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

**Year:** 2019

**Version:** Accepted version (Final draft)

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**Please cite the original version:**

Kuparinen, A., & Hutchings, J. A. (2019). When phenotypes fail to illuminate underlying genetic processes in fish and fisheries science. *ICES Journal of Marine Science*, 76(4), 999-1006.  
<https://doi.org/10.1093/icesjms/fsz002>

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

3  
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15 **Abstract**

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

30

31

32

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

35

36

37 **Introduction**

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

54

55 **The words ‘evolution’ and ‘genetic’ enter the lexicon of fisheries science**

56 Concerns regarding the selective removal of large, old individuals by fishing date from at least  
57 the 19<sup>th</sup> Century in Newfoundland (Hutchings *et al.*, 2002) and the UK (Smith, 1994) and as a  
58 possibly general feature of fisheries in the early 20<sup>th</sup> Century (Ricker, 1981). Following the  
59 detailed work by Handford *et al.* (1977) and Ricker (1981), the evolutionary consequences of

60 such selection gained the attention of a wider audience in the late 1980s and early 1990s.  
61 Analyses of fitness landscapes of Atlantic cod (*Gadus morhua* L.) (Grey and Law 1989;  
62 Hutchings, 1995; Heino *et al.*, 2002) and other species (Stokes *et al.*, 1993), coupled with  
63 empirical selection experiments on Atlantic silverside (*Menidia menidia*; Conover and Munch,  
64 2002), revealed that increased mortality, especially when size-selective, can cause genetically  
65 based reductions in fish age and size at maturity over a few generations. Traces of fishing-  
66 induced evolution (hereafter FIE) have since been investigated in numerous populations of  
67 marine and freshwater species subject to intensive fishing (see reviews by Devine *et al.*, 2012;  
68 Audzijonyte *et al.*, 2013; Heino *et al.*, 2015). The emerging message was that decreasing trends  
69 in the age and size at maturity of fishes can reflect evolutionary shifts towards younger maturing,  
70 faster growing phenotypes which, in the presence of high fishing mortality, have higher  
71 individual fitness than later maturing, slower growing individuals (Dieckmann and Heino, 2007;  
72 Law, 2007; Heino *et al.*, 2015). As phrased by Richard Law (2007), in the presence of selection  
73 and heritability, some evolutionary responses in fish life histories to intensive fishing seem  
74 inevitable based on the principles of the breeder's equation,  $R = h^2S$ , where the response to  
75 selection,  $R$ , is a function of trait heritability,  $h^2$ , and the selection differential,  $S$ . Of course, this  
76 need not mean that phenotypic trends similar to those predicted by FIE models actually reflect  
77 selection responses to fisheries.

78

### 79 **Hypothesized FIE is instead population replacement**

80 On the Baltic Sea coast of Estonia, in Matsalu Bay, Eurasian perch (*Perca fluviatilis* L.) age and  
81 size at maturity decreased across a 24-year period. The change in perch life-histories was  
82 coincident with a dramatic change in fishing intensity from the Soviet-regulated 1980s to the

83 unregulated fishing period associated with the early decades of Estonian independence (Pukk *et*  
84 *al.*, 2013). As estimated from scale growth patterns, the trend in perch life-histories looked very  
85 similar to trends claimed to be reflective of FIE in other fish species across the North Sea and the  
86 Atlantic; indeed, the most dramatic phenotypic shifts matched the years when fishing intensity  
87 dramatically increased.

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

101

## 102 **What constitutes the evidence for FIE – academic side-tracks**

103 Debate about the adequateness of phenotypic observations to test for FIE, as opposed to the  
104 necessity of obtaining supportive genetic evidence, has gained unduly much attention in fisheries  
105 biology. At its core, the debate stems from the impossibility of conclusively demonstrating that

106 detectable temporal trends in fish phenotypes reflect life-history evolution caused by fishing.  
107 Even common-garden experiments have failed in this respect. The selection experiment  
108 conducted on silverside by Conover and Munch (2002) is in many ways a cornerstone study of  
109 FIE, as it demonstrated how rapidly life-history traits can change under highly intense size-  
110 selective harvesting. But as soon as harvesting was relaxed and populations were allowed to  
111 recover, phenotypic traits in one of the selected lines rapidly shifted towards their original values  
112 (Conover *et al.*, 2009). Either stabilizing selection in the absence of ‘fishing’ was very strong or  
113 a large component of the original phenotypic shifts were related to plastic changes in growth and  
114 maturity, possibly in response to changes in population density.

