This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Ahti, Pauliina Anna; Kuparinen, Anna; Uusi-Heikkilä, Silva

Title: Size does matter : the eco-evolutionary effects of changing body size in fish

Year: 2020

Version: Accepted version (Final draft)

Copyright: © Canadian Science Publishing, 2020

Rights: In Copyright

Rights url: <http://rightsstatements.org/page/InC/1.0/?language=en>

Please cite the original version:

Ahti, P. A., Kuparinen, A., & Uusi-Heikkilä, S. (2020). Size does matter : the eco-evolutionary effects of changing body size in fish. *Environmental Reviews*, 28(3), 311-324.
<https://doi.org/10.1139/er-2019-0076>

Environmental Reviews

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

Journal:	<i>Environmental Reviews</i>
Manuscript ID	er-2019-0076.R2
Manuscript Type:	Review
Date Submitted by the Author:	20-Apr-2020
Complete List of Authors:	Ahti, Pauliina; University of Jyväskylä , Department of Biological and Environmental Science Kuparinen, Anna; University of Jyväskylä , Department of Biological and Environmental Science Uusi-Heikkilä, Silva; University of Jyväskylä , Department of Biological and Environmental Science
Is this manuscript invited for consideration in a Special Issue? :	Not applicable (regular submission)
Keyword:	body size, fisheries, environmental change, evolution, life-history trait

SCHOLARONE™
Manuscripts

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

Pauliina A. Ahti^{1*}, Anna Kuparinen¹ & Silva Uusi-Heikkilä¹

¹ Department of Biological and Environmental Sciences, P.O. Box 35, 40014 University of Jyväskylä, Finland

*Corresponding author: Pauliina A. Ahti, Department of Biological and Environmental Sciences, P.O. Box 35, 40014 University of Jyväskylä, Finland, telephone: +358-41-492-4459, e-mail: pauliina.a.s.ahti@jyu.fi

Word count: 10534

Draft

Abstract

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

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

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.

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

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

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

Here, we review the recent literature on the causes and consequences of changing body size in fish and its links to ecological and evolutionary processes. While there is a large selection of important and relevant literature focusing on body size in fish (Uusi-Heikkilä et al. 2008; Devine et al. 2012; Enberg et al. 2012; Audzijonyte et al. 2013; Heino et al. 2013, 2015; Diaz 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

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

The ecological theories behind different stressors as selection agents

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

Temperature and dissolved oxygen

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

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

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

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

Harvesting and natural predators

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

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

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

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

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

Individual level consequences of selection

Changing body size

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

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

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

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

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

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

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

Changes in growth rate

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

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

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

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

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

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

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

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

Big and bold? Linking body size and behaviour

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

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

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

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

Changes in reproduction

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

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

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

Bigger size appears to be beneficial, as it allows for increased egg production, better access to nesting territories, and improved nest digging (Fleming and Gross 1994). Further, the changes in body size are often accompanied with associated changes in population age structure. The truncation of age structure can potentially enhance the effects of declining body size at individual and population level. As an example, longevity may be advantageous as it can increase population recruitment variability (in timing), particularly in long-lived fish species, thereby making the population less vulnerable in unstable environments (Longhurst 2002). Maternal age can also contribute to the fitness of offspring. The larvae of older black rockfish (*Sebastes melanops*) showed over three times faster growth rate than the larvae of younger rockfish, and they survived starvation better (Berkeley et al. 2004). Since body size and reproductive output are often positively correlated (Barneche et al. 2018), changes in individual body size can have multigenerational impacts, truncate the population age and size structure, and potentially lower the population growth rate.

How do changes in body size translate to population dynamics?

The intrinsic rate of per-capita population growth rate (r) can be thought of as a population level analogue to LRS. Although r cannot be directly translated from LRS, body size is a strong correlate for both (Denney et al. 2002; Anderson et al. 2008). Indeed, Uusi-Heikkilä et

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

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

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

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

Genetic and phenotypic variation

While selective harvesting is known to affect several traits in harvested populations (Walsh et al. 2006), the nature of selection can affect the outcome. Some fish populations have not 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

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

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

In some cases fishing can result both in strong directional selection and in declining population size, therefore being a candidate for the cause of potentially irreversible changes in genetic and phenotypic variation. Empirical (Hauser et al. 2002) and experimental (Uusi-Heikkilä et al. 2015) studies as well as a meta-analysis of 140 fish species (Pinsky and Palumbi 2014) have shown that harvest can lead to declines in genetic variation (both 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

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

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

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

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

Ecosystem-level effects of the changing body size

Predator-prey relationship

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

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

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

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

Trophic cascade

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

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

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

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

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

Conclusion

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

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

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

Acknowledgements

This work was supported by funding from the Emil Aaltonen Foundation (PAA), the Academy of Finland AK (grant no. 317495), SUH (grant no. 325107), Discovery Grant from the National Sciences and Engineering Research Council of Canada (NSERC to AK), the European Research Council (COMPLEX-FISH 400820 to AK), and the Finnish Cultural Foundation (SUH). The authors thank the two anonymous referees as well as the editing team.

Draft

852

853 **References:**

854 Agrawal, A.A. 2001. Phenotypic Plasticity in the Interactions and Evolution of Species.

855 Science. **294**: 321–327. doi:10.1126/science.1060701.

856 Allain, G., Petitgas, P., Grellier, P., and Lazure, P. 2003. The selection process from larval to

857 juvenile stages of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay investigated by858 Lagrangian simulations and comparative otolith growth. Fish. Oceanogr. **12**(4–5): 407–

859 418. doi:10.1046/j.1365-2419.2003.00245.x.

860 Allendorf, F.W., and Hard, J.J. 2009. Human-induced evolution caused by unnatural

861 selection through harvest of wild animals. PNAS. **3**: 9987–9994. doi:10.17226/12692.

862 Anderson, C.N.K., Chih-hao, H., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J.,

863 May, R.M., and Sugihara, G. 2008. Why fishing magnifies fluctuations in fish

864 abundance. Nature. **452**: 835–839. doi:10.1038/nature06851.

865 Andrews, J.W., Murai, T., and Gibbons, G. 1973. The influence of dissolved oxygen on the

866 growth of channel catfish. Trans. Am. Fish. Soc. **102**(4): 835–838. doi:10.1577/1548-

867 8659(1973)102<835.

868 Arandia-Gorostidi, N., Huete-Stauffer, T.M., Alonso-Saez, L., and Moran, X.A.G. 2017.

869 Testing the metabolic theory of ecology with marine bacteria: different temperature

870 sensitivity of major phylogenetic groups during the spring phytoplankton bloom.

871 Environ. Microbiol. **19**(11): 4493–4505. doi:10.1111/1462-2920.13898.

872 Ashton, K.G., and Feldman, C.R. 2003. Bergmann's rule in nonavian reptiles: turtles follow

873 it, lizards and snakes reverse it. Evolution. **57**(5): 1151–1163. doi:10.1111/j.0014-

874 3820.2003.tb00324.x.

