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### Size does matter – the eco-evolutionary effects of changing body size in fish

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1           **Size does matter – the eco-evolutionary effects of changing body size in fish**

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## 22 **Abstract**

23 Body size acts as a proxy for many fitness-related traits. Body size is also subject to  
24 directional selection from various anthropogenic stressors such as increasing water  
25 temperature, decreasing dissolved oxygen, fisheries, as well as natural predators. Changes in  
26 individual body size correlate with changes in fecundity, behaviour, and survival, and can  
27 propagate through populations and ecosystems by truncating age and size structures and  
28 changing predator-prey dynamics. In this review, we will explore the causes and  
29 consequences of changing body size in fish in the light of recent literature and relevant  
30 theories. We will investigate the central role of body size in ecology by first discussing the  
31 main selective agents that influence body size: fishing, increasing water temperature,  
32 decreasing dissolved oxygen, and predation. We will then explore the impacts of these  
33 changes at the individual, population and ecosystem levels. Considering the relatively high  
34 heritability of body size, we will discuss how a change in body size can leave a genetic  
35 signature in the population and translate to a change in the evolutionary potential of the  
36 species.

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38 **Keywords:** body size, fisheries, environmental change, evolution, life-history trait, plasticity

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## 45 **Introduction**

46 Historically, before the influence of modern human and industrialisation, most species  
47 responded to the changing climate by shifting ranges (Cabanne et al. 2016). In the present  
48 day, as anthropogenically driven, rapidly changing climate is accompanied by a range of  
49 other selective agents, biological responses are likely to be more complex (Parmesan et al.  
50 2000). Threats such as increasing temperature (Barnett et al. 2005), acidification (Orr et al.  
51 2005), reduced dissolved oxygen (Garcia et al. 2005), pollution (Moore 2008), overfishing  
52 (Jackson et al. 2001), and habitat destruction (Nordhaus et al. 2018) are posing serious  
53 challenges to our oceans, often acting in concert. To survive the change, species have three  
54 options: disperse to a more suitable habitat, adjust through phenotypic plasticity, or adapt  
55 through evolutionary change. How well an organism can respond to a change depends largely  
56 on its plasticity and evolutionary potential (Hoffmann and Willi 2008).

57 Conventionally, research has focused on either ecological responses such dispersal or  
58 phenotypic plasticity, or evolutionary responses such as genetic adaptation, and this  
59 distinction was based on the assumption that ecological and evolutionary responses occur at  
60 vastly different time scales. However, it is now widely documented that evolutionary change  
61 can occur over ecologically relevant timescales (Stockwell et al. 2003; Carroll et al. 2007),  
62 and that these processes are not independent of each other (Hanski 2012). Consequently, to  
63 fully understand the ecological and evolutionary processes in nature, we need to move  
64 beyond just documenting the ecological or evolutionary change, towards exploring the impact  
65 of the change in a wider concept.

66 Many natural and anthropogenic stressors are inducing selection pressure on a key ecological  
67 trait: the body size of an organism. Body size, like many other traits, has both plastic  
68 (Crozier and Hutchings 2014) and genetic (Mousseau and Roff 1987; Garcia De Leaniz et al.

69 2007) components. It acts as an easy-to-measure proxy for many life-history characters such  
70 as lifetime reproductive success (Barneche et al. 2018), size and age at maturity (Jensen  
71 1996), and survival (White et al. 2013). Many functions in an organism's life, including  
72 energetics, resource use, susceptibility to predators, species interactions and several  
73 population parameters are functions of its body size (Werner and Gilliam 1984).

74 The question whether organisms have the evolutionary potential to respond to anthropogenic  
75 stressors fast enough is becoming increasingly more important. Unlike terrestrial organisms,  
76 fishes, being immersed in water, are in an intimate contact with their physical and chemical  
77 environment making them particularly sensitive to any changes in their environment (Cossins  
78 and Crawford 2005). Compared to air, oxygen availability in the water is much lower and due  
79 to the higher viscosity of water, more effort is needed to utilise it (Verberk et al. 2011).

80 Increasing water temperature and decreasing oxygen content, even without the pressure from  
81 fisheries, have been predicted to lead to sharp declines in fish body sizes (van Rijn et al.  
82 2017). Regardless of the cause, changes in body size occur at the level of an individual, and  
83 scale up to population, community and ecosystem levels (Pörtner 2002; Pörtner and Peck  
84 2010). The nature of the change, whether it is plastic or genetic, determines whether the  
85 change is likely to be reversible or lead to adaptation. The more the trait under selection  
86 changes, and the more links there are between the trait variation and ecological interactions,  
87 the more important the role of contemporary evolution to ecological processes becomes  
88 (Hairston et al. 2005).

89 Here, we review the recent literature on the causes and consequences of changing body size  
90 in fish and its links to ecological and evolutionary processes. While there is a large selection  
91 of important and relevant literature focusing on body size in fish (Uusi-Heikkilä et al. 2008;  
92 Devine et al. 2012; Enberg et al. 2012; Audzijonyte et al. 2013; Heino et al. 2013, 2015; Diaz  
93 Pauli and Heino 2014; Diaz Pauli and Sih 2017; Hollins et al. 2018), much of it tends to focus

94 on fishing as a selective agent. We believe it is necessary to expand our investigations into  
95 how different selective agents (i.e. not only fishing) affect body size, a key measure in  
96 ecology and a central theme in several ecological theories. To achieve this, we draw attention  
97 to not only fishing, but also to what we consider to be the main (or at least relatively well-  
98 studied) abiotic factors i.e. increasing temperature and dissolved oxygen, as well as a major  
99 biotic factor i.e. predation, in driving selection on body size. Other agents exist as well, such  
100 as pH, water chemistry, primary production, light, and mate choice, and more studies are  
101 needed to understand their role in selection. Additionally, there is currently a knowledge gap  
102 on how different selection agents or stressors interact, and we call for more research effort on  
103 the synergistic effects of multiple stressors. It should also be noted, that a single selective  
104 agent may select for various traits such as body size, growth rate, and natural mortality  
105 schedules. The majority of the current literature is descriptive, and fails to consider the far-  
106 reaching effects of changing body size. Given the rapidly changing environment, and the  
107 various selection pressures imposed by it, it is crucial to investigate the role of changing body  
108 size in a wider perspective beyond fisheries science, to understand how those changes may  
109 affect the entire ecosystem over ecological and evolutionary time.

110 With body size, we refer to metrics such as asymptotic length, size at age, body mass, as well  
111 as growth rate. Although size at age is a state, and growth is a process, these metrics are  
112 closely linked, as growth is necessary in order to reach a certain size (Enberg et al. 2012).  
113 Also, size at age can be considered a proxy for growth (Heino et al. 2015). We will first  
114 provide an overview of the main ecological theories behind the mechanistic functioning of  
115 different selective agents, namely increasing temperature coupled with decreasing dissolved  
116 oxygen, fishing, and predation. We will then use examples from relevant literature to discuss  
117 how changes in body size can influence other life-history traits of an individual fish, and

118 propagate through different levels of biological organisation through to population and  
119 ecosystem levels, at ecologically and evolutionarily relevant time scales (Fig.1).

120

## 121 **The ecological theories behind different stressors as selection agents**

122 In this section, we summarise the selection agents we focus on, namely: temperature,  
123 dissolved oxygen, harvesting and natural predators, and provide an overview of the main  
124 ecological theories behind the selective mechanisms (Fig. 2).

### 125 *Temperature and dissolved oxygen*

126 Temperature is known to affect organisms at community, population and individual levels.  
127 This effect is embodied by three rules: the Bergmann's rule, (Bergmann 1847), the James'  
128 rule (James 1970), and the Temperature – Size –rule (Atkinson 1994). The Bergmann's rule  
129 predicts that, at the community level, organisms in cold habitats are larger than those in  
130 warmer habitats. While not universal (Belk and Houston 2002; Ashton and Feldman 2003;  
131 Fisher et al. 2010), many taxa including birds and mammals (Meiri et al. 2003) as well as  
132 marine (Fernández-torres et al. 2018; Saunders and Tarling 2018) and freshwater (Knouft  
133 2004; Daufresne et al. 2009; Rypel 2014) fishes are known to conform to Bergmann's rule.  
134 This rule is known to apply particularly to freshwater species in cold waters (Rypel 2014).  
135 However, at least for freshwater fish, this pattern may be disrupted by non-native species  
136 (Blanchet et al. 2010). At the population level, James' rule (James 1970) predicts that within  
137 species, populations with smaller body size tend to be found in warmer habitats. As with  
138 Bergmann's rule, James' rule is not universal, but does hold for some fishes in the marine  
139 (Pörtner et al. 2008; Cappo et al. 2013) as well as freshwater (Daufresne et al. 2009)  
140 environments. Temperature is a particularly important aspect in the life of ectothermic  
141 organisms, such as most fishes, as they rely on external source for body heat. The well-

142 established temperature-size –rule (Atkinson 1994) predicts that at lower temperatures  
143 organisms grow slower but reach larger size at maturity (or inversely at higher temperatures  
144 organisms have higher growth rate but lower final size). Indeed, it has been proposed that  
145 shrinking body size is one of the universal responses to global warming, alongside with range  
146 shifts and life cycle mismatches (Daufresne et al. 2009; Sheridan and Bickford 2011).

