriately reflects genetically different adaptive responses to environmental change. Spatial mismatches between management units and biological or evolutionary units can negatively influence the effectiveness of efforts to alleviate the impacts of fishing and climate change. An empirically strong example of such spatial mismatches is emerging for Atlantic cod that inhabit coastal waters of Skagerrak (marine waters bounded by Norway, Sweden and Denmark). Commercial fisheries for Norwegian cod south of 62° are managed as part of a single North Sea cod management unit (www.ices.dk). Yet, for almost a decade, a compelling argument has been made that cod inhabiting fjords and coastal waters along the Norwegian Skagerrak are genetically distinctive from North Sea cod (Knutsen *et al.*, 2011).

Recent analyses of single nucleotide polymorphism (SNP) data have revealed the co-existence of two genotype clusters: a ‘fjord’ ecotype dominates the waters of the inner fjords, whereas a ‘North Sea’ ecotype is often predominant in outer-fjord waters (Knutsen *et al.*, 2018). These ecotypes appear to differ in growth rate (Kuparinen *et al.*, 2016; Knutsen *et al.*, 2018) and spawning success (Roney *et al.*, 2018). Thus, despite their high dispersal capabilities and concomitant potential for gene flow, genomic research has revealed the co-existence of genetically differentiated ecotypes of Atlantic cod at spatial scales exceedingly smaller than those at which harvest strategies, and other management actions, are assigned.

Ecological consequences of the genetic trait architecture

Traditionally, quantitative traits such as age at maturity are assumed to be controlled by many genes with small, additive effects (Roff, 2002). Under this assumption, the traits of offspring typically reflect the average of the parental trait values, and changes in the population average trait value can be predicted by the breeder’s equation. This model predicts that trait change from one generation to the next is the product of heritability and the change in the trait value from birth to reproductive ages (that is, the change in the trait value average owing to selection). However, the hypothesis that life-history traits are controlled by multiple loci has recently been challenged by the newly discovered genetic architecture of age at maturity in Atlantic salmon (*Salmo salar*). Barson *et al.* (2015) found that the time salmon spend at sea before reproductive migration back to fresh water is strongly regulated by a single locus with sexually dimorphic expression of heterozygotes.

The detected mode of inheritance obviously largely differs from the principles of traditional quantitative genetics and suggests that responses to fishing-induced selection might differ considerably from predictions based on the premise that multiple, rather than single, loci underpin the genetic architecture of life-history traits. Indeed, simulations contrasting the single-locus scenario (with sexually dimorphic expression) with the scenario in which sea-age at maturity is determined by multiple loci with additive effects suggests that the eco-evolutionary consequences of targeting large, old individuals can fundamentally differ (Kuparinen and Hutchings, 2017). Multiple-locus control leads to decreasing age at maturity if fishing targets old individuals, whereas no clear change in age at maturity can be detected under single-locus control. Instead, single-locus control leads to increased variability in age at maturity both temporally and among replicated simulations (resembling evolutionary trajectories of individual populations) (Kuparinen and Hutchings, 2017).

In practice, such an outcome means that a lack of phenotypic trends in an intensively harvested population need not imply that fishing has not caused genetic change. Whilst acknowledging increased stochasticity in the single-locus scenarios, the simulations suggest that ecologically identical populations can evolve in different directions under the same selection pressure, such that differences in phenotypes among populations need not constitute a reliable signal of differences in the ecological properties of the populations in response to the fishing pressures they experience. In brief, ecological differences through time or across space among populations need not necessarily imply analogous genetic differences. Below, we illustrate this, using a management strategy for Atlantic salmon in Canada.

Evaluation of a salmon fishing management strategy in light of genomics of maturity

As fisheries scientists become increasingly aware of the potential evolutionary consequences of fishing, management strategies accounting for evolutionary consequences of fishing have increasingly been called for (*e.g*., Jörgensen *et al.*, 2007). For example, 'spawn-at-least-once' strategies and upper size limits are likely to cause unwanted selection towards smaller, earlier maturing phenotypes (Kuparinen *et al.*, 2009), such that alternative methods to regulate fishing are being sought.