- 875 Atkinson, D. 1994. Temperature and organism size - a biological law for ectotherms. *Adv.*
876 *Ecol. Res.* **25**: 1–58. doi:10.1016/S0065-2504(08)60212-3.
- 877 Audzijonyte, A., Barneche, D.R., Baudron, A.R., Belmaker, J., Clark, T.D., Marshall, C.T.,
878 Morrongiello, J.R., and van Rijn, I. 2019. Is oxygen limitation in warming waters a valid
879 mechanism to explain decreased body sizes in aquatic ectotherms? *Glob. Ecol.*
880 *Biogeogr.* **28**(2): 64–77. doi:10.1111/geb.12847.
- 881 Audzijonyte, A., and Kuparinen, A. 2016. The role of life histories and trophic interactions in
882 population recovery. *Conserv. Biol.* **30**(4): 734–743. doi:10.1111/cobi.12651.
- 883 Audzijonyte, A., Kuparinen, A., and Fulton, E.A. 2013. How fast is fisheries-induced
884 evolution? Quantitative analysis of modelling and empirical studies. *Evol. Appl.* **6**(4):
885 585–595. doi:10.1111/eva.12044.
- 886 Bailey, K.M., Ciannelli, L., Hunsicker, M., Rindorf, A., Neuenfeldt, S., and Mo, C. 2010.
887 Comparative analysis of marine ecosystems: workshop on predator – prey interactions.
888 *Biol. Lett.* **6**: 579–581. doi:10.1098/rsbl.2010.0326.
- 889 Bailey, N., Bailey, D.M., Bellini, L.C., Fernandes, P.G., Fox, C., S, H., Holmes, S., Howe, J.,
890 Hughes, S., Magill, S., McIntyre, F., McKee, D., Ryan, M.R., Smith, I.P., Tyldesley, G.,
891 Watret, R., and Turrell, W.R. 2011. The West of Scotland marine ecosystem: A review
892 of scientific knowledge. *Mar. Scotl. Sci. Rep.* 0911: 1–288.
- 893 Bailly, D., Cassemiro, F.A.S., Agostinho, C.S., Marques, E.E., and Agostinho, A.A. 2014.
894 The metabolic theory of ecology convincingly explains the latitudinal diversity gradient
895 of Neotropical freshwater fish. *Ecology* **95**(2): 553–562. doi: 10.1890/13-0483.1.
- 896 Barneche, D.R., Kulbicki, M., Floeter, S.R., Friedlander, A.M., and Allen, A.P. 2016.
897 Energetic and ecological constraints on population density of reef fishes. *Proc. R. Soc. B*

- 898 **283**: 20152186. <http://dx.doi.org/10.1098/rspb.2015.2186>.
- 899 Barneche, D.R., Robertson, D.R., White, C.R., and Marshall, D.J. 2018. Fish reproductive-
900 energy output increases disproportionately with body size. *Science*. **360**: 642–645. doi:
901 10.1126/science.aao6868.
- 902 Barnett, T.P., Pierce, D.W., AchutaRao, K.M., J, G.P., D, S.B., Gregory, J.M., and
903 Washington, W.M. 2005. Penetration of human-induced warming into the world's
904 oceans. *Science*. **309**: 284–287. doi:10.1126/science.1112418.
- 905 Barson, N.J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G.H., Fiske, P., Jacq, C.,
906 Jensen, A.J., Johnston, S.E., Karlsson, S., Kent, M., Moen, T., Niemelä, E., Nome, T.,
907 Næsje, T.F., Orell, P., Romakkaniemi, A., Sægrov, H., Urdal, K., Erkinaro, J., Lien, S.,
908 and Primmer, C.R. 2015. Sex-dependent dominance at a single locus maintains variation
909 in age at maturity in salmon. *Nature* **528**: 405–408. doi:10.1038/nature16062.
- 910 Baudron, A.R., Needle, C.L., and Marshall, C.T. 2011. Implications of a warming North Sea
911 for the growth of haddock *Melanogrammus aeglefinus*. *J. Fish Biol.* **78**(7): 1874–1889.
912 doi:10.1111/j.1095-8649.2011.02940.x.
- 913 Baudron, A.R., Needle, C.L., Rijnsdorp, A.D., and Tara Marshall, C. 2014. Warming
914 temperatures and smaller body sizes: Synchronous changes in growth of North Sea
915 fishes. *Glob. Chang. Biol.* **20**(4): 1023–1031. doi:10.1111/gcb.12514.
- 916 Becks, L., Ellner, S.P., Jones, L.E., and Hairston, N.G. 2012. The functional genomics of an
917 eco-evolutionary feedback loop: Linking gene expression, trait evolution, and
918 community dynamics. *Ecol. Lett.* **15**(5): 492–501. doi:10.1111/j.1461-
919 0248.2012.01763.x.
- 920 Belk, M.C., and Houston, D.D. 2002. Bergmann's rule in ectotherms: A test using freshwater

- 921 fishes. *Am. Nat.* **160**(6): 803–808. doi:10.1086/343880.
- 922 Benoît, H.P., Swain, D.P., Hutchings, J.A., Knox, D., Doniol-Valcroze, T., and Bourne, C.M.
 923 2018. Evidence for reproductive senescence in a broadly distributed harvested marine
 924 fish. *Mar. Ecol. Prog. Ser.* **592**: 207–224. doi:10.3354/meps12532.
- 925 Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004. Maternal Age as a Determinant of
 926 Larval Growth and Survival in a Marine Fish, *Sebastes Melanops*. *Ecology* **85**(5): 1258–
 927 1264. doi:10.1890/03-0706.
- 928 Bergmann, C. 1847. About the relationships between heat conservation and body size of
 929 animals. *Goett. Stud. (Original in German)* **1**:595–708.
- 930 Bernatchez, L. 2016. On the maintenance of genetic variation and adaptation to
 931 environmental change: considerations from population genomics in fishes. *J. Fish Biol.*
 932 **89**(6): 2519–2556. doi:10.1111/jfb.13145.
- 933 Beverton, R.J.H., Hylan, A., Østvedt, O.J., Alvsvaag, J., and Iles, T.C. 2004. Growth,
 934 maturation, and longevity of maturation cohorts of Norwegian spring-spawning herring.
 935 *ICES J. Mar. Sci.* **61**(2): 165–175. doi:10.1016/j.icesjms.2004.01.001.
- 936 Biro, P.A., Abrahams, M. V., Post, J.R., and Parkinson, E.A. 2004. Predators select against
 937 high growth rates and risk-taking behaviour in domestic trout populations. *Proc. R. Soc.*
 938 *B Biol. Sci.* **271**(1554): 2233–2237. doi:10.1098/rspb.2004.2861.
- 939 Biro, P.A., and Post, J.R. 2008. Rapid depletion of genotypes with fast growth and bold
 940 personality traits from harvested fish populations. *Proc. Natl. Acad. Sci.* **105**(8): 2919–
 941 2922. doi:10.1073/pnas.0708159105.
- 942 Blanchet, S., Beauchard, O., and Tedesco, P.A. 2010. Non-native species disrupt the
 943 worldwide patterns of freshwater fish body size: implications for Bergmann's rule. *Ecol.*