147 Declines in body size has been observed in marine (Daufresne et al. 2009; Cheung et al.  
148 2012; Baudron et al. 2014) as well as freshwater (Baudron et al. 2011; Forster et al. 2012)  
149 fishes, ranging from warm water to cold water species in every ocean basin as well as in  
150 freshwater environments (Daufresne et al. 2009; Cheung et al. 2012). ).

151 Coupled with increasing water temperature is a decreased level of dissolved oxygen. Warm  
152 water, whether marine or fresh, holds less oxygen than cold water, and water mass can  
153 become under-saturated with oxygen due to excess organic carbon and other anthropogenic  
154 processes (Rabalais et al. 2010). Oxygen limitation together with increasing temperature may  
155 have synergistic effects on aquatic life, as limited oxygen can further impair the tolerance for  
156 warmer temperatures (Pörtner and Knust 2007; Verberk et al. 2016). Warm water causes two  
157 opposing effects: on the one hand warmer water holds less oxygen, on the other hand warmer  
158 temperature increases the anabolic oxygen demand of fish, complicating the oxygen need vs.  
159 oxygen supply -equation. Following this imbalance, it has been suggested that the surface  
160 area of the gills cannot meet the oxygen demand of large bodies, a phenomenon explained by  
161 the Gill-Oxygen Limitation (GOL) theory (Pauly 1981; Pauly and Cheung 2018).

162 Consequently, small body size may become favourable. However, while the trend of  
163 decreasing body size with increasing temperature and decreasing oxygen is evident in both  
164 marine (Pörtner and Knust 2007) and freshwater (Andrews et al. 1973; Pedersen 1987; Pauli  
165 et al. 2017) environments, the underlying mechanisms of the GOL theory are currently  
166 debated. It has been suggested that the scaling of gills with body mass, which the GOL theory

167 is based on, is erroneous, and because gills are a folded surface, they can indeed scale  
168 proportionally with body mass (Lefevre et al. 2017). Lefevre et al. (2017) suggest that it is  
169 the oxygen demand that determines the gill surface area, and not *vice versa*. Instead of gill  
170 size determining the body size of an individual, lifestyle and habitat determine the demand  
171 for oxygen, which in turn determines the size of an individual (Lefevre et al. 2017).  
172 Audzijonyte et al. (2019) further discuss this approach, and point out that gills are dynamic  
173 and some fish are capable of increasing or decreasing their mass-specific oxygen  
174 consumption within days. Increasing the gill size comes with costs, however, as dynamic  
175 modification of gills is likely to incur energetic costs and fish may be more susceptible to  
176 parasites, diseases, and toxins in the water (Audzijonyte et al. 2019). Indeed, as with many  
177 things in nature, fish growth and size are optimised, rather than maximised (Enberg et al.  
178 2012). Audzijonyte et al. (2019) also discuss the potential role of acclimation as well as  
179 epigenetic and evolutionary responses to temperature changes. They suggest that while  
180 acclimation is unlikely to fully compensate for the increased metabolic rate as temperature  
181 increases, adaptation is undoubtedly occurring through epigenetic and evolutionary responses  
182 (Audzijonyte et al. 2019). However, Audzijonyte et al. (2019), limit their epigenetic and  
183 evolutionary discussion mainly to temperature, and not changing oxygen levels. Additionally,  
184 they highlight alternative intrinsic and extrinsic explanations for the decrease in body size to  
185 encourage further research into the mechanisms behind decreasing body size with  
186 temperature in aquatic ectotherms.

187 The metabolic theory of ecology (MTE) provides a link between the different levels of  
188 biological organisation. Metabolism, the process how body converts food to energy to  
189 maintain life, sets the pace for all biological activities (West et al. 1997; Brown et al. 2004;  
190 Savage et al. 2004b, 2004a; West and Brown 2005). Allometric scaling laws demonstrate  
191 how body size and temperature create the borders for a finite energy budget, which the

192 organism must then allocate to survival, growth and reproduction (West et al. 1997; Brown et  
193 al. 2004; Savage et al. 2004b, 2004a; West and Brown 2005). The Kleiber's law predicts that  
194 the respiratory metabolic rate (R) scales with body mass (M) to the power of  $\frac{3}{4}$  ( $R \propto M^{\frac{3}{4}}$ )  
195 (Kleiber 1932). Using the fundamental laws of biology, chemistry and physics, this theory  
196 was further expanded by West, Brown and Enquist (1997) to use multiples of  $\frac{3}{4}$  to scale up  
197 and predict essentially any biological process from genomes to ecosystems (Brown et al.  
198 2004; Savage et al. 2004a; West and Brown 2005). This framework became known as the  
199 'quarter power law', or metabolic theory of ecology, and it demonstrates how body size and  
200 metabolism can be powerful in predicting not only biological traits in the individual but also  
201 functions at the population and ecosystem level. Indeed, MTE has been successful in  
202 predicting the latitudinal diversity gradient (Bailly et al. 2014), population density (Barneche  
203 et al. 2016), species distribution and abundance (White et al. 2017), and life-span variation  
204 (Scarnecchia et al. 2015) in fish, as well as estimating the flux and storage of carbon in  
205 marine, freshwater and terrestrial ecosystems (Schramski et al. 2015). However, there are  
206 several studies not supporting MTE in the aquatic realm (Terribile and Diniz-Filho 2009;  
207 Arandia-Gorostidi et al. 2017) and a scientific debate over the validity of MTE remains  
208 (Kozłowski and Konarzewski 1998, 2005; Brown et al. 2004, 2005; Savage et al. 2004b;  
209 Etienne et al. 2006).

### 210 *Harvesting and natural predators*

211 Given that most fisheries are highly size-selective and target large individuals, and that body  
212 size is known to have a relatively high heritability (Mousseau and Roff 1987; Garcia De  
213 Leaniz et al. 2007), fisheries have the potential to induce evolutionary changes in fished  
214 populations when the strength of selection is adequately high (Allendorf and Hard 2009;  
215 Heino et al. 2015). Using basic quantitative genetics, the expected response to selection  
216 caused by fishing can be estimated from the breeder's equation  $R = h^2S$ , where over a single

217 generation, the expected evolutionary response  $R$  in a trait depends on the selection  
218 differential  $S$  and trait heritability  $h^2$  (Lush 1937). Following this equation, the selection on  
219 body size, regardless of the cause, can leave a genetic signature in the population. Indeed,  
220 experimental (Uusi-Heikkilä et al. 2015), empirical (Hunter et al. 2015), and mathematical  
221 modelling (Ratner and Lande 2001) work is suggesting harvest induced evolution is  
222 occurring.

223 Natural selection often drives selection on body size towards different direction than  
224 anthropogenic selective agents. While fisheries often target large body size, natural mortality  
225 tends to favour large body size (Edeline et al. 2007; Olsen and Moland 2011). Juvenile fish  
226 experience very high rates of mortality during their early life-history stages, and this  
227 mortality is often non-random with respect to size (Sogard 1997). From the prey's point of  
228 view, the "bigger is better" hypothesis (Miller et al. 1988) suggests that for a prey larva,  
229 bigger body size is better, as it increases survival from predators. Consequently, it should be  
230 beneficial to grow fast and grow large in order to avoid predators. Organisms rarely grow to  
231 their full potential, however, as the presence of compensatory growth (Metcalf and  
232 Monaghan 2001) in nature illuminates, and growth is rather optimised than maximised  
233 (Enberg et al. 2012).

234 From the predator's point of view, the optimal foraging theory (MacArthur and Pianka 1966)  
235 suggests that a predator will choose a strategy that ensures the most energy gain at the least  
236 cost, in order to maximise fitness. Following that prey body size is thought to be positively  
237 correlated with predator encounter rate, and negatively with capture rate, the prey  
238 vulnerability curve tends to be dome-shaped (Fuiman and Magurran 1994). A dome-shaped  
239 curve would suggest that both smaller and larger individuals are at less risk from predators,  
240 and the middle-sized individuals are at the highest risk.

241 We have here focussed on what we consider to be the main selection agents on body size.  
242 While increasing temperature, decreasing dissolved oxygen, and harvesting tend to select  
243 towards smaller body size, natural selection in the form of predator avoidance may select for  
244 either small or large body size.