One sattempt to protect larger, older spawners and to minimize selection against these phenotypes exists for Atlantic salmon in Québec, Canada, where regulations stipulate that fish longer than 63 cm (*i.e.*, 2 sea-winter (SW) and previous spawners) must be released in some rivers (Québec, 2016). Following principles of traditional quantitative genetics and the assumption that age at maturity is determined by multiple loci with small additive effects (Roff, 2002), this management strategy should favour older (>1 SW) age at maturity, eventually increasing the abundance of such phenotypes. However, in the presence of sexually dimorphic, single-locus control of age at maturity (Barson *et al.*, 2015), we find that the consequences of focusing fishing pressure on younger individuals are far from intuitive.

To explore the ecological and evolutionary impacts of fishing exclusively 1 SW salmon, we conducted individual-based simulations, where the eco-evolutionary dynamics of the populations were tracked through time across 100-year periods prior to, during, and after fishing (model details are fully described by Kuparinen and Hutchings, 2017). The targeting of 1 SW mature salmon generated selection favouring older age at maturity such that maturity tended to evolve towards older ages to a greater extent than in the absence of fishing. To some extent, single-locus control buffered against this selection, leading to smaller and more variable evolutionary shifts in age at maturity than in the multi-locus scenario (Fig. 1; 1st row). Given that alleles favouring delayed maturity in the single-locus control scenario are sexually divergent, later maturity among females than males carrying the same alleles led to a lower proportion of females in the spawning population (Fig. 1; 2nd row).

Salmon evolved more rapidly to older ages at maturity in the multi-locus scenario, thus avoiding more efficiently the targeting of 1 SW salmon, as reflected by lower catches. By contrast, in the single-locus scenario, the higher abundance of 1 SW salmon led to greater stability in catch (Fig. 1; 3rd row). The same pattern is reflected by the proportion of mature fish in the population, compared to the unexploited population size: in the presence of fishing, the prevalence of 1 SW fish under the single-locus scenario means greater losses of mature fish to fisheries and, conversely, a lower proportion of mature fish remaining for spawning (Fig. 2). In the absence of fishing, however, the pattern is reversed, as the single-locus scenario facilitates higher abundance of 1 SW mature fish when compared to the multi-locus scenario, where fish have evolved to mature later (Fig. 1; 4th row).

In summary, single-locus control of age at maturity buffers against evolutionary impacts of fishing (Fig. 1) and maintains higher life-history diversity. This makes the life-history structure more robust to changing selection pressures, leading to smaller temporal changes in catch. When fishing pressure is relaxed, the rate of population recovery should be faster under the single-locus scenario, as a larger proportion of the population is mature. On the other hand, there is considerably greater uncertainty in both evolutionary and ecological population properties under the single-locus scenario, notably with respect to population size (Fig. 2), increasing the challenge in evaluating conservation status. When coupled with environmental stochasticity and extreme disturbances, greater uncertainty in population demographic dynamics can negatively, sometimes severely, affect population viability (Lande, 1993).

Future directions

In the present overview, we have highlighted cases for which genomic analyses have proven instrumental in the rejection of hypotheses that have been well-motivated, based on phenotypic and ecological properties of individuals and populations. In this concluding section, we explore how the ongoing rapid development of genetic methods (e.g., RNA-seq), markers (e.g., SNPs) and candidate genes (or chromosomal inversions) is likely to provide new insights into the ecological dynamics of fish species and the functioning of aquatic ecosystems (Oomen and Hutchings, 2017).