- 944 Lett. **13**: 421–431. doi:10.1111/j.1461-0248.2009.01432.x.
- 945 Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf,
 946 V.H.W., Schreiber, S.J., Urban, M.C., and Vasseur, D. 2011. Why intraspecific trait
 947 variation matters in community ecology. Trends Ecol. Evol. **26**(4): 183–192.
 948 doi:10.1016/j.tree.2011.01.009.
- 949 Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.).
 950 ICES J. Mar. Sci. **52**(1): 1–10. doi:10.1016/1054-3139(95)80010-7.
- 951 Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., and West, G.B. 2004. Toward a
 952 metabolic theory of ecology. Ecology **85**(7): 1771–1789. doi:10.1890/03-9000.
- 953 Brown, J.H., West, G.B., and Enquist, B.J. 2005. Yes, West, Brown and Enquist’s model of
 954 allometric scaling is both mathematically correct and biologically relevant. Funct. Ecol.
 955 **19**(4): 735–738. doi:10.1111/j.1365-2435.2005.01022.x.
- 956 Cabanne, G.S., Calderón, L., Trujillo Arias, N., Flores, P., Pessoa, R., d’Horta, F.M., and
 957 Miyaki, C.Y. 2016. Effects of Pleistocene climate changes on species ranges and
 958 evolutionary processes in the Neotropical Atlantic Forest. Biol. J. Linn. Soc. **119**(4):
 959 856–872. doi:10.1111/bij.12844.
- 960 Cappel, M., Marriott, R.J., and Newman, S.J. 2013. James’s rule and causes and consequences
 961 of a latitudinal cline in the demography of John’s Snapper (*Lutjanus johnii*) in coastal
 962 waters of Australia. Fish. Bull. **111**(4): 309–324. doi:10.7755/FB.111.4.2.
- 963 Carlson, S.M., Edeline, E., Asbjørn Vøllestad, L., Haugen, T.O., Winfield, I.J., Fletcher,
 964 J.M., Ben James, J., and Stenseth, N.C. 2007. Four decades of opposing natural and
 965 human-induced artificial selection acting on Windermere pike (*Esox lucius*). Ecol. Lett.
 966 **10**(6): 512–521. doi:10.1111/j.1461-0248.2007.01046.x.

- 967 Carroll, S.P., Hendry, A.P., Reznick, D.N., and Fox, C.W. 2007. Evolution on ecological
968 time-scales. *Funct. Ecol.* **21**(3): 387–393. doi:10.1111/j.1365-2435.2007.01289.x.
- 969 Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Deng Palomares,
970 M.L., Watson, R., and Pauly, D. 2012. Shrinking of fishes exacerbates impacts of global
971 ocean changes on marine ecosystems. *Nat. Clim. Chang.* **3**(3): 254–258.
972 doi:10.1038/nclimate1691.
- 973 Clark, T.D., Donaldson, M.R., Pieperhoff, S., Drenner, S.M., Lotto, A., Cooke, S.J., Hinch,
974 S.G., Patterson, D.A., and Farrell, A.P. 2012. Physiological benefits of being small in a
975 changing world: Responses of coho salmon (*Oncorhynchus kisutch*) to an acute thermal
976 challenge and a simulated capture event. *PLoS One* **7**(6): 1–8.
977 doi:10.1371/journal.pone.0039079.
- 978 Cline, T.J., Ohlberger, J., and Schindler, D.E. 2019. Effects of warming climate and
979 competition in the ocean for life-histories of Pacific salmon. *Nat. Ecol. Evol.* **3**: 935–
980 942. doi:10.1038/s41559-019-0901-7.
- 981 Conover, D.O., and Munch, S.B. 2002. Sustaining fisheries yields over evolutionary time
982 scales. *Science.* **297**: 94–97. doi:10.1126/science.1074085.
- 983 Cossins, A.R., and Crawford, D.L. 2005. Fish as models for environmental genomics. *Nat.*
984 *Rev. Genet.* **6**(4): 324–333. doi:10.1038/nrg1590.
- 985 Costello, C., Ovando, D., Clavelle, T., Strauss, C.K., Hilborn, R., Melnychuk, M.C., Branch,
986 T.A., Gaines, S.D., Szuwalski, C.S., Cabral, R.B., Rader, D.N., and Leland, A. 2016.
987 Global fishery prospects under contrasting management regimes. *Proc. Natl. Acad. Sci.*
988 **113**(18): 5125–5129. doi:10.1073/pnas.1520420113.
- 989 Crozier, L.G., and Hutchings, J.A. 2014. Plastic and evolutionary responses to climate change

- 990 in fish. *Evol. Appl.* **7**(1): 68–87. doi:10.1111/eva.12135.
- 991 Daufresne, M., Lengfellner, K., and Sommer, U. 2009. Global warming benefits the small in
992 aquatic ecosystems. *PNAS* **106**(31): 12788–12793. doi:10.1007/BF00291885.
- 993 Day, T., Abrams, P.A., Chase, J.M., Day, T., Abrams, P.A., and Chase, I.J.M. 2002. The role
994 of size-specific predation in the evolution and diversification of prey life histories.
995 *Evolution*. **56**(5): 877–887. <https://www.jstor.org/stable/3061628>.
- 996 Denney, N.H., Jennings, S., and Reynolds, J.D. 2002. Life-history correlates of maximum
997 population growth rates in marine fishes. *Proc. R. Soc. B Biol. Sci.* **269**(1506): 2229–
998 2237. doi:10.1098/rspb.2002.2138.
- 999 Devine, J.A., Wright, P.J., Pardoe, H.E., and Heino, M. 2012. Comparing rates of
1000 contemporary evolution in life-history traits for exploited fish stocks. *Can. J. Fish.*
1001 *Aquat. Sci.* **69**(6): 1105–1120. doi:10.1139/f2012-047.
- 1002 Diaz Pauli, B., and Heino, M. 2014. What can selection experiments teach us about fisheries-
1003 induced evolution? *Biol. J. Linn. Soc.* **111**(3): 485–503. doi:10.1111/bij.12241.
- 1004 Diaz Pauli, B., and Sih, A. 2017. Behavioural responses to human-induced change: Why
1005 fishing should not be ignored. *Evol. Appl.* **10**(3): 231–240. doi:10.1111/eva.12456.
- 1006 Dick, E.J., Beyer, S., Mangel, M., and Ralston, S. 2017. A meta-analysis of fecundity in
1007 rockfishes (genus *Sebastes*). *Fish. Res.* **187**: 73–85. Elsevier B.V.
1008 doi:10.1016/j.fishres.2016.11.009.
- 1009 Douhard, M., Lemaitre, J.-F., Bonenfant, C., Berger, V., Gaillard, J.-M., Gamelon, M., and
1010 Plard, F. 2015. Early-late life trade-offs and the evolution of ageing in the wild. *Proc. R.*
1011 *Soc. B Biol. Sci.* **282**(1806): 20150209. doi:10.1098/rspb.2015.0209.
- 1012 Dukes, J.S., and Mooney, H.A. 1999. Does global change increase the Success of Biological