245

## 246 **Individual level consequences of selection**

### 247 *Changing body size*

248 Temperature was found to be the main cause of declining body size in an empirically based  
249 study in the North Sea (Baudron et al. 2014). The study used over 40 years of data from  
250 several databases, and found reductions in the body size of six out of eight commercially  
251 important species (Baudron et al. 2014). In the northern North Sea, haddock  
252 (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), herring (*Clupea harengus*),  
253 Norwegian pout (*Trisopterus esmarkii*), and in the southern North Sea whiting, sole (*Solea*  
254 *solea*) and female plaice (*Pleuronectes platessa*) all expressed a decrease of 16% on average  
255 in asymptotic length ( $L_{\infty}$ ), coinciding with an increase of < 2 % in the seawater temperatures  
256 (Baudron et al. 2014). Similarly, a comprehensive study by Daufresne et al. (2009) used  
257 long-term analyses of fishes (brown trout, herring, sprat) in the Baltic Sea and French rivers,  
258 experimental plankton data, and a review of other published work to show a decrease in size-  
259 at-age and mean body sizes at individual, population and community level. These changes  
260 applied in both freshwater and marine environments.

261 In addition to temperature, fishing alone is thought to exert selection pressure on body size.  
262 On the west coast of Scotland, the Firth of Clyde was once a productive estuary supporting  
263 commercially important demersal fisheries, mainly targeting cod (*Gadus morhua*), haddock  
264 (*M. aeglefinus*) and whiting (*M. merlangus*) (Bailey et al. 2011). After decades of intense

265 harvest and the collapse of many fisheries, a decrease in age and size at maturation was  
266 demonstrated in all three species using probabilistic maturation reaction norms (PMRNs)  
267 (Hunter et al. 2015). The significant decline in the abundance of large fish in the Clyde may  
268 be partially explained by these changes in age and size at maturation (Hunter et al. 2015).  
269 Temperature and abundance were shown to have only marginal effects on this and the shift  
270 towards earlier age and smaller size at maturation was attributed at least in part to fishing  
271 (Hunter et al. 2015).

272 Disentangling the effects of changing temperature and fishing can be notoriously difficult and  
273 more research effort is needed to understand the potential synergistic effects of multiple  
274 stressors. In an attempt to differentiate between the effects of fishing and temperature,  
275 Genner et al. (2010) investigated the variability of demersal fish assemblages in the English  
276 Channel. They documented size-dependent responses to changing climate and fishing, and  
277 showed that the temporal trends in the abundance of smaller-bodied fish followed thermal  
278 trends, while the abundance of large-bodied fish declined steadily and independently of the  
279 thermal regime. Large-bodied fish also showed the greatest declines in body size. Regardless  
280 of the root cause of changing body size, the combination of climate change and fisheries may  
281 act in concert. Daufresne et al. (2009) noticed that reduction in body size was larger in marine  
282 species subjected to heavy fishing than in species not subject to such heavy fishing,  
283 suggesting the potential presence of additive effects. Clark et al. (2012) in turn showed that in  
284 coho salmon (*Oncorhynchus kisutch*), smaller individuals showed a clear advantage in  
285 recovery following exhaustive exercise mimicking catch- and release fishing, suggesting that  
286 fishing-induced selection against large individuals may be enhanced by the better stress-  
287 related survival of smaller individuals. Importantly, different stressors may affect fish at  
288 different stages of their life, and the effects of the stressor may carry over to different life-  
289 stages (Cline et al. 2019). Although not directly measuring size *per se*, Cline et al. (2019)

290 studied the sockeye salmon (*Oncorhynchus nerka*) and showed that increased temperature  
291 during the freshwater phase increased the prevalence of salmon spending only one year in  
292 freshwater. This carried over to the ocean life-history by increasing the sockeye maturation  
293 age and hence the time of returning to the natal river (Cline et al. 2019). At the same time,  
294 hatchery augmented pink and chum salmon compete with the sockeye salmon in the ocean,  
295 and the size of returning sockeye negatively correlates with the biomass of hatchery-produced  
296 salmon. Cline et al. (2019) suggest that competition reduces the size of sockeye salmon,  
297 which then drives delayed maturation, highlighting the complexity of several selection agents  
298 acting on life-history traits. The different responses of different size-class fishes stress the  
299 importance of considering the life histories of individual species when predicting responses to  
300 any natural or anthropogenic stressors.

301 Predation is one of the most important selective forces driving the evolution of life histories  
302 (Day et al. 2002). Depending on the context, predation can drive evolution towards smaller  
303 (Heins et al. 2016) or larger (Reznick et al. 2001) body size, as would be the prediction of the  
304 dome-shaped curve of prey vulnerability as a result of optimal foraging. Understanding the  
305 selection caused by predation is particularly timely, as the potential increase in invasive  
306 species is thought to be among the consequences of climate change (Dukes and Mooney  
307 1999; Rahel and Olden 2008; Mainka and Howard 2010). Invasive species can markedly alter  
308 local ecosystem function and drive changes in the life history evolution of native species. For  
309 instance, an illegally introduced invasive pike in the Alaskan Scout Lake preys on the native  
310 threespine stickleback (*Gasterosteus aculeatus*) (Heins et al. 2016). It has caused  
311 significant, directional changes in the life history traits of the stickleback, towards declining  
312 size and age at maturity. The sticklebacks shifted from maturing at age two to reaching  
313 maturity already at one year of age, at a significantly smaller size (Heins et al. 2016). An  
314 opposite effect was seen in the well-known guppy (*Poecilia reticulata*) experiments. Reznick

315 et al. (2001) showed that guppies in the high-predation environment grew faster, but also  
316 reached higher asymptotic lengths than those inhabiting low-predation sites. Reznick et al.  
317 (2001) suggested that the higher growth rate and higher asymptotic length were in part due to  
318 high-predation areas also having higher resource availability. This could be caused by abiotic  
319 factors such as the higher light level in the area resulting in higher primary productivity, or it  
320 could be a consequence of predators lowering prey biomass thus freeing more nutrients per  
321 capita (Reznick et al. 2001). Compared to selection induced by fisheries, natural selection  
322 often operates in the opposite direction, favouring larger size (Olsen and Moland 2011). The  
323 fitness landscape then becomes dynamic, moving towards the direction of the stronger  
324 selection force (Edeline et al. 2007).

325 Over the last two decades, experimental studies have started to reveal the genetic basis of  
326 changing body size. However, while experimental studies allow for the control of  
327 confounding factors, they lack the density dependence present in nature and thus alone cannot  
328 be directly translated to describe processes taking place in the nature. Most of this  
329 experimental evidence comes from harvesting studies on both freshwater and marine/  
330 brackish species, and the results have indicated no differences in the mechanistic changes as a  
331 result of harvest depending on the salinity of the water. Following positively size-selective  
332 harvest (i.e., large individuals removed from the population, selection similar to most  
333 fisheries) of the Atlantic silverside (*Menidia menidia*) over four generations, Conover and  
334 Munch (2002) reported significantly lower body weight and slower growth rate of the  
335 positively size-selected line. Later, using the same selection lines, Salinas et al. (2012)  
336 showed that some of these changes were reversible, some partially reversible, and some did  
337 not show any signs of reversibility after five generations of the cessation of fishing. While  
338 this common garden approach suggested that some of the changes were likely to be genetic,  
339 the direct evidence for genetic changes caused by size-selective harvesting was provided over

340 a decade later. Van Wijk et al. (2013) subjected guppies to three generations of positively and  
341 negatively size-selective harvest and quantified the phenotypic and genetic responses to  
342 selection. The phenotypic responses to directional selection were similar to those observed by  
343 Conover and Munch (2002): positively size-selective harvest led to a reduction in adult body  
344 size. Van Wijk et al. (2013) used 17 candidate loci to study genetic changes in response to  
345 size-selective harvesting, and demonstrated changes in seven of them. At least three of their  
346 candidate loci were associated with body size. Following a similar harvest design over five  
347 generations, an experimental study on zebrafish (*Danio rerio*) provided further evidence on  
348 declining body size and changes in associated life-history characters after intensive  
349 directional selection (Uusi-Heikkilä et al. 2015). Uusi-Heikkilä et al. (2015) utilised 384  
350 single nucleotide polymorphisms (SNPs) and identified 21 outlier SNPs responding to  
351 directional selection, thus demonstrating contemporary evolutionary changes in the  
352 experimentally exploited populations. With the same experimental selection lines, Uusi-  
353 Heikkilä et al. (2017) studied harvest-induced changes in gene expression by sequencing the  
354 transcriptomes of individual fishes. They demonstrated that size-selective harvesting had  
355 changed the expression of over 4 000 genes and some of these changes were associated with  
356 changes at the sequence level. Importantly, they showed that the changes in gene expression  
357 were slow to reverse. Further, in 2019, Therkildsen and colleagues showed that the  
358 phenotypic responses to harvest selection may in fact be underlain by divergent genomic  
359 shifts, meaning fishing may potentially cause genomic changes comparable to distinct  
360 populations in nature (Therkildsen et al. 2019). Experimental studies such as these can further  
361 our understanding of the nature of the changes, and help us monitor and manage fish  
362 populations in an efficient way.