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

129           From a science-communication perspective, the outburst of studies on FIE and the debate  
130 surrounding the efficacy of various methodologies to detect FIE have undoubtedly increased the  
131 evolutionary awareness of fisheries scientists and managers. On the other hand, the debate  
132 surrounding the evidence of evolution distanced many from the core objectives of fisheries  
133 science: (i) sustainable harvesting; (ii) provision of science advice to decision-makers over  
134 managerially meaningful time frames (usually less than 10 years); and (iii) maintenance of the  
135 diversity, stability, and functioning of aquatic ecosystems (but see Law and Plank, 2018). Thus,  
136 the question of whether phenotypic changes in fishes reflect evolution is somewhat irrelevant;  
137 what matters is the degree to which FIE affects things such as species resilience, recovery  
138 following depletion, and population sustainability under exploitation (*e.g.*, Hutchings and Fraser  
139 2008).

140

#### 141 **What can genetic diversity tell about population structure?**

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

150           Despite its popularity in the management of natural populations and the assessment of  
151 species extinction probabilities, the rule has never been conclusively validated (*e.g.*, Jamieson



152 and Allendorf, 2012; Franklin *et al.*, 2014a,b). Strikingly, in contrast to expectations, there are  
153 numerous examples of naturally small but ecologically and genetically stable fish populations  
154 whose estimated values of  $N_e$  and  $N_c$  fall well below those specified by the 50/500 rule, and even  
155 further below the 100/1000 rule recommended by Frankham *et al.* (2014a).

156 One such set of brook trout (*Salvelinus fontinalis*) populations is located on Cape Race,  
157 Newfoundland. These trout are isolated (gene flow is unable to supply genetic variation), not  
158 currently subjected to human interference (including fishing) and likely never have been, and  
159 exhibit adaptive variability in life history (Hutchings, 1993). The effective number of breeders  
160 ( $N_b$ ) has been estimated for several of the populations (Wood *et al.*, 2014). The median  $N_b$  for the  
161 19 populations is 46; for 11 of the populations,  $N_b$  is less than 50. Waples *et al.* (2013) have  
162 estimated the ratio of  $N_b/N_e$  for vertebrates with overlapping generations to be 1.06. If one  
163 applies this ratio to the estimates of  $N_b$  for the trout populations, the median effective population  
164 size is 49 and the range in  $N_e$  for all 19 populations is 16 to 264. In another set of brook trout  
165 populations, almost all estimates of  $N_e$  for 14 naturally small riverine populations were less than  
166 500, and several were less than 50 (Ruzzante *et al.*, 2016). Whiteley *et al.* (2010) estimated  
167 contemporary  $N_e$  to be less than 100 in several isolated populations of cutthroat trout  
168 (*Oncorhynchus clarkii*) in southeastern Alaska.

169 As noted by Fraser (2017), and experimentally explored in *Drosophila melanogaster* by  
170 Schou *et al.* (2017), there are likely to be numerous different factors responsible for shaping,  
171 maintaining or removing genetic diversity in populations that have small  $N_e$ , rendering  
172 application of the 50/500 rule increasingly problematic. That said, one could make the argument  
173 that those populations that persist despite low  $N_e$  are able to do so because they were able to

174 purge genetic loads. Thus, the 50/500 rule may be useful in cases where data are sparse and rules  
175 must be relied upon (Franklin *et al.*, 2014b).

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

190

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

192 A fundamental challenge to successful management and threat mitigation is to correctly match  
193 the spatial scale of marine fish management units with a spatial scale that appropriately reflects  
194 genetically different adaptive responses to environmental change. Spatial mismatches between  
195 management units and biological or evolutionary units can negatively influence the  
196 effectiveness of efforts to alleviate the impacts of fishing and climate change. An empirically

197 strong example of such spatial mismatches is emerging for Atlantic cod that inhabit coastal  
198 waters of Skagerrak (marine waters bounded by Norway, Sweden and Denmark). Commercial  
199 fisheries for Norwegian cod south of 62° are managed as part of a single North Sea cod  
200 management unit ([www.ices.dk](http://www.ices.dk)). Yet, for almost a decade, a compelling argument has been  
201 made that cod inhabiting fjords and coastal waters along the Norwegian Skagerrak are  
202 genetically distinctive from North Sea cod (Knutsen *et al.*, 2011).