One obvious application is stock identification (Hard, 1995; Bernatchez *et al.*, 2017). Currently, the distinction between separately managed units in the marine realm is made arbitrarily, from an ecological and (or) evolutionary perspective, while recent research findings suggest much finer scale structuring of populations, likely driven by local adaptations and reproductive barriers (e.g., Knutsen *et al.*, 2011, 2018; Roney *et al.*, 2018). While in theory distinct marine populations could be identified by rigorous sampling across wide spatial scales (Bernatchez *et al.*, 2017), there are several practical problems. Assuming stable and symmetric dispersal, genetic differentiation should increase by distance, but in practice dispersal especially at the larval stage is largely driven by oceanographic currents, which further depend on climatic regimes. Coupling oceanographic model projections with genetic sampling and analyses (so-called ‘seascape genetics’) has, therefore, been suggested as an effective way to improve the identification of populations, their migration patterns, and to estimate connectivity of populations (Baltasar-Soares *et al*., 2017). Similarly, improved clarity of the fluxes that govern neutral genetic diversity (and, thus, reduced noise in the data) facilitates the detection of candidate genes and functionally coding genome regions responsible for ecologically important traits (Baltasar-Soares *et al*., 2017).

From the fundamental ecological point of view, intensive sampling of genetic diversity is likely to shed some light on macroecological properties, such as population boundaries, dispersal, gene flow and adaptation (Hard, 1995). One area of research that has benefitted tremendously from concerted efforts in this regard is our understanding of the consequences of interactions between farmed and wild Atlantic salmon (superbly reviewed by Glover *et al*., 2017). It might also provide insights into the underlying causes of drastic changes in population abundances, although genetic signals of bottlenecks can also be easily masked by noise or other confounding processes (see the discussion above; Cano *et al*., 2008).

More detailed knowledge about the drivers of population dynamics and demographic properties of populations clearly requires information from life histories and changes in key fitness-related traits. Apart from the traditional way to sample phenotypes, genetic sampling has potential to contribute, given that candidate genes or genomic regions for key traits can be known at least with some accuracy. At an extreme, allele frequencies of so-called ‘supergenes’ coding for fitness-related traits (e.g., Erickson *et al*., 2018) and life-history strategies (or large parts thereof, such as *vgll3* for Atlantic salmon (Barson *et al*., 2015) and *greb1L* in steelhead, *Oncorhynchus mykiss* (Micheletti *et al*., 2018)) have potential to inform proxies of population age and size structure and the reproductive capacity of the population. Such tools are only available for few species, but new genomic discoveries are likely to occur in the near future (Macqueen *et al.*, 2017).

Although the primary focus of this perspective has been on phenotypes, genotypes and populations, these entities do not exist independently of the ecosystems of which they are part. Genomic tools can be used, for example, to clarify feeding links among species through genetic analyses of gut contents (Leray *et al.*, 2013). Environmental DNA (Taberlet *et al.*, 2018) has potential to identify incipient changes to community structure resulting from species invasions and distributional shifts. The increased resolution of trophic structure and food-web dynamics offered by genomic analyses can thus strengthen efforts to implement ecosystem-based fisheries management (Kuparinen and Uusi-Heikkilä, 2018).

Concordant with arguments made two decades ago (Browman, 2000; Hutchings, 2000), the ultimate value of studying the ecology and evolution of fishes lies in the hope of strengthening our capacity to predict how short- and long-term anthropogenic, biological, and physical environmental perturbations influence individual life history, resilience, per capita population growth, community interactions, and ecosystem stability. Viewed in this light, the capacity of genomics to illuminate our understanding of the causal mechanisms and consequences of phenotypic change has never been greater.

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Table 1 The probabilities of postponing maturity beyond threshold ages for $\text{Vgll3}_{\text{TOP}}$ genotype × sex, as estimated by Barson *et al.* (2015). These probabilities were utilized in salmon fishing simulations, in the model where the age at maturity was coded by one locus having two alleles (0 and 1). The table is reproduced from Kuparinen and Hutchings (2017).