363 *Changes in growth rate*

364 The fight for survival begins from the egg phase, and continues through the larval stage into  
365 adulthood and eventual mortality. This survival is often non-random with respect to size. The  
366 ‘bigger is better’ –hypothesis suggests that fast and large-growing larvae may better avoid  
367 predators. The size-selective mortality of the sprat *Spratelloides gracilis* provided evidence  
368 for this hypothesis, as selection was operating against small and slow growing individuals  
369 (Meekan et al. 2006). Allain et al. (2003) reported similar trends in anchovies (*Engraulis*  
370 *encrasicolus*) and attributed survival to faster larval growth rate. While juvenile stage is of  
371 crucial importance as it determines the future cohort sizes, juvenile growth rates can be  
372 altered by size selective harvest (Conover and Munch 2002; Walsh et al. 2006), changing  
373 temperatures (Meekan et al. 2003; Baudron et al. 2011, 2014; Rogers et al. 2011), and  
374 predation (Reznick et al. 2001; Heins et al. 2016).

375 Body size and growth rate are closely associated, and for animals with indeterminate growth  
376 this close association is often described by the von Bertalanffy equation. There is a strong  
377 negative correlation between the von Bertalanffy (vB) growth parameters  $L_{\infty}$  = asymptotic  
378 length, and  $k$  = the intrinsic individual growth rate, suggesting a presence of trade-off.

379 Following this, if asymptotic length decreases, the growth rate would be expected to increase  
380 (and *vice versa*). However, depending on the selective agent, selection on body size may  
381 influence growth rate differently.

382 Baudron et al. (2011) used over three decades of length and age data to fit the von Bertalanffy  
383 growth model and investigated the growth response of North Sea haddock (*Melanogrammus*  
384 *aeglefinus*) to different temperature scenarios. They showed that increasing temperature was  
385 linked with a decrease in  $L_{\infty}$ . This finding was coupled with an increase in the growth rate  
386 during early life stages (Baudron et al. 2011), in line with the vB growth model (where  $L_{\infty}$   
387 and intrinsic individual growth rate correlate negatively), and as predicted by the  
388 Temperature-Size –rule. A similar increase in juvenile growth rate with an increasing

389 temperature appears to be relatively common, as it has also been detected in the North Sea  
390 cod (Rindorf et al. 2008), Northeast Arctic cod (Michalsen et al. 1998), and Norwegian  
391 coastal cod (Otterlei et al. 1999),, and holds true across spatial scales (Brander 1995). In  
392 some cases, temperature may select directly for increased juvenile growth rate. Thresher et al.  
393 (2007) examined otolith data dating back to 1861, and reported a significant change in the  
394 growth rate of six out of eight studied species. Three of these species were shallow water  
395 fishes (< 250 m), and thus had been subjected to increasing water temperatures over the past  
396 century, and showed increasing juvenile growth rates. The remaining three species were  
397 deep-water species, and temperature reconstructions inferred from deep-water corals fitted the  
398 growth curves of the older, deep-water species which showed no increase in juvenile growth  
399 rates (Thresher et al. 2007). More recently, Morrongiello et al. (2019) were the first to report  
400 fishing-induced shifts in thermal reaction norms in marine fish, highlighting the potential  
401 synergistic effects of harvest and changing temperature. By fishing out the largest individuals  
402 that have a high thermal capacity, we might be weakening the species' adaptive potential to  
403 respond to climate change (Morrongiello et al. 2019).

404 While the fish in the study by Morrongiello et al. (2019) attained faster adult growth rates  
405 (partially due to release from density dependence as a result of fishing), a typical selection  
406 pressure from fisheries tends to select towards lower growth rate (Enberg et al. 2012).  
407 Empirical studies of the Alpine freshwater whitefish *Coregonus palaea* (Nusslé et al. 2009),  
408 *Coregonus albellus*, and *Coregonus fatioi* (Nusslé et al. 2011), all subject to steady and heavy  
409 fishing pressure, have shown declines in the average adult (but not juvenile) growth rate as  
410 well as significant selection differentials over several generations. Studies in the laboratory  
411 have provided further evidence for changes in growth rate. Experimental harvesting studies  
412 have revealed declines in juvenile growth rate following positively size-selective harvest over  
413 four generations (Conover and Munch 2002). The parental harvest extended its influence to

414 the next generation, causing changes also in the larval growth rates. The larvae of positively  
415 size-selected parents evolved to grow slower than the larvae of negatively size-selected  
416 parents, potentially subjecting slow-growing larvae to higher predation pressure in nature  
417 (Conover and Munch 2002).

418 It is thought that the natural mortality of many fish populations has been increasing in the  
419 recent decades (Gislason et al. 2010). Following the presence of life history trade-offs in  
420 nature (Jensen 1996; Douhard et al. 2015), it could be that increased growth rate early in life  
421 is associated with increased mortality late in life. Indeed, accelerated growth rate is known to  
422 be linked to shorter lifespan in many species, (Metcalf and Monaghan 2003), and a recent  
423 meta-analysis suggested a link between growth rate and natural mortality in fish (Gislason et  
424 al. 2010). The link between faster growth rate and higher natural mortality (or shorter life-  
425 span, which in a controlled laboratory environment corresponds to higher natural mortality)  
426 has also been shown experimentally in three-spined sticklebacks (Lee et al. 2013). By  
427 inducing changes in fish growth rate, we may be indirectly altering fish natural mortality  
428 rates, too.

#### 429 *Big and bold? Linking body size and behaviour*

430 Body size is known to correlate with many behavioural traits, which can enhance or reduce  
431 individual fitness. For example, after five generations of harvesting, small Atlantic silverside  
432 (*Menidia menidia*) showed reduced willingness to forage under a threat of predation  
433 compared to the large ones, potentially reducing individual energy flow and therefore  
434 reducing fitness (Walsh et al. 2006). Later, using the same experimental populations, Salinas  
435 et al. (2012) showed that the changes in food consumption did not recover after the cessation  
436 of fishing. This kind of change in food consumption is likely to influence the population  
437 growth rate and productivity (Conover and Munch 2002). Uusi-Heikkilä et al. (2015)

438 investigated behavioural changes in juvenile zebrafish, and showed that negatively size-  
439 selected fish (i.e. small individuals removed) were more active, explorative and bolder than  
440 positively size-selected fish (i.e. large individuals removed), and that this shift in behaviour  
441 was accompanied by genetic changes (but see Sbragaglia et al. 2019). Although not  
442 demonstrated by the zebrafish study, it can be speculated that larger fish have higher energy  
443 demand and therefore they are more active and bolder in search of food (Réale et al. 2010).  
444 This in turn could make them more vulnerable not only to natural predators but also to fishing  
445 gear.

446 Fishing gear selection is a two-way street. While behaviour can influence the vulnerability to  
447 fishing, selective fishing can cause behavioural changes. As an example, Sutter et al. (2012)  
448 focused on behaviour instead of size, and showed that aggression, intensity of parental care,  
449 and reproductive fitness positively correlated with vulnerability to angling. Similarly,  
450 physiological traits such as anaerobic swimming performance and metabolic demand are  
451 known to be linked to vulnerability to fishing (Killen et al. 2015). Fishing can also be the  
452 cause of behavioural changes, as the gear retention probability depends on the fishing gear in  
453 question, and the selection curves are often non-linear with respect to size (Kuparinen et al.  
454 2009). Since size and behavioural traits are linked, and fishing often selects a certain size  
455 regime, the selection likely affects behavioural traits too. Obviously, vulnerability also  
456 depends on the fishing gear at hand. Behavioural changes associated with body size have also  
457 been studied in the context of fish farming, as it provides a semi-natural laboratory to study  
458 contemporary evolution. Farmed fish that have been selected for higher growth rates are  
459 expressing changes in boldness (Biro et al. 2004). The fish under selection tend to take more  
460 risks while foraging, grow faster and survive at a lower rate than their wild conspecifics (Biro  
461 et al. 2004; Biro and Post 2008).