- 1013 Invaders? *Trends Ecol. Evol.* **14**(4): 135–139. doi:10.1016/S0169-5347(98)01554-7.
- 1014 Dunlop, E.S., Eikeset, A.M., and Stenseth, N.C. 2015. From genes to populations: How
1015 fisheries-induced evolution alters stock productivity. *Ecol. Appl.* **25**(7): 1860–1868.
1016 doi:10.1890/14-1862.1.
- 1017 Edeline, E., Carlson, S.M., Stige, L.C., Winfield, I.J., Fletcher, J.M., James, J.B., Haugen,
1018 T.O., Vollestad, L.A., and Stenseth, N.C. 2007. Trait changes in a harvested population
1019 are driven by a dynamic tug-of-war between natural and harvest selection. *Proc. Natl.*
1020 *Acad. Sci.* **104**(40): 15799–15804. doi:10.1073/pnas.0705908104.
- 1021 Edeline, E., Le Rouzic, A., Winfield, I.J., Fletcher, J.M., James, J. Ben, Stenseth, N.C., and
1022 Vøllestad, L.A. 2009. Harvest-induced disruptive selection increases variance in fitness-
1023 related traits. *Proc. R. Soc. B Biol. Sci.* **276**: 4163–4171. doi:10.1098/rspb.2009.1106.
- 1024 Elmer, K.R., and Meyer, A. 2011. Adaptation in the age of ecological genomics: Insights
1025 from parallelism and convergence. *Trends Ecol. Evol.* **26**(6): 298–306.
1026 doi:10.1016/j.tree.2011.02.008.
- 1027 Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S.,
1028 and Heino, M. 2012. Fishing-induced evolution of growth: Concepts, mechanisms and
1029 the empirical evidence. *Mar. Ecol.* **33**(1): 1–25. doi:10.1111/j.1439-0485.2011.00460.x.
- 1030 Etienne, R.S., Apol, M.E.F., and Olff, H. 2006. Demystifying the West, Brown & Enquist
1031 model of the allometry of metabolism. *Funct. Ecol.* **20**(2): 394–399. doi:10.1111/j.1365-
1032 2435.2006.01136.x.
- 1033 Fernández-Torres, F., Ariel, P., and Olalla-Tárraga, M.Á. 2018. Shallow water ray-finned
1034 marine fishes follow Bergmann's rule. *Basic Appl. Ecol.* **33**: 99–110.
1035 doi:10.1016/j.baae.2018.09.002.

- 1036 Fisher, J.A.D., Frank, K.T., and Leggett, W.C. 2010. Breaking Bergmann's rule: truncation
1037 of Northwest Atlantic marine fish body sizes. *Ecology* **91**(9): 2499–2505.
1038 doi:10.1890/09-1914.1.
- 1039 Fleming, I.A., and Gross, M.R. 1994. Breeding competition in a Pacific Salmon (Coho:
1040 *Oncorhynchus kisutch*): Measures of natural and sexual selection. *Evolution*. **48**(3):
1041 637– 657. doi:10.2307/2410475.
- 1042 Forster, J., Hirst, A.G., and Atkinson, D. 2012. Warming-induced reductions in body size are
1043 greater in aquatic than terrestrial species. *Proc. Natl. Acad. Sci.* **109**(47): 19310–19314.
1044 doi:10.1073/pnas.1210460109.
- 1045 Frank, K.T., Petrie, B., Choi, S. J., and Leggett, W.C., 2005. Trophic cascades in a formerly
1046 cod-dominated ecosystem. *Science*. **308**: 1621–1623. doi: 10.1126/science.1113075.
- 1047 Fraser, D.J. 2013. The emerging synthesis of evolution with ecology in fisheries science.
1048 *Can. J. Fish. Aquat. Sci.* **70**(9): 1417–1428. doi:10.1139/cjfas-2013-0171.
- 1049 Fuiman, L.A., and Magurran, A.E. 1994. Development of predator defences in fishes. *Rev.*
1050 *Fish Biol. Fish.* **4**(2): 145–183. doi:10.1007/BF00044127.
- 1051 Garcia De Leaniz, C., Fleming, I.A., Einum, S., Verspoor, E., Jordan, W.C., Consuegra, S.,
1052 Aubin-Horth, N., Lajus, D., Letcher, B.H., Youngson, A.F., Webb, J.H., Vøllestad, L.A.,
1053 Villanueva, B., Ferguson, A., and Quinn, T.P. 2007. A critical review of adaptive
1054 genetic variation in Atlantic salmon: Implications for conservation. *Biol. Rev.* **82**(2):
1055 173–211. doi:10.1111/j.1469-185X.2006.00004.x.
- 1056 Garcia, H.E., Boyer, T.P., Levitus, S., Locarnini, R.A., and Antonov, J. 2005. On the
1057 variability of dissolved oxygen and apparent oxygen utilization content for the upper
1058 world ocean: 1955 to 1998. *Geophys. Res. Lett.* **32**(9): 1–4.

- doi:10.1029/2004GL022286.
- Genner, M.J., Sims, D.W., Southward, A.J., Budd, G.C., Masterson, P., Mchugh, M., Rendle, P., Southall, E.J., Wearmouth, V.J., and Hawkins, S.J. 2010. Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Glob. Chang. Biol.* **16**(2): 517–527. doi:10.1111/j.1365-2486.2009.02027.x.
- Gislason, H., Daan, N., Rice, J.C., and Pope, J.G. 2010. Size, growth, temperature and the natural mortality of marine fish. *Fish Fish.* **11**(2): 149–158. doi:10.1111/j.1467-2979.2009.00350.x.
- Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T., and Fox, J.A. 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* **8**(10): 1114–1127. doi:10.1111/j.1461-0248.2005.00812.x.
- Hanski, I. 2012. Eco-evolutionary dynamics in a changing world. *Ann. N. Y. Acad. Sci.* **1249**: 1–17. doi:10.1111/j.1749-6632.2011.06419.x.
- Haugen, T.O., Aass, P., Stenseth, N.C., and Vøllestad, L.A. 2008. Changes in selection and evolutionary responses in migratory brown trout following the construction of a fish ladder. *Evol. Appl.* **1**(2): 319–335. doi:10.1111/j.1752-4571.2008.00031.x.
- Hauser, L., Adcock, G.J., Smith, P.J., Bernal Ramirez, J.H., and Carvalho, G.R. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proc. Natl. Acad. Sci.* **99**(18): 11742–11747. doi:10.1073/pnas.172242899.
- Hayward, A., and Gillooly, J.F. 2011. The cost of sex: Quantifying energetic investment in gamete production by males and females. *PLoS One* **6**(1): e16557. doi:10.1371/journal.pone.0016557.