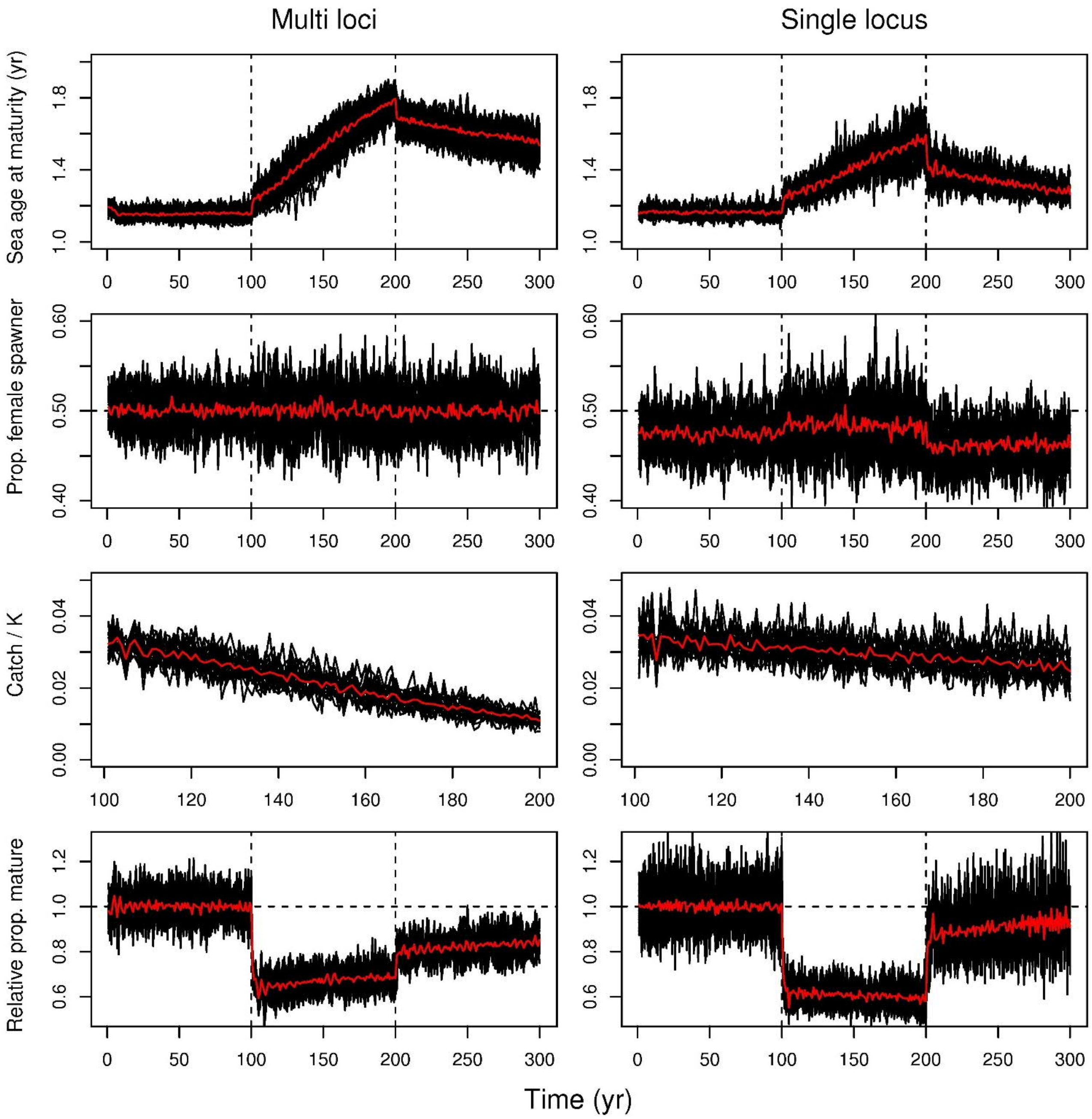
Sex		**Homozygote (11)**	**Heterozygote (10 or 01)**	**Homozygote (00)**
Female	2 SW → 3 SW	0.754	0.949	0.983
	1 SW → 2 SW	0.101	0.404	0.665
Male	2 SW → 3 SW	0.266	0.277	0.835
	1 SW → 2 SW	0.058	0.061	0.467