462 In addition to fishing and fish farming, behavioural characters may be indirectly impacted by  
463 temperature. Given that fishes are mainly ectothermic, increasing water temperature will  
464 likely affect metabolic rates, which in turn may alter feeding behaviour and activity. Scott et  
465 al. (2017) showed that this kind of response is size dependant. On the Great Barrier Reef in  
466 Australia, the common coral trout (*Plectropomus leopardus*) shows more active foraging  
467 behaviour during hotter months than colder months, but when the water temperature exceeds  
468 30 °C, foraging frequency declines. This may suggest the presence of a temperature  
469 threshold, beyond which *P. leopardus* cannot compensate the increased basal metabolic rate  
470 with increased foraging activity (Scott et al. 2017). They also showed that larger individuals  
471 spent more time completely inactive in increasing temperatures compared to their smaller  
472 conspecifics (Scott et al. 2017). This kind of behavioural change may have far-reaching  
473 effects, from non-sufficient foraging and abnormal spawning-related movements to predator-  
474 prey relationships (Scott et al. 2017). Studying the same species, Johansen et al. (2015)  
475 demonstrated, that while *P. leopardus*, a predatory species, may be able to increase food  
476 intake in response to increased metabolic demand due to increased water temperature, the  
477 lower trophic levels may not be able to provide this energy. This highlights the importance of  
478 considering the wider ecosystem, not just one species, when predicting the influence of  
479 natural or anthropogenic stressors.

480 An interesting link between changing sea temperature, body size and activity level was also  
481 discovered by van Rijn et al. (2017). They studied 74 fish species across space in the  
482 Mediterranean Sea, ranging from small bottom-associated gobies to large pelagic tunas, and  
483 demonstrated that body size decreased with increasing temperature as predicted by the  
484 Temperature-Size –rule. Additionally, they found that the activity level of the species was  
485 strongly correlated with the decrease in body size, so that large, active species showed the  
486 strongest decline in size in response to increasing temperature (van Rijn et al. 2017). This

487 highlights the complexity of several selective agents acting simultaneously. As discussed  
488 above, fisheries selection may select for a certain type of behaviour or activity level, and as  
489 shown here, activity level is linked to body size response to warming. This provides an  
490 interesting connection between fishing, changing temperature, activity level and body size,  
491 and warrants for further research into the potential synergistic effects of multiple stressors.

#### 492 *Changes in reproduction*

493 A commonly used proxy for individual fitness is the lifetime reproductive success (LRS),  
494 which can simply be described as the total number of offspring an individual produces during  
495 its lifetime (Mousseau and Roff 1987). The reproductive output of an individual tends to  
496 increase with body size (Hixon et al. 2014), thus contributing to the individual fitness. In a  
497 meta-analysis of 342 species of marine fishes from 15 different orders, Barneche et al. (2018)  
498 quantified this increase, and estimated how selection towards smaller body size may reduce  
499 fecundity. They controlled for phylogenetic nonindependence and scaled female mass and  
500 reproductive energy output, including fecundity, egg volume and egg energy, to show that  
501 large females reproduce disproportionately more than small females. Similar trend has been  
502 seen in experimental studies, where positively size-selected harvest has led to reduction in  
503 fecundity (lower spawning probability, fewer eggs both absolutely and relatively) in zebrafish  
504 (Uusi-Heikkilä et al. 2015). Similarly, a study on the Atlantic silverside subjected to five  
505 generations of size-selective harvest showed marked reductions in egg volume, larval size at  
506 hatching, larval growth rate, and larval survival probability (Walsh et al. 2006). The  
507 correlation of body size and fecundity has been documented in various fish species both intra-  
508 (Dick et al. 2017) and inter-specifically (Savage et al. 2004b; Hayward and Gillooly 2011). It  
509 is important to note, however, that the strength of the correlation depends on the species in  
510 question (Barneche et al. 2018), and that like other animals in the wild (Nussey et al. 2013),  
511 at least some fish experience actuarial (Beverton et al. 2004; Uriarte et al. 2016) and

512 reproductive (Reznick et al. 2006; Benoît et al. 2018) senescence, meaning that the  
513 reproductive capacity of fish may not increase indefinitely with size. Therefore, predictions  
514 about reproductive capacity based on body size alone should be made with caution.

515 The mechanisms of how larger body size benefits the reproductive output vary, however, and  
516 some are related to behaviour. In coho salmon (*O. kisutch*), larger female body size has been  
517 associated with an advantage in mate and territory selection (Fleming and Gross 1994).

518 Bigger size appears to be beneficial, as it allows for increased egg production, better access to  
519 nesting territories, and improved nest digging (Fleming and Gross 1994). Further, the

520 changes in body size are often accompanied with associated changes in population age

521 structure. The truncation of age structure can potentially enhance the effects of declining

522 body size at individual and population level. As an example, longevity may be advantageous

523 as it can increase population recruitment variability (in timing), particularly in long-lived fish

524 species, thereby making the population less vulnerable in unstable environments (Longhurst

525 2002). Maternal age can also contribute to the fitness of offspring. The larvae of older black

526 rockfish (*Sebastes melanops*) showed over three times faster growth rate than the larvae of

527 younger rockfish, and they survived starvation better (Berkeley et al. 2004). Since body size

528 and reproductive output are often positively correlated (Barneche et al. 2018), changes in

529 individual body size can have multigenerational impacts, truncate the population age and size

530 structure, and potentially lower the population growth rate.

531

### 532 **How do changes in body size translate to population dynamics?**

533 The intrinsic rate of per-capita population growth rate ( $r$ ) can be thought of as a population

534 level analogue to LRS. Although  $r$  cannot be directly translated from LRS, body size is a

535 strong correlate for both (Denney et al. 2002; Anderson et al. 2008). Indeed, Uusi-Heikkilä et

536 al. (2015) modelled their results from the zebrafish studies, and found that in the absence of  
537 fishing, positively size-selected (large individuals removed) population had a slower  
538 population growth rate than negatively and randomly size-selected populations. In their  
539 modelling study, Audzijonyte and Kuparinen (2016) showed that earlier maturation that  
540 evolved during fishing, reduced  $r$  after fishing had been halted. They also showed that  
541 decreased adult body size reduced the reproductive output and increased adult natural  
542 mortality. However, species' age-specific survival and trophic position was also important in  
543 determining  $r$ : a species inhabiting offshore environment and exposed to few predators did  
544 not suffer, in terms of population growth rate, as much from reduced body size as a species  
545 living near shore and being intensively predated by other fish. A density dependent  
546 population response to fishing was predicted by the model of Dunlop et al. (2015), who  
547 observed that as fishing began,  $r$  first declined as the largest individuals were removed from  
548 the reproductive pool, but once density dependent processes started regulating the population,  
549  $r$  and reproductive output increased. After moratorium, the opposite occurred: at first  $r$   
550 increased temporarily, but was eventually counter-acted by density dependent processes,  
551 leading to reduction in  $r$  (Dunlop et al. 2015). This kind of delayed response can explain how  
552 evolution may impede stock recovery after harvest (Dunlop et al. 2015).

553 The form of selection will affect the outcome of the selection: stabilising selection favours  
554 the intermediate phenotype, and disruptive selection favours the extreme phenotypes.  
555 Directional selection occurs when selection favours one phenotype over another so that the  
556 frequency of this phenotype in a population becomes higher than before selection. On the one  
557 hand, studies have shown that stabilising selection can lead to decreasing phenotypic and  
558 genetic variation (Olsen et al. 2009), which is known to reduce population fitness (Reed and  
559 Frankham 2003). On the other hand, if the selection is disruptive, it may increase the genetic  
560 variance in a population (Edeline et al. 2009), potentially increasing population fitness. Thus,

561 by understanding the selection mode of different fishing methods, and the genetic outcome  
562 they may produce, we could minimise the damage that harvesting can cause.

563 While human-induced trait-selection may drive selection in one direction, natural selection  
564 may favour another direction. This trend was quantified by Carlson et al. (2007) as they  
565 studied the effect of natural selection and harvest-induced selection on Windermere pike  
566 (*Esox lucius*). They showed that while fishery selection favoured small pike, natural selection  
567 acted against small pike. Further, natural selection was stabilising, suggesting that bigger  
568 body size is not always beneficial, while harvest-induced selection was disruptive, likely a  
569 sign that the smallest and the largest individuals were not caught by the fishery (Carlson et al.  
570 2007). Thus, harvest-induced selection may modify the natural adaptive landscape of  
571 populations. Changes in the adaptive peak were further explored by Edeline et al. (2007), as  
572 they showed that the adaptive peak moves in the direction imposed by the stronger selective  
573 force, and that trait changes follow the movement of the peak. The modification of the  
574 adaptive peak is dynamic, so that during fishing, harvest selection was the dominating force,  
575 and when fishing was relaxed, natural selection became the dominating force. After the  
576 fishing pressure ceased, a shift toward faster growth was accompanied by a decrease in  
577 reproductive investment, suggesting a trade-off between growth and reproductive investment  
578 (Edeline et al. 2007). These movements of the adaptive peak were seen under a relatively low  
579 fishing pressure (1.1-7.3%), while commercial fishing pressure is typically in the order of 45-  
580 99% (Edeline et al. 2007).