- 1082 Heino, M., Baulier, L., Boukal, D.S., Ernande, B., Johnston, F.D., Mollet, F.M., Pardoe, H.,
 1083 Therkildsen, N.O., Uusi-Heikkilä, S., Vainikka, A., Arlinghaus, R., Dankel, D.J.,
 1084 Dunlop, E.S., Eikeset, A.M., Enberg, K., Engelhard, G.H., Jørgensen, C., Laugen, A.T.,
 1085 Masumura, S., Nusslé, S., Urbach, D., Whitlock, R., Rijnsdorp, A.D., and Dieckmann,
 1086 U. 2013. Can fisheries-induced evolution shift reference points for fisheries
 1087 management? *ICES J. Mar. Sci.* **70**(4): 707–721. doi:10.1093/icesjms/fst077.
- 1088 Heino, M., Díaz Pauli, B., and Dieckmann, U. 2015. Fisheries-Induced Evolution. *Annu.*
 1089 *Rev. Ecol. Evol. Syst.* **46**(1): 461–480. doi:10.1146/annurev-ecolsys-112414-054339.
- 1090 Heins, D.C., Knoper, H., and Baker, J.A. 2016. Consumptive and non-consumptive effects of
 1091 predation by introduced northern pike on life-history traits in threespine stickleback.
 1092 *Evol. Ecol. Res.* **17**(3): 355–372.
- 1093 Hixon, M.A., Johnson, D.W., and Sogard, S.M. 2014. BOFFFFs: on the importance of
 1094 conserving old-growth age structure in fishery populations. *ICES J. Mar. Sci.* **71**(8):
 1095 2171–2185. doi:10.1093/icesjms/fst200.
- 1096 Hoffmann, A.A., and Willi, Y. 2008. Detecting genetic responses to environmental change.
 1097 *Nat. Rev. Genet.* **9**(6): 421–432. doi:10.1038/nrg2339.
- 1098 Hollins, J., Thambithurai, D., Köeck, B., Crespel, A., Bailey, D.M., Cooke, S.J., Lindström,
 1099 J., Parsons, K.J., and Killen, S.S. 2018. A Physiological perspective on fisheries-induced
 1100 evolution. *Evol. Appl.* **11**: 561–576. doi:10.1111/eva.12597.
- 1101 Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H.,
 1102 Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J.,
 1103 Vandermeer, J., and Wardle, D.A. 2005. Effects of biodiversity on ecosystem
 1104 functioning: A consensus of current knowledge. *Ecol. Monogr.* **75**(1): 3–35.
 1105 doi:10.1890/04-0922.

- 1106 Hunter, A., Speirs, D.C., and Heath, M.R. 2015. Fishery-induced changes to age and length
1107 dependent maturation schedules of three demersal fish species in the Firth of Clyde.
1108 Fish. Res. **170**: 14–23. doi:10.1016/j.fishres.2015.05.004.
- 1109 Hutchings, J.A., and Baum, J.K. 2005. Measuring marine fish biodiversity: Temporal
1110 changes in abundance, life history and demography. Philos. Trans. R. Soc. B Biol. Sci.
1111 **360**(1454): 315–338. doi:10.1098/rstb.2004.1586.
- 1112 Hutchinson, W.F., Van Oosterhout, C., Rogers, S.I., and Carvalho, G.R. 2003. Temporal
1113 analysis of archived samples indicates marked genetic changes in declining North Sea
1114 cod (*Gadus morhua*). Proc. R. Soc. B Biol. Sci. **270**(1529): 2125–2132.
1115 doi:10.1098/rspb.2003.2493.
- 1116 Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J.,
1117 Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange,
1118 C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., and
1119 Warner, R.R. 2001. Historical overfishing and the recent collapse of coastal ecosystems.
1120 Science. **293**(5530): 629–637. doi:10.1126/science.1059199.
- 1121 Jakobsdóttir, K.B., Pardoe, H., Magnússon, Á., Björnsson, H., Pampoulie, C., Ruzzante,
1122 D.E., and Marteinsdóttir, G. 2011. Historical changes in genotypic frequencies at the
1123 Pantophysin locus in Atlantic cod (*Gadus morhua*) in Icelandic waters: Evidence of
1124 fisheries-induced selection? Evol. Appl. **4**(4): 562–573. doi:10.1111/j.1752-
1125 4571.2010.00176.x.
- 1126 James, F. 1970. Geographic size variation in birds and its relationship to climate. Ecology
1127 **51**:365–390.
- 1128 Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of
1129 reproduction and survival. Can. J. Fish. Aquat. Sci. **53**(4): 820–822. doi:10.1139/f95-

- 1130 233.
- 1131 Johansen, J.L., Pratchett, M.S., Messmer, V., Coker, D.J., Tobin, A.J., and Hoey, A.S. 2015.
- 1132 Large predatory coral trout species unlikely to meet increasing energetic demands in a
- 1133 warming ocean. *Sci. Rep.* **5**: 1–8. doi:10.1038/srep13830.
- 1134 Killen, S., Nati, J., and Suski, C. 2015. Catchability of individual fish by trawling is driven by
- 1135 capacity for anaerobic metabolism. *Proc. R. Soc. B Biol. Sci.* **282**: 20150603. doi:
- 1136 10.1098/rspb.2015.0603.
- 1137 Kleiber, M. 1932. Body size and metabolism. *Hilgardia* **6**(11): 315 - 353.
- 1138 Knouft, J.H. 2004. Latitudinal variation in the shape of the species body size distribution : an
- 1139 analysis using freshwater fishes. *Oecologia* **139**: 408–417. doi:10.1007/s00442-004-
- 1140 1510-x.
- 1141 Kozłowski, J., and Konarzewski, M. 1998. Is West, Brown and Enquist’s model of allometric
- 1142 scaling mathematically correct and biologically relevant? *Funct. Ecol.* **18**: 283–289.
- 1143 doi:10.1111/j.0269-8463.2004.00830.x.
- 1144 Kozłowski, J., and Konarzewski, M. 2005. West, Brown and Enquist’s model of allometric
- 1145 scaling again: the same questions remain. *Funct. Ecol.* **19**: 739–743. doi:10.1111/j.1365-
- 1146 2435.2005.01021.x.
- 1147 Kuparinen, A., Boit, A., Valdovinos, F.S., Lassaux, H., and Martinez, N.D. 2016. Fishing-
- 1148 induced life-history changes degrade and destabilize harvested ecosystems. *Sci. Rep.*
- 1149 **6**(1): 22245. doi:10.1038/srep22245.
- 1150 Kuparinen, A., and Hutchings, J.A. 2016. Genetic architecture of age at maturity can generate
- 1151 either directional or divergent and disruptive harvest-induced evolution. *Philos. Trans.*
- 1152 *R. Soc. B Biol. Sci.* **372**: 20160035. doi:10.1098/rstb.2016.0035.