Figure legends

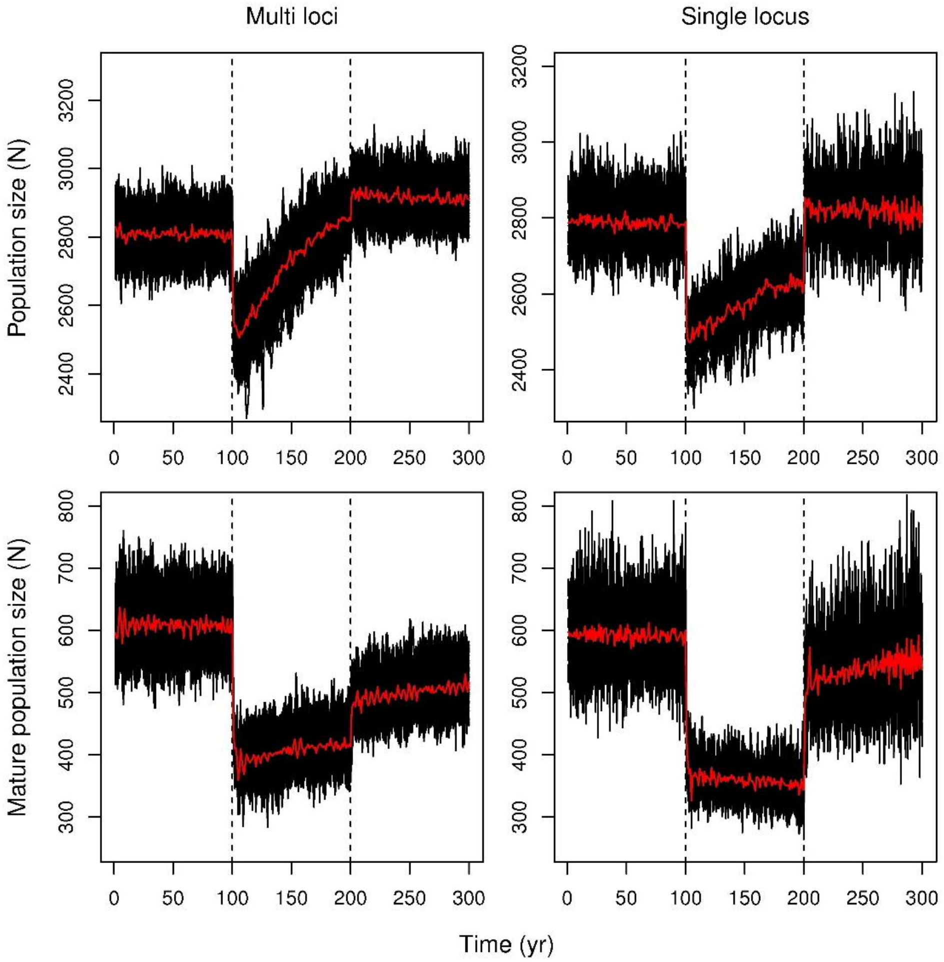
Fig. 1 The role of genetic architecture of the age at maturity on eco-evolutionary impacts of salmon fishing targeting 1SW (sea-winter) mature fish prior to, during, and after fishing (F=0.4, corresponding to a harvest rate of 33%). The evolution of sea age at maturity is shown in the topmost panels. The second panel row shows the proportion of females in the spawning population. The third panel row describes the number of salmon caught, standardized by the population carrying capacity (5000 individuals); note that the abscissa in this row of figures differs from those of the other rows, as it is focused on the fishing period only. The fourth panel row illustrates the proportion of mature individuals in the population, standardized by the size of the unfished population. In each panel, 20 independent simulation runs are shown with black lines and the averages across them by a red solid line. Vertical dashed lines mark the beginning and the end of the fishing period (years 100-200).

Fig. 2 The sizes of the entire and the mature populations under multi-locus and single-locus control of age at maturity. Figure components are the same as in Fig. 1.

Fig. 1


Multi loci
Single locus
Sea age at maturity (yr)
1.0
1.4
1.8
Prop. female spawner
0.40
0.50
0.60
Catch / K
0.00
0.02
0.04
Relative prop. mature
0.6
0.8
1.0
1.2
0
50
100
150
200
250
300
120
140
160
180
Time (yr)

553 **Fig. 2**


Multi loci
Single locus
Population size (N)
Mature population size (N)
2400
2600
2800
3000
3200
300
400
500
600
700
800
0
50
100
150
200
250
300
Time (yr)