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

211

## 212 **Ecological consequences of the genetic trait architecture**

213 Traditionally, quantitative traits such as age at maturity are assumed to be controlled by many  
214 genes with small, additive effects (Roff, 2002). Under this assumption, the traits of offspring  
215 typically reflect the average of the parental trait values, and changes in the population average  
216 trait value can be predicted by the breeder’s equation. This model predicts that trait change from  
217 one generation to the next is the product of heritability and the change in the trait value from  
218 birth to reproductive ages (that is, the change in the trait value average owing to selection).  
219 However, the hypothesis that life-history traits are controlled by multiple loci has recently been

220 challenged by the newly discovered genetic architecture of age at maturity in Atlantic salmon  
221 (*Salmo salar*). Barson *et al.* (2015) found that the time salmon spend at sea before reproductive  
222 migration back to fresh water is strongly regulated by a single locus with sexually dimorphic  
223 expression of heterozygotes.

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

236         In practice, such an outcome means that a lack of phenotypic trends in an intensively  
237 harvested population need not imply that fishing has not caused genetic change. Whilst  
238 acknowledging increased stochasticity in the single-locus scenarios, the simulations suggest that  
239 ecologically identical populations can evolve in different directions under the same selection  
240 pressure, such that differences in phenotypes among populations need not constitute a reliable  
241 signal of differences in the ecological properties of the populations in response to the fishing  
242 pressures they experience. In brief, ecological differences through time or across space among

243 populations need not necessarily imply analogous genetic differences. Below, we illustrate this,  
244 using a management strategy for Atlantic salmon in Canada.

245

### 246 **Evaluation of a salmon fishing management strategy in light of genomics of maturity**

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

253         One attempt to protect larger, older spawners and to minimize selection against these  
254 phenotypes exists for Atlantic salmon in Québec, Canada, where regulations stipulate that fish  
255 longer than 63 cm (*i.e.*, 2 sea-winter (SW) and previous spawners) must be released in some  
256 rivers (Québec, 2016). Following principles of traditional quantitative genetics and the  
257 assumption that age at maturity is determined by multiple loci with small additive effects (Roff,  
258 2002), this management strategy should favour older (>1 SW) age at maturity, eventually  
259 increasing the abundance of such phenotypes. However, in the presence of sexually dimorphic,  
260 single-locus control of age at maturity (Barson *et al.*, 2015), we find that the consequences of  
261 focusing fishing pressure on younger individuals are far from intuitive.

262         To explore the ecological and evolutionary impacts of fishing exclusively 1 SW salmon,  
263 we conducted individual-based simulations, where the eco-evolutionary dynamics of the  
264 populations were tracked through time across 100-year periods prior to, during, and after fishing  
265 (model details are fully described by Kuparinen and Hutchings, 2017). The targeting of 1 SW

266 mature salmon generated selection favouring older age at maturity such that maturity tended to  
267 evolve towards older ages to a greater extent than in the absence of fishing. To some extent,  
268 single-locus control buffered against this selection, leading to smaller and more variable  
269 evolutionary shifts in age at maturity than in the multi-locus scenario (Fig. 1; 1<sup>st</sup> row). Given that  
270 alleles favouring delayed maturity in the single-locus control scenario are sexually divergent,  
271 later maturity among females than males carrying the same alleles led to a lower proportion of  
272 females in the spawning population (Fig. 1; 2<sup>nd</sup> row).