- 1153 Kuparinen, A., Kuikka, S., and Merilä, J. 2009. Estimating fisheries-induced selection:
1154 Traditional gear selectivity research meets fisheries-induced evolution. *Evol. Appl.* **2**(2):
1155 234–243. doi:10.1111/j.1752-4571.2009.00070.x.
- 1156 Lee, W.S., Monaghan, P., and Metcalfe, N.B. 2013. Experimental demonstration of the
1157 growth rate-lifespan trade-off. *Proc. R. Soc. B Biol. Sci.* **280**:20122370.
1158 doi:10.1098/rspb.2012.2370.
- 1159 Lefevre, S., McKenzie, D.J., and Nilsson, G.E. 2017. Models projecting the fate of fish
1160 populations under climate change need to be based on valid physiological mechanisms.
1161 *Glob. Chang. Biol.* **23**(9): 3449–3459. doi:10.1111/gcb.13652.
- 1162 Longhurst, A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish
1163 populations. *Fish. Res.* **56**(2): 125–131. doi: 10.1016/S0165-7836(01)00351-4.
- 1164 Lush, J. L. 1937. *Animal Breeding Plans*, Collegiate Press Inc, Ames, IA.
- 1165 MacArthur, R.H., and Pianka, E.R. 1966. On optimal use of a patchy environment. *Am. Nat.*
1166 **100**(916): 603–609. doi:10.1086/282454.
- 1167 Mainka, S.A., and Howard, G.W. 2010. Climate change and invasive species: Double
1168 jeopardy. *Integr. Zool.* **5**(2): 102–111. doi:10.1111/j.1749-4877.2010.00193.x.
- 1169 Marty, L., Dieckmann, U., and Ernande, B. 2015. Fisheries-induced neutral and adaptive
1170 evolution in exploited fish populations and consequences for their adaptive potential.
1171 *Evol. Appl.* **8**(1): 47–63. doi:10.1111/eva.12220.
- 1172 McCormick, M.I. 2009. Behaviourally mediated phenotypic selection in a disturbed coral
1173 reef environment. *PLoS One* **4**(9): e7096. doi:10.1371/journal.pone.0007096.
- 1174 Meekan, M.G., Carleton, J.H., McKinnon, A.D., Flynn, K., and Furnas, M. 2003. What
1175 determines the growth of tropical reef fish larvae in the plankton: Food or temperature?

- 1176 Mar. Ecol. Prog. Ser. **256**: 193–204. doi:10.3354/meps256193.
- 1177 Meekan, M.G., Vigliola, L., Hansen, A., Doherty, P.J., Halford, A., and Carleton, J.H. 2006.
- 1178 Bigger is better: Size-selective mortality throughout the life history of a fast-growing
- 1179 clupeid, *Spratelloides gracilis*. Mar. Ecol. Prog. Ser. **317**: 237–244.
- 1180 doi:10.3354/meps317237.
- 1181 Meiri, S., Dayan, T., and Aviv, T. 2003. On the validity of Bergmann's rule. J. Biogeogr. **30**:
- 1182 331–351. doi:10.1046/j.1365-2699.2003.00837.x.
- 1183 Metcalfe, N.B., and Monaghan, P. 2001. Compensation for a bad start: Grow now, pay later?
- 1184 Trends Ecol. Evol. **16**(5): 254–260. doi:10.1016/S0169-5347(01)02124-3.
- 1185 Metcalfe, N.B., and Monaghan, P. 2003. Growth versus lifespan: Perspectives from
- 1186 evolutionary ecology. Exp. Gerontol. **38**(9): 935–940. doi:10.1016/S0531-
- 1187 5565(03)00159-1.
- 1188 Michalsen, K., Ottersen, G., and Nakken, O. 1998. Growth of northeast Arctic cod in relation
- 1189 to ambient temperature. ICES J. Mar. Sci. **55**: 863–877. doi: 10.1006/jmsc.1998.0364.
- 1190 Miller T.J., Crowder L.B., Rice J.A., Marschall, E.A. 1988 Larval size and recruitment
- 1191 mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci.
- 1192 **45**:1657–1670.
- 1193 Moore, C.J. 2008. Synthetic polymers in the marine environment: A rapidly increasing, long-
- 1194 term threat. Environ. Res. **108**(2): 131–139. doi:10.1016/j.envres.2008.07.025.
- 1195 Morrongiello, J.R., Sweetman, P.C., and Thresher, R.E. 2019. Fishing constrains phenotypic
- 1196 responses of marine fish to climate variability. J. Anim. Ecol. **88**(11): 1645–1656.
- 1197 doi:10.1111/1365-2656.12999.
- 1198 Mousseau, T.A., and Roff, D.A. 1987. Natural selection and the heritability of fitness

- 1199 components. *Heredity*. **59**(59): 181–197. doi:10.1038/hdy.1987.113.
- 1200 Murawski, S.A. 2010. Rebuilding depleted fish stocks: the good, the bad, and, mostly, the
1201 ugly. *ICES J. Mar. Sci.* **67**(9): 1830–1840. doi:10.1093/icesjms/fsq125.
- 1202 Neuenhoff, R.D., Swain, D.P., Cox, S.P., McAllister, M.K., Trites, A.W., Walters, C.J., and
1203 Hammill, M.O. 2019. Continued decline of a collapsed population of Atlantic cod
1204 (*Gadus morhua*) due to predation-driven Allee effects. *Can. J. Fish. Aquat. Sci.* **76**(1):
1205 168–184. doi:10.1139/cjfas-2017-0190.
- 1206 Nilsson, J., Flink, H., and Tibblin, P. 2019. Predator–prey role reversal may impair the
1207 recovery of declining pike populations. *J. Anim. Ecol.* **88**: 927–939. doi:10.1111/1365-
1208 2656.12981.
- 1209 Nordhaus, I., Roelke, D.L., Vaquer-Sunyer, R., and Winter, C. 2018. Coastal systems in
1210 transition: From a ‘natural’ to an ‘anthropogenically-modified’ state. *Estuar. Coast.*
1211 *Shelf Sci.* **211**: 1–5. doi:10.1016/j.ecss.2018.08.001.
- 1212 Nussey, D.H., Froy, H., Lemaitre, J.F., Gaillard, J.M., and Austad, S.N. 2013. Senescence in
1213 natural populations of animals: Widespread evidence and its implications for bio-
1214 gerontology. *Ageing Res. Rev.* **12**(1): 214–225. doi:10.1016/j.arr.2012.07.004.
- 1215 Nusslé, S., Bornand, C.N., and Wedekind, C. 2009. Fishery-induced selection on an Alpine
1216 whitefish: Quantifying genetic and environmental effects on individual growth rate.
1217 *Evol. Appl.* **2**(2): 200–208. doi:10.1111/j.1752-4571.2008.00054.x.
- 1218 Nusslé, S., Bréchon, A., and Wedekind, C. 2011. Change in individual growth rate and its
1219 link to gill-net fishing in two sympatric whitefish species. *Evol. Ecol.* **25**(3): 681–693.
1220 doi:10.1007/s10682-010-9412-3.
- 1221 Ohlberger, J. 2013. Climate warming and ectotherm body size - from individual physiology