### 581 *Genetic and phenotypic variation*

582 While selective harvesting is known to affect several traits in harvested populations (Walsh et  
583 al. 2006), the nature of selection can affect the outcome. Some fish populations have not  
584 managed to recover following depletion, but others show signs of reversal after intense

585 harvest (Murawski 2010; Costello et al. 2016). While the recovery of a population likely  
586 depends on several factors, extrinsic and intrinsic, the effect of fishing depends on the form  
587 of selection it causes. Edeline et al. (2009) demonstrated empirically that harvest-induced  
588 selection in pike could actually increase variance in fitness related traits such as body size,  
589 when the harvest is disruptive. Disruptive selection leads to a higher fitness for the  
590 phenotypic extremes, which gives raise to increased trait variability (Edeline et al. 2009). An  
591 opposing effect of fishing has been seen in the brown trout (*Salmo trutta*) (Haugen et al.  
592 2008), and Atlantic cod (Olsen et al. 2009) where stabilising selection led to a decrease in  
593 phenotypic variance with respect to body size. Furthermore, the nature of genetic architecture  
594 of the trait under selection may influence the outcome of the harvest-induced selection  
595 (Kuparinen and Hutchings 2016). A striking example of the importance of the genetic  
596 patterns behind inherited traits comes from the Atlantic salmon (*S. salar*), where the genetic  
597 architecture behind age at maturity was recently identified to be controlled by a large effect  
598 locus explaining nearly 40% of phenotypic variation in age at maturity (Barson et al. 2015).  
599 Simulations indicate that if the trait (here age at maturity) is under the control of a single  
600 sexually dimorphic locus, the selection response is likely divergent or disruptive, and if the  
601 trait is controlled by multiple loci, the response is uni-directional (Kuparinen and Hutchings  
602 2016).

603 According to classic evolutionary theory, for populations with small effective population size  
604 ( $N_e$ ) and little genetic variation, the evolutionary potential to respond to future challenges  
605 may be limited and the consequences of genetic drift and stochastic events may be serious.  
606 Selection and declining population size may cause erosion in the genetic variation of a  
607 population, potentially leading to the accumulation of deleterious alleles and therefore  
608 decreasing the population fitness (Marty et al. 2015). A genetic bottleneck has the potential to  
609 cause inbreeding depression in populations with small effective population size (Palstra and

610 Ruzzante 2008), and in the worst case this could send the population into an extinction  
611 vortex.

612 However, the empirical evidence for reduced genetic variation as a result of harvest or in  
613 small populations is contradictory. While heavy harvesting has been associated with lower  
614 genetic diversity in some populations (Hauser et al. 2002; Pinsky and Palumbi 2014), others  
615 show no signs of this (Ruzzante et al. 2001; Therkildsen et al. 2010). This maintenance of  
616 genetic diversity may be due to large effective population size despite harvesting  
617 (Therkildsen et al. 2010) or the mixing of populations (Ruzzante et al. 2001). Additionally, a  
618 recent meta-analysis (Wood et al. 2016) found no correlation between declining population  
619 size and genetic variation. Similarly, the consequences of reduced genetic diversity in nature  
620 can be variable. An experimental relocation study found no correlation between reduced  
621 genetic variability and fitness (survival and growth) (Yates et al. 2019). Instead, the habitat  
622 quality had a significant effect on the fitness of individuals and species extinction (Yates et  
623 al. 2019). While this study highlights the importance of habitat conservation, it does not  
624 inform on the importance of genetic variation on an evolutionary time scale. It has been  
625 suggested that, in addition to genetic variation, factors such as epigenetic variation, soft  
626 sweeps from standing genetic variation, polygenic and balancing selection, as well as  
627 repeated adaptation may help maintain the evolutionary potential of species (Bernatchez  
628 2016).

629 In some cases fishing can result both in strong directional selection and in declining  
630 population size, therefore being a candidate for the cause of potentially irreversible changes  
631 in genetic and phenotypic variation. Empirical (Hauser et al. 2002) and experimental (Uusi-  
632 Heikkilä et al. 2015) studies as well as a meta-analysis of 140 fish species (Pinsky and  
633 Palumbi 2014) have shown that harvest can lead to declines in genetic variation (both  
634 sequence and gene expression level). Genetic diversity has been shown to correlate with

635 population fitness and to explain almost 20% of the variation in it (Reed and Frankham  
636 2003). Additionally, high genetic (Reusch et al. 2008) as well as phenotypic (Morrongiello et  
637 al. 2019) diversity can buffer ecosystems from extreme climatic events by ensuring  
638 complimentary genotypes and improving recovery after perturbations. Apart from avoiding  
639 genetic bottleneck and maintaining evolutionary potential, another reason for the importance  
640 of preserving genetic variation is that it may be linked to the rate of evolution. In the  
641 Trinidadian guppies, for instance, male guppies showed a higher rate of evolution than  
642 female guppies, apparently due to higher genetic variation in males (Reznick et al. 1997). The  
643 lower genetic variation in females likely slowed down the evolutionary change in age and  
644 size at maturity (Reznick et al. 1997). Now, with a rapidly changing environment, fast  
645 adaptation may be needed, highlighting the role of genetic variation as it holds the  
646 evolutionary key for the swift adaptation of species to their environment.

647 In the recent years, studies have found declines in genetic and phenotypic variation, but the  
648 root cause of these is somewhat unclear. Olsen et al. (2009) used nine decades of  
649 commercially and recreationally harvested cod length data from the Norwegian Skagerrak  
650 coast and showed that while the mean length of juvenile Atlantic cod had not changed, the  
651 variation had decreased. They found evidence for selection against both large and fast-  
652 growing, and small and slow-growing juveniles, likely a sign of stabilising selection. The  
653 reasons behind this were speculated to be various and non-exclusive, such as climatic  
654 conditions, trends in biotic factors (abundance of conspecifics, predator-prey relationships),  
655 changes in breeding phenology, natural selection, or harvest (Olsen et al. 2009). In the same  
656 location, Rogers et al. (2011) showed that temperature and population density had a  
657 pronounced effect on the variation in the growth rates of juvenile Atlantic cod. While warm  
658 spring temperatures resulted in larger juvenile cod, they also reduced length variation within  
659 a cohort (Rogers et al. 2011). While the cod on the Norwegian coast showed declines in

660 phenotypic variation, the North Sea cod off the coast of Flamborough Head, UK, has shown  
661 declines in genetic variation (Hutchinson et al. 2003). This decline coincided with the time of  
662 high population exploitation rates, shifts towards younger age and smaller size at maturity,  
663 and demographic changes on a population level (Hutchinson et al. 2003).

664 Intra-specific variation in life-history traits such as age or size at maturation can affect  
665 ecological dynamics on population level, irrespective of whether the trait variation is  
666 genetically based or not (Bolnick et al. 2011). Life-history variation within species can  
667 stabilise ecosystems and dampen temporal variability, a phenomenon known as the portfolio  
668 effect. The heavily exploited sockeye salmon in Bristol Bay, Alaska, shows a high degree of  
669 population and life-history diversity (Schindler et al. 2010). Schindler et al. (2010) quantified  
670 this variability by modelling empirical data and showed that because of the life-history  
671 variation, the temporal variability in annual salmon returns is 2.2 times lower than what it  
672 would be if the population were homogenous with respect to life histories. This is important,  
673 as salmon fishery is a major source of income to the local communities, and therefore low  
674 variation in income is desirable (Schindler et al. 2010). This study highlights the importance  
675 of preserving within species variation from both ecological and economic perspective  
676 (Schindler et al. 2010).

677 A study on Atlantic cod in Iceland has provided cues to the link between life-history variation  
678 and genetic changes. Jakobsdóttir et al. (2011) used a historical data set spanning nearly six  
679 decades to study the genotypic frequencies in Atlantic cod. They showed that the frequency  
680 of *Pan* I<sup>BB</sup> genotype decreased over the course of 60 years, and that this decrease coincided  
681 with the increases in fishing effort and intensity, as well as with the collapse of the numbers  
682 of older individuals in the population (Jakobsdóttir et al. 2011). Their results strongly suggest  
683 that the different *Pan* I genotypes correspond to different life-history strategies, so that  
684 different *Pan* I genotypes mature at different ages (Jakobsdóttir et al. 2011). As suggested by

685 the portfolio effect, the decrease in intra-specific life-history variation may make the  
686 population more vulnerable to stochastic events or adverse conditions (Bolnick et al. 2011).  
687 Ignoring the genetic and phenotypic variation and evolutionary potential of species can  
688 reduce the efficiency of conservation efforts or even make some actions harmful.