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

283 In summary, single-locus control of age at maturity buffers against evolutionary impacts  
284 of fishing (Fig. 1) and maintains higher life-history diversity. This makes the life-history  
285 structure more robust to changing selection pressures, leading to smaller temporal changes in  
286 catch. When fishing pressure is relaxed, the rate of population recovery should be faster under  
287 the single-locus scenario, as a larger proportion of the population is mature. On the other hand,  
288 there is considerably greater uncertainty in both evolutionary and ecological population

289 properties under the single-locus scenario, notably with respect to population size (Fig. 2),  
290 increasing the challenge in evaluating conservation status. When coupled with environmental  
291 stochasticity and extreme disturbances, greater uncertainty in population demographic dynamics  
292 can negatively, sometimes severely, affect population viability (Lande, 1993).

293

## 294 **Future directions**

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

302         One obvious application is stock identification (Hard, 1995; Bernatchez *et al.*, 2017).  
303 Currently, the distinction between separately managed units **in the marine realm is made**  
304 arbitrarily, from an ecological and (or) evolutionary perspective, while recent research findings  
305 suggest much finer scale structuring of populations, likely driven by local adaptations and  
306 reproductive barriers (e.g., Knutsen *et al.*, 2011, 2018; Roney *et al.*, 2018). While in theory  
307 distinct **marine** populations could be identified by rigorous sampling across wide spatial scales  
308 (Bernatchez *et al.*, 2017), there are several practical problems. Assuming stable and symmetric  
309 dispersal, genetic differentiation should increase by distance, but in practice dispersal especially  
310 at the larval stage is largely driven by oceanographic currents, which further depend on climatic  
311 regimes. Coupling oceanographic model projections with genetic sampling and analyses (so-

312 called ‘seascape genetics’) has, therefore, been suggested as an effective way to improve the  
313 identification of populations, their migration patterns, and to estimate connectivity of populations  
314 (Baltasar-Soares *et al.*, 2017). Similarly, improved clarity of the fluxes that govern neutral  
315 genetic diversity (and, thus, reduced noise in the data) facilitates the detection of candidate genes  
316 and functionally coding genome regions responsible for ecologically important traits (Baltasar-  
317 Soares *et al.*, 2017).

318         From the fundamental ecological point of view, intensive sampling of genetic diversity is  
319 likely to shed some light on macroecological properties, such as population boundaries,  
320 dispersal, gene flow and adaptation (Hard, 1995). One area of research that has benefitted  
321 tremendously from concerted efforts in this regard is our understanding of the consequences of  
322 interactions between farmed and wild Atlantic salmon (superbly reviewed by Glover *et al.*,  
323 2017). It might also provide insights into the underlying causes of drastic changes in population  
324 abundances, although genetic signals of bottlenecks can also be easily masked by noise or other  
325 confounding processes (see the discussion above; Cano *et al.*, 2008).

326         More detailed knowledge about the drivers of population dynamics and demographic  
327 properties of populations clearly requires information from life histories and changes in key  
328 fitness-related traits. Apart from the traditional way to sample phenotypes, genetic sampling has  
329 potential to contribute, given that candidate genes or genomic regions for key traits can be  
330 known at least with some accuracy. At an extreme, allele frequencies of so-called ‘supergenes’  
331 coding for fitness-related traits (e.g., Erickson *et al.*, 2018) and life-history strategies (or large  
332 parts thereof, such as *vgl3* for Atlantic salmon (Barson *et al.*, 2015) and *greb1L* in steelhead,  
333 *Oncorhynchus mykiss* (Micheletti *et al.*, 2018)) have potential to inform proxies of population  
334 age and size structure and the reproductive capacity of the population. Such tools are only



335 available for few species, but new genomic discoveries are likely to occur in the near future  
336 (Macqueen *et al.*, 2017).

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

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

352

### 353 **Acknowledgements**

354 We thank Dylan Fraser for information on salmon fishery management in Québec. The  
355 manuscript has been greatly improved by comments and criticisms offered by Philip McGinnity,  
356 Stewart Grant, and an anonymous reviewer. This work was supported by funding from the  
357 Academy of Finland (grant no. 317495), Discovery Grants from the National Sciences and

358 Engineering Research Council of Canada (NSERC; AK and JAH), and the European Research  
359 Council (COMPLEX-FISH 400820) to AK.

360

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524

525 **Table 1** The probabilities of postponing maturity beyond threshold ages for VglI3<sub>TOP</sub> genotype ×  
 526 sex, as estimated by Barson *et al.* (2015). These probabilities were utilized in salmon fishing  
 527 simulations, in the model where the age at maturity was coded by one locus having two alleles (0  
 528 and 1). The table is reproduced from Kuparinen and Hutchings (2017).