- 1222 to community ecology. *Funct. Ecol.* **27**(4): 991–1001. doi:10.1111/1365-2435.12098.
- 1223 Ohlberger, J., Ward, E.J., Schindler, D.E., and Lewis, B. 2017. Demographic changes in
1224 Chinook salmon across the Northeast Pacific Ocean. *Fish Fish.* **19**: 533–546.
1225 doi:10.1111/faf.12272.
- 1226 Olsen, E.M., Carlson, S.M., Gjøsæter, J., and Stenseth, N.C. 2009. Nine decades of
1227 decreasing phenotypic variability in Atlantic cod. *Ecol. Lett.* **12**(7): 622–631.
1228 doi:10.1111/j.1461-0248.2009.01311.x.
- 1229 Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B., and Dieckmann,
1230 U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of
1231 northern cod. *Nature* **428**: 4–7. doi:10.1038/nature02453.1.
- 1232 Olsen, E.M., and Moland, E. 2011. Fitness landscape of Atlantic cod shaped by harvest
1233 selection and natural selection. *Evol. Ecol.* **25**(3): 695–710. doi:10.1007/s10682-010-
1234 9427-9.
- 1235 Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A.,
1236 Gruber, N., Ishida, A., Joos, F., Key, R.M., Lindsay, K., Maier-Reimer, E., Matear, R.,
1237 Monfray, P., Mouchet, A., Najjar, R.G., Plattner, G.-K., Rodgers, K.B., Sabine, C.L.,
1238 Sarmiento, J.L., Schlitzer, R., Slater, R.D., Totterdell, I.J., Weirig, M.-F., Yamanaka, Y.,
1239 and Yool, A. 2005. Anthropogenic ocean acidification over the twenty-first century and
1240 its impact on calcifying organisms. *Nature* **437**(4): 681–686. doi:10.1038/nature04095.
- 1241 Otterlei, E., Nyhammer, G., Folkvord, A., and Stefansson, S. O. 1999. Temperature- and size-
1242 dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a
1243 comparative study of Norwegian coastal cod and northeast Arctic cod. *Can. J. Fish.*
1244 *Aquat. Sci.* **56**: 2099–2111.

- 1245 Palkovacs, E.P., Kinnison, M.T., Correa, C., Dalton, C.M., and Hendry, A.P. 2011. Fates
1246 beyond traits: ecological consequences of human-induced trait change. *Evol. Appl.* **5**:
1247 183–191. doi:10.1111/j.1752-4571.2011.00212.x.
- 1248 Palkovacs, E.P., Marshall, M.C., Lamphere, B.A., Lynch, B.R., Weese, D.J., Fraser, D.F.,
1249 Reznick, D.N., Pringle, C.M., and Kinnison, M.T. 2009. Experimental evaluation of
1250 evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Philos.*
1251 *Trans. R. Soc. B Biol. Sci.* **364**: 1617–1628. doi:10.1098/rstb.2009.0016.
- 1252 Palkovacs, E.P., and Post, D.M. 2009. Experimental evidence that phenotypic divergence in
1253 predators drives community divergence in prey. *Ecology* **90**(2): 300–305.
1254 doi:10.1890/08-1673.1.
- 1255 Palstra, F.P., and Ruzzante, D.E. 2008. Genetic estimates of contemporary effective
1256 population size: What can they tell us about the importance of genetic stochasticity for
1257 wild population persistence? *Mol. Ecol.* **17**(15): 3428–3447. doi:10.1111/j.1365-
1258 294X.2008.03842.x.
- 1259 Parmesan, C., Root, T.L., and Willig, M.R. 2000. Impacts of Extreme Weather and Climate on
1260 Terrestrial Biota. *Bull. Am. Meteorol. Soc.* **81**(3): 443–450.
1261 doi:http://dx.doi.org/10.1108/17506200710779521.
- 1262 Pauli, B.D., Kolding, J., Jeyakanth, G., and Heino, M. 2017. Effects of ambient oxygen and
1263 size-selective mortality on growth and maturation in guppies. *Conserv. Physiol.* **5**: 1–13.
1264 doi:10.1093/conphys/cox010.
- 1265 Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a
1266 generalization of von Bertalanffy's theory of growth. *Meeresforschung* **28**: 251–282.
- 1267 Pauly, D., and Cheung, W.W.L. 2018. Sound physiological knowledge and principles in

- 1268 modeling shrinking of fishes under climate change. *Glob. Chang. Biol.* **24**(1): e15–e26.
1269 doi:10.1111/gcb.13831.
- 1270 Pedersen, L. 1987. Energy budgets for juvenile Rainbow Trout at various oxygen
1271 concentrations. *Aquaculture* **62**: 289–298. doi:10.1016/0044-8486(87)90171-2
- 1272 Persson, L., Andersson, J., Wahlström, E., and Eklöv, P. 1995. Size-specific interactions in
1273 lake systems: predator gape limitation and prey growth rate and mortality. *Ecology*
1274 **77**(3): 900–911. doi:10.2307/2265510.
- 1275 Pinsky, M.L., and Palumbi, S.R. 2014. Meta-analysis reveals lower genetic diversity in
1276 overfished populations. *Mol. Ecol.* **23**(1): 29–39. doi:10.1111/mec.12509.
- 1277 Pörtner, H.O. 2002. Climate variations and the physiological basis of temperature dependent
1278 biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comp.*
1279 *Biochem. Physiol. Part A* **132**: 739–761. doi:10.1016/S1095-6433(02)00045-4.
- 1280 Pörtner, H.O., Bock, C., Knust, R., Lannig, G., Lucassen, M., Mark, F.C., and Sartoris, F.J.
1281 2008. Cod and climate in a latitudinal cline: Physiological analyses of climate effects in
1282 marine fishes. *Clim. Res.* **37**(2–3): 253–270. doi:10.3354/cr00766.
- 1283 Pörtner, H.O., and Knust, R. 2007. Climate change affects marine fishes through the oxygen
1284 limitation of thermal tolerance. *Science*. **315**: 95–98. doi:10.1126/science.1135471.
- 1285 Pörtner, H.O., and Peck, M.A. 2010. Climate change effects on fishes and fisheries: Towards
1286 a cause-and-effect understanding. *J. Fish Biol.* **77**(8): 1745–1779. doi:10.1111/j.1095-
1287 8649.2010.02783.x.
- 1288 Rabalais, N.N., Díaz, R.J., Levin, L.A., Turner, R.E., Gilbert, D., and Zhang, J. 2010.
1289 Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* **7**:
1290 585–619. doi:10.5194/bg-7-585-2010.

- 1291 Rahel, F.J., and Olden, J.D. 2008. Assessing the effects of climate change on aquatic invasive
1292 species. *Conserv. Biol.* **22**(3): 521–533. doi:10.1111/j.1523-1739.2008.00950.x.
- 1293 Ratner, S., and Lande, R. 2001. Demographic and evolutionary responses to selective
1294 harvesting in populations with discrete generations. *Ecology* **82**(11): 3093–3104.
1295 doi:10.1890/0012-9658(2001)082[3093:DAERTS]2.0.CO;2.
- 1296 Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V., and Montiglio, P.O. 2010.
1297 Personality and the emergence of the pace-of-life syndrome concept at the population
1298 level. *Philos. Trans. R. Soc. B Biol. Sci.* **365**(1560): 4051–4063.
1299 doi:10.1098/rstb.2010.0208.
- 1300 Reed, D.H., and Frankham, R. 2003. Correlation between fitness and genetic diversity.
1301 *Conserv. Biol.* **17**(1): 230–237. doi:10.1046/j.1523-1739.2003.01236.x.
- 1302 Reusch, T.B.H., Ehlers, A., Hämmerli, A., and Worm, B. 2008. Ecosystem recovery after
1303 climatic extremes enhanced by genotypic diversity. *Proc. Natl. Acad. Sci.* **102**(8): 2826–
1304 2831. doi:10.1073/pnas.091092498.
- 1305 Reznick, Butler, and Rodd. 2001. Life-History Evolution in Guppies. VII. The Comparative
1306 Ecology of High- and Low-Predation Environments. *Am. Nat.* **157**(2): 126.
1307 doi:10.2307/3079254.
- 1308 Reznick, D., Bryant, M., and Holmes, D. 2006. The evolution of senescence and post-
1309 reproductive lifespan in guppies (*Poecilia reticulata*). *PLoS Biol.* **4**(1): 0136–0143.
1310 doi:10.1371/journal.pbio.0040007.
- 1311 Reznick, D.A., Bryga, H., and Endler, J. 1990. Experimentally induced life-history evolution
1312 in a natural population. *Nature*. **346**: 357 – 359. doi:10.1038/346357a0.
- 1313 Reznick, D.N., Shaw, F.H., Rodd, F.H., and Shaw, R.G. 1997. Evaluation of the rate of