689

## 690 **Ecosystem-level effects of the changing body size**

### 691 *Predator-prey relationship*

692 An ecosystem consists of the abiotic environment and the species and their functional  
693 characters that live in it (Hooper et al. 2005). Predator-prey relationships are the cornerstone  
694 of ecosystem dynamics (Bailey et al. 2010), and a phenotypic change in one species can  
695 induce ecological and evolutionary changes in other species interacting with it (Agrawal  
696 2001). The predator-prey relationship is characterised by prey survival on the one hand, and  
697 predator foraging strategy on the other hand. As a result, a change in the body size of one  
698 species can affect the other species in the food web. Most predatory fish tend to be gape-  
699 limited, and thus both prey and predator body size are likely to influence the outcome of  
700 predator-prey encounters. The predator gape-limitation determines when prey will reach a  
701 size refuge from the predator, which in turn can have community-wide effects. Persson et al.  
702 (1995) studied size-structured perch (*Perca fluviatilis*) populations in four lakes in Sweden.  
703 Two of these lakes had perch, and two had perch and pike (*Esox lucius*). All lakes had  
704 predators, because perch are known to be cannibalistic. Given that predatory perch is smaller  
705 than predatory pike, in lakes with perch only, perch reached size refuge earlier than in lakes  
706 with also pike present. Persson et al. (1995) found that the lakes differed in size dependent  
707 mortality and growth rates as well as perch habitat use, so that the presence of pike increased  
708 the size when perch reached size refuge, increased the growth rate and limited their resource

709 use. In the lakes with no pike present, perch utilised both the hypolimnion and epilimnion  
710 habitats and thus were also found below the thermocline. The authors attributed these  
711 differences to the differences in the size when perch reached size refuge, illustrating how  
712 size-dependent predation can feed back to the ecosystem function by altering the habitat use  
713 of the species (Persson et al. 1995). Growth rate and body size may even determine who  
714 becomes a prey and who is a predator. A study by Nilsson et al. (2019) documented a  
715 predator-prey role reversal for pike and stickleback. While pike is usually a predator and  
716 stickleback is a prey, they provided evidence that juvenile pike mortality is size-dependant  
717 and corresponds to stickleback gape limitation (Nilsson et al. 2019). In the presence of  
718 increasing water temperature or human induced changes in body size and growth rate, this  
719 kind of predator-prey role reversals may add to the hindrance of population recovery.

720 While size-dependent predation can have ecological effects on the environment as described  
721 in the above study by Persson et al. (1995), the cause and effect is likely more complex. Size-  
722 related evolutionary and ecological changes can also drive changes in the ecosystem, and  
723 these may further feed back into the ecosystem. In their experimental study, Palkovacs et al.  
724 (2009) compared the effects of ecological (invasive guppies, *P. reticulata*), evolutionary  
725 (different guppy life-histories as a result of different predation pressure) and co-evolutionary  
726 (coevolution of guppies and the small fish *Rivulus*) agents driving ecosystem change in  
727 Trinidadian river ecosystems. They concluded that guppy evolution and guppy-*Rivulus*  
728 coevolution caused significant changes in the surrounding ecosystem, while guppy invasion  
729 did not. Another example of evolutionary change affecting the ecosystem comes from the  
730 gape-limited predatory alewife (*Alosa pseudoharengus*), which has diverged in its foraging  
731 traits (Palkovacs and Post 2009). Anadromous alewives are capable of preying on larger prey  
732 than their landlocked counterparts, and this has in turn significantly affected the size structure  
733 of its prey, crustacean zooplankton (Palkovacs and Post 2009). These studies provide

734 evidence that evolutionary changes in one species can have an impact on the entire  
735 ecosystem. Human-induced evolutionary changes on various species and their effects on  
736 ecosystems have further been reviewed by Palkovacs et al. (2011) and Fraser (2013).

737 *Trophic cascade*

738 The tale of Atlantic cod is an iconic example of how changes have propagated through  
739 different levels of biological organisation in nature. The intensely fished northern cod  
740 population in southern Labrador and eastern Newfoundland collapsed in the early 1990s, and  
741 despite a decades long moratorium, the stocks have not fully recovered (Neuenhoff et al.  
742 2019; Sguotti et al. 2019). The reasons for the lack of recovery are complex, and include  
743 several hypotheses such as changing sea water temperatures, predation by seals, continued  
744 fishing, and life-history changes due to fishing (Swain et al. 2011). Olsen et al. (2004)  
745 showed that the fishery collapse was preceded by a rapid phenotypic change toward younger  
746 age and smaller size at maturity, and the study strongly suggested there was an evolutionary  
747 component behind this change. It is likely that this has contributed to the slow recovery of the  
748 stocks (Olsen et al. 2004), and similar trends have been recorded in many other top predators  
749 (Hutchings and Baum 2005). The collapse of cod and other large predator populations in the  
750 northwest Atlantic marine ecosystem led to a cascade involving four trophic levels (Frank et  
751 al. 2005). Following the collapse of large predators, the abundance of smaller fish and  
752 benthic macroinvertebrates increased markedly. The increase in smaller fish in turn  
753 influenced the abundance of zooplankton and phytoplankton, followed by a response in  
754 nitrate concentrations. This top-down trophic cascade has likely further impeded the recovery  
755 of the cod population by altering food webs (Frank et al. 2005).

756 Similarly, in the Northeast Pacific, marked declines in the abundance of the oldest and largest  
757 individuals of Chinook salmon (*O. tshawytscha*), and changes in the age and size structure of

758 the population coincide with a decline in the length-at-age of the fish (Ohlberger et al. 2017).  
759 Intriguingly, while the decrease in the length-at-age was clear, the cause of it was not.  
760 Ohlberger et al. (2017) hypothesised that the changes could be a result of size-selective  
761 harvesting, changing temperatures, interspecific competition, or, more likely, predation by  
762 large apex predators such as the resident killer whale, the numbers of which have increased  
763 following a harvest ban in the 1970s. The loss of the oldest and largest individuals of the  
764 Chinook salmon population are of concern because it can have a negative impact on the long-  
765 term viability of the population (Ohlberger et al. 2017). Another ecosystem-level example  
766 comes from the Northwest Atlantic, where the combination of size-selective harvest and  
767 changing climate caused reductions in the body sizes of functional top predators, which in  
768 turn contributed to the increase in prey biomass (Shackell et al. 2009). This demographic  
769 change was also weakly associated with a decline in zooplankton and an increase in  
770 phytoplankton abundance, indicating a cascading effect through the food web involving three  
771 trophic levels (Shackell et al. 2009).

772 As discussed, not only fishing, but also changing water temperature has been associated with  
773 shifts towards smaller body size in fish, affecting populations and communities. A  
774 comprehensive meta-analysis by Daufresne et al. (2009) demonstrated an increase in the  
775 proportion of small-sized species with increasing temperature, in terms of both species  
776 richness and abundance (Daufresne et al. 2009). The latter result includes a latitude-related  
777 component, and is in line with not only the temperature-size rule, but also ecogeographical  
778 rules such as the Bergmann's rule or the James' rule (Daufresne et al. 2009). Warming-  
779 induced changes in body size and resulting consequences at the population and community  
780 level have also been reviewed by Ohlberger (2013). These are important studies showing how  
781 the changing climate can have an impact at individual, population and community level, and  
782 even change the species composition of an ecosystem.

783 The explicit demonstration of changes propagating through different levels of biological  
784 organisation is challenging, but in addition to empirical examples discussed above, modelling  
785 and microcosm studies are showing similar trends. In a modelling study, Kuparinen et al.  
786 (2016) used a network model to demonstrate how declining body size together with advanced  
787 maturation may magnify fluctuations in fished populations. They showed that this fluctuation  
788 can extend to other species in the ecosystem, and may continue long after fishing has ceased  
789 (Kuparinen et al. 2016). A microcosm study on predator-prey (rotifer – algae) interactions  
790 showed that the prey evolution affected the growth of predator population more than the  
791 actual abundance of prey, and that the changes in predator abundance in turn affected the  
792 prey evolution, suggesting an eco-evolutionary feedback loop (Becks et al. 2012). While  
793 these particular results cannot be directly extrapolated to fish communities, changes in fish  
794 body size are likely to influence other species too, especially when predation is gape-limited.  
795 Indeed, examples of parallel evolution in fishes such as the cichlids, threespine sticklebacks,  
796 and guppies are illuminating the tight linkage there exists between the genetics of an  
797 individual and the ecological environment surrounding it (Elmer and Meyer 2011).