529

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

530

531 **Figure legends**

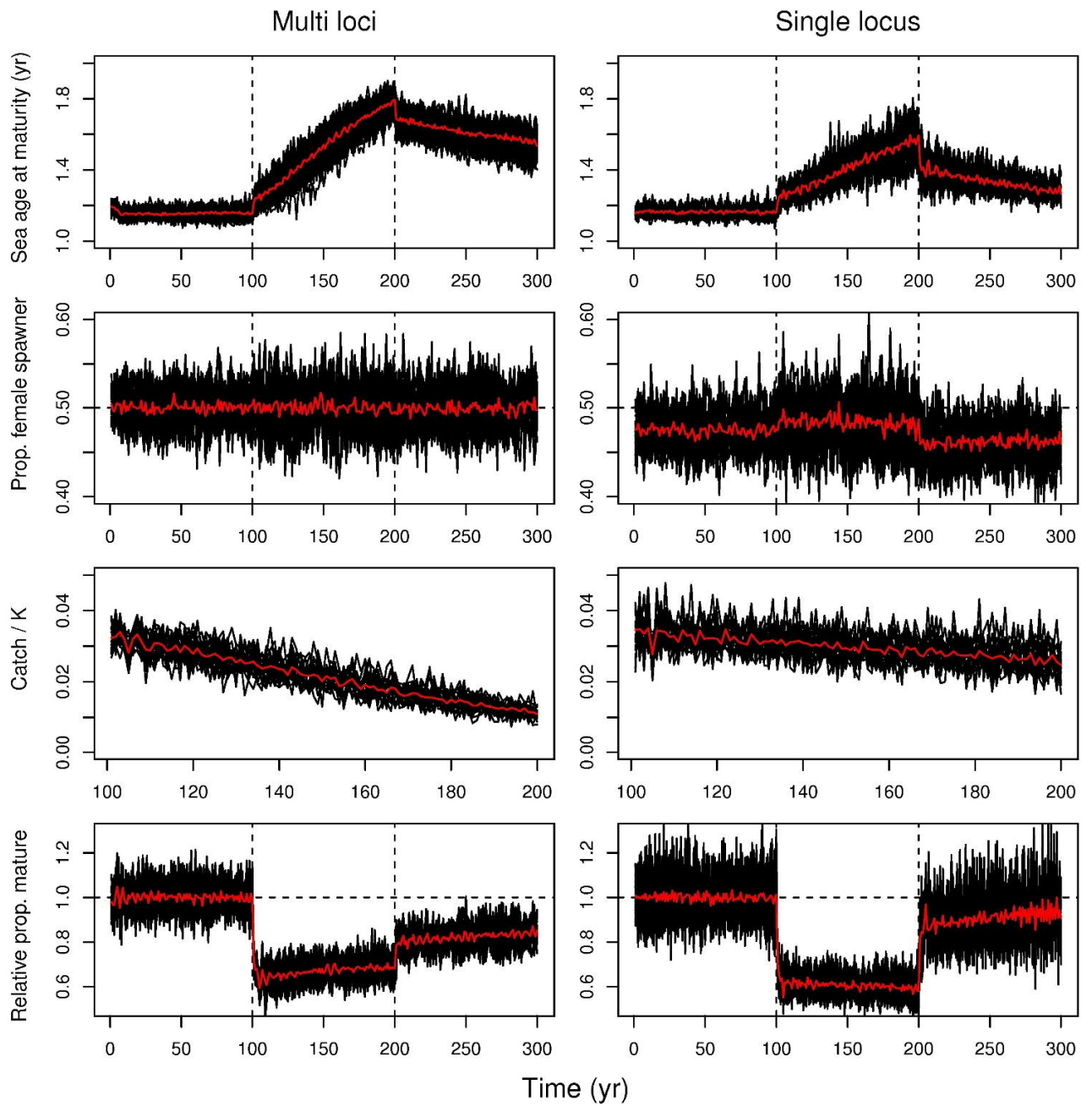
532

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

544

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

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