- 1314 evolution in natural Populations of Guppies (*Poecilia reticulata*). *Science*. **275**(5308):
 1315 1934–1937. doi:10.1126/science.275.5308.1934.
- 1316 van Rijn, I., Buba, Y., DeLong, J., Kiflawi, M., and Belmaker, J. 2017. Large but uneven
 1317 reduction in fish size across species in relation to changing sea temperatures. *Glob.*
 1318 *Chang. Biol.* **23**(9): 3667–3674. doi:10.1111/gcb.13688.
- 1319 Rindorf, A., Jensen, H., and Schrum, C. 2008. Growth, temperature, and density relationships
 1320 of North Sea cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **65**(3): 456–470.
 1321 doi:10.1139/f07-150.
- 1322 Rogers, L.A., Stige, L.C., Olsen, E.M., Knutsen, H., Chan, K.-S., and Stenseth, N.C. 2011.
 1323 Climate and population density drive changes in cod body size throughout a century on
 1324 the Norwegian coast. *Proc. Natl. Acad. Sci.* **108**(5): 1961–1966.
 1325 doi:10.1073/pnas.1010314108.
- 1326 Ruzzante, D.E., Taggart, C.T., Doyle, R.W., and Cook, D. 2001. Stability in the historical
 1327 pattern of genetic structure of Newfoundland cod (*Gadus morhua*) despite the
 1328 catastrophic decline in population size from 1964 to 1994. *Conserv. Genet.* **2**(3): 257–
 1329 269. doi:10.1023/A:1012247213644.
- 1330 Rypel, A.L. 2014. The cold-water connection: Bergmann’s rule in North American
 1331 freshwater fishes. *Am. Nat.* **183**(1): 147–156. doi:10.1086/674094.
- 1332 Salinas, S., Perez, K.O., Duffy, T.A., Sabatino, S.J., Hice, L.A., Munch, S.B., and Conover,
 1333 D.O. 2012. The response of correlated traits following cessation of fishery-induced
 1334 selection. *Evol. Appl.* **5**(7): 657–663. doi:10.1111/j.1752-4571.2012.00243.x.
- 1335 Saunders, R.A., and Tarling, G.A. 2018. Southern Ocean mesopelagic fish comply with
 1336 Bergmann’s rule. *Am. Nat.* **191**(3): 343–351. doi:10.1086/695767.

- 1337 Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B., and Charnov, E.L. 2004a. Effects of
1338 body size and temperature on population growth. *Am. Nat.* **163**(3): 429–441.
1339 doi:10.1086/381872.
- 1340 Savage, V.M., Gillooly, J.F., Woodruff, W., West, G., Allen, A.P., Enquist, B.J., and
1341 Brown, J.H. 2004b. The predominance of quarter-power scaling in biology. *Funct. Ecol.*
1342 **18**: 257–282. doi:10.1093/aesa/79.1.219.
- 1343 Sbragaglia, V., Gliese, C., Bierbach, D., Honsey, A.E., Uusi-Heikkilä, S., and Arlinghaus, R.
1344 2019. Size-selective harvesting fosters adaptations in mating behaviour and reproductive
1345 allocation, affecting sexual selection in fish. *J. Anim. Ecol.* **88**(9): 1343–1354.
1346 doi:10.1111/1365-2656.13032.
- 1347 Scarnecchia, D.L., Gordon, B.D., Schooley, J.D., Ryckman, L.F., Schmitz, B.J., Miller, S.E.,
1348 and Lim, Y. 2015. Southern and Northern Great Plains (United States) paddlefish stocks
1349 within frameworks of Acipenseriform life history and the metabolic theory of ecology.
1350 *Rev. Fish. Sci.* **19**(3): 279–298. doi:10.1080/10641262.2011.598123.
- 1351 Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and
1352 Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited
1353 species. *Nature* **465**(7298): 609–612. doi:10.1038/nature09060.
- 1354 Schramski, J.R., Dell, A.I., Grady, J.M., Sibly, R.M., and Brown, J.H. 2015. Metabolic
1355 theory predicts whole-ecosystem properties. *Proc. Natl. Acad. Sci.* **112**(8): 2617–2622.
1356 doi:10.1073/pnas.1423502112.
- 1357 Scott, M., Heupel, M., Tobin, A., and Pratchett, M. 2017. A large predatory reef fish species
1358 moderates feeding and activity patterns in response to seasonal and latitudinal
1359 temperature variation. *Sci. Rep.* **7**(1): 1–9. doi:10.1038/s41598-017-13277-4.

- 1360 Sguotti, C., Otto, S.A., Frelat, R., Langbehn, T.J., Plambech Ryberg, M., Lindegren, M.,
 1361 Durant, J.M., Stenseth, N.C., and Möllmann, C. 2019. Catastrophic dynamics limit
 1362 Atlantic cod recovery. *Proc. R. Soc. B.* **286**: 20182877 doi:10.5061/dryad.037jr6v.
- 1363 Shackell, N.L., Frank, K.T., Fisher, J.A.D., Petrie, B., and Leggett, W.C. 2009. Decline in top
 1364 predator body size and changing climate alter trophic structure in an oceanic ecosystem.
 1365 *Proc. R. Soc. B Biol. Sci.* **277**(1686): 1353–1360. doi:10.1098/rspb.2009.1020.
- 1366 Sheridan, J.A., and Bickford, D. 2011. Shrinking body size as an ecological response to
 1367 climate change. *Nat. Clim. Chang.* **1**(8): 401–406. doi:10.1038/nclimate1259.
- 1368 Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review.
 1369 *Bull. Mar. Sci.* **60**(3): 1129–1157.
- 1370 Stockwell, C.A., Hendry, A.P., and Kinnison, M.T. 2003. Contemporary evolution meets
 1371 conservation biology. *TREE.* **18**(2): 94–101. doi:10.1016/S0169-5347(02)00044-7.
- 1372 Sutter, D.A.H., Suski, C.D., Philipp, D.P., Klefoth, T., Wahl, D.H., Kersten, P., Cooke, S.J.,
 1373 and Arlinghaus, R. 2012. Recreational fishing selectively captures individuals with