798

## 799 **Conclusion**

800 Changes in body size at an individual level can propagate through different levels of  
801 biological organisation. Given the current rapid environmental change, organisms will have  
802 to adjust, adapt or move, probably quicker than ever before. Adaptation requires evolutionary  
803 change, and evolutionary change requires building material: genetic variability. Evolutionary  
804 change can occur at ecologically relevant time scales, and therefore it is vital for conservation  
805 biologists and decision makers to understand both the ecology of an organism, and the  
806 genetic architecture that enables evolution. Changes in body size and correlated life history

807 characters following harvest, changing temperature and dissolved oxygen, as well as  
808 predation have been demonstrated empirically (Nusslé et al. 2009, 2011; Baudron et al. 2014;  
809 Hunter et al. 2015; Ohlberger et al. 2017), experimentally (Reznick et al. 1990; Conover and  
810 Munch 2002; van Wijk et al. 2013; Uusi-Heikkilä et al. 2015), as well as through  
811 mathematical modelling (Kuparinen et al. 2016). Consequently, the outcomes of these  
812 changes can vary from behavioural changes (McCormick 2009; Sutter et al. 2012) to changes  
813 in reproductive output (Hixon et al. 2014), and can extend their influence to the next  
814 generation (van Wijk et al. 2013), and the entire ecosystem (Frank et al. 2005) regardless of  
815 whether the change is genetic or not (Bolnick et al. 2011). The genetic basis of the change  
816 matters, however, because first, genetic change allows for the evolutionary adaptation to the  
817 changing environment, and second, evolutionary change may be hard if not impossible to  
818 reverse (Salinas et al. 2012; Uusi-Heikkilä et al. 2017). Should the changes be indeed genetic,  
819 and therefore likely hard to reverse, the consequences that extend from declining body  
820 through to population size and stability (Audzijonyte and Kuparinen 2016) to ecosystem  
821 functions (Frank et al. 2005; Ohlberger et al. 2017), may also be hard to reverse.

822 In addition to reversibility, understanding the genetic basis of the changes occurring in nature  
823 is vital from the biodiversity management perspective. From the multiple stressors affecting  
824 our oceans today, some are easier controlled than others. Managing fisheries selection  
825 regimes, for instance, is easier and quicker to control than changing climate. If we utilise the  
826 genetic knowledge and fishing methods that conserve variation, we may be maintaining a  
827 higher genetic variability (Edeline et al. 2009), as well as population stability (Bolnick et al.  
828 2011). Higher genetic variability, in turn, is what forms the basis for evolutionary potential.  
829 In this way, we may better conserve the biodiversity not only now, but also in the future.

830

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1453 **Figure 1.** A summary of how different external stressors may affect fish body size, and how  
1454 the change in body size or associated life-history traits may propagate through different levels  
1455 of biological organisation. The superscript denotes an example study on the topic. 1) Hunter  
1456 et al. 2015; 2) Nusslé et al. 2009, 2011; 3) Conover and Munch 2002; 4) van Wijk et al. 2013;  
1457 5) Uusi-Heikkilä et al. 2015; 6) Uusi-Heikkilä et al. 2017; 7) Walsh et al. 2006; 8) Salinas et  
1458 al. 2012; 9) Biro et al. 2004, Biro and Post 2008; 10) Uusi-Heikkilä et al. 2008; 11) Uusi-  
1459 Heikkilä et al. 2015; 12) Barneche et al. 2018; 13) Dick et al. 2017; 14) Savage et al. 2004;  
1460 15) Fleming and Gross 1994; 16) Berkeley et al. 2004; 17) Hixon et al. 2014; 18)  
1461 Audzijonyte and Kuparinen 2016; 19) Dunlop et al. 2007; 20) Hauser et al. 2002; 21) Pinsky  
1462 and Palumbi 2014; 22) Hutchinson et al. 2003; 23) Jakobsdóttir et al. 2011; 24) Olsen et al.  
1463 2009; 25) Reznick et al. 1997; 26) Edeline et al. 2007; 27) Olsen et al. 2004; 28) Frank et al.  
1464 2005; 29) Ohlberger et al. 2017; 30) Shackell et al. 2009; 31) Daufresne et al. 2009; 32)  
1465 Kuparinen et al. 2016; 33) Becks et al. 2012; 34) Elmer and Meyer 2011; 35) Heins et al.  
1466 2016; 36) Reznick et al. 2001; 37) Persson et al 1995; 38) Nilsson et al. 2019.

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1468 **Figure 2.**

1469 A summary of the main ecological theories behind the discussed stressors as selection agents.  
1470 1) Bergmann 1847; 2) James 1970; 3) Atkinson 1994; 4) West et al. 1997; 5) Pauly 1981; 6)  
1471 Lefevre et al. 2017; Audzijonyte et al 2019 7) Lush 1937; 8) Miller et al. 1988; 9) MacArthur  
1472 and Pianka 1966.

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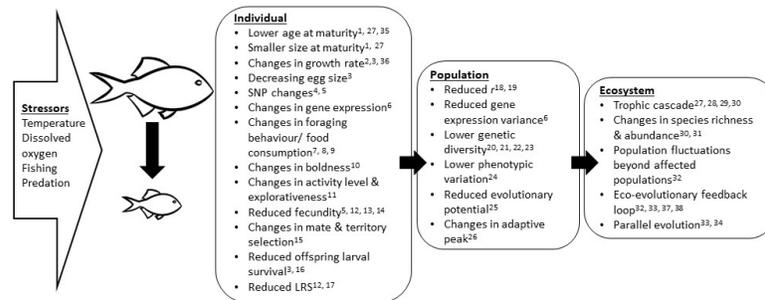
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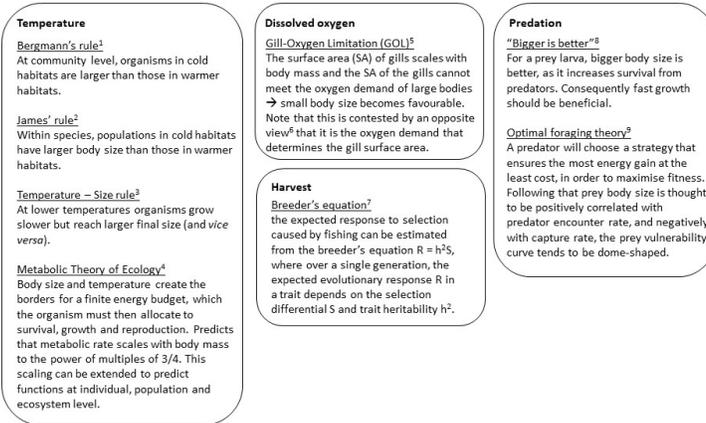
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A summary of how different external stressors may affect fish body size, and how the change in body size or associated life-history traits may propagate through different levels of biological organisation. The superscript denotes an example study on the topic. 1) Hunter et al. 2015; 2) Nusslé et al. 2009, 2011; 3) Conover and Munch 2002; 4) van Wijk et al. 2013; 5) Uusi-Heikkilä et al. 2015; 6) Uusi-Heikkilä et al. 2017; 7) Walsh et al. 2006; 8) Salinas et al. 2012; 9) Biro et al. 2004, Biro and Post 2008; 10) Uusi-Heikkilä et al. 2008; 11) Uusi-Heikkilä et al. 2015; 12) Barneche et al. 2018; 13) Dick et al. 2017; 14) Savage et al. 2004; 15) Fleming and Gross 1994; 16) Berkeley et al. 2004; 17) Hixon et al. 2014; 18) Audzijonyte and Kuparinen 2016; 19) Dunlop et al. 2007; 20) Hauser et al. 2002; 21) Pinsky and Palumbi 2014; 22) Hutchinson et al. 2003; 23) Jakobsdóttir et al. 2011; 24) Olsen et al. 2009; 25) Reznick et al. 1997; 26) Edeline et al. 2007; 27) Olsen et al. 2004; 28) Frank et al. 2005; 29) Ohlberger et al. 2017; 30) Shackell et al. 2009; 31) Daufresne et al. 2009; 32) Kuparinen et al. 2016; 33) Becks et al. 2012; 34) Elmer and Meyer 2011; 35) Heins et al. 2016; 36) Reznick et al. 2001; 37) Persson et al. 1995; 38) Nilsson et al. 2019.

338x190mm (96 x 96 DPI)

A summary of the main ecological theories behind different stressors as selection agents



A summary of the main ecological theories behind the discussed stressors as selection agents. 1) Bergmann 1847; 2) James 1970; 3) Atkinson 1994; 4) West et al. 1997; 5) Pauly 1981; 6) Lefevre et al. 2017; Audzijonyte et al 2019 7) Lush 1937; 8) Miller et al. 1988; 9) MacArthur and Pianka 1966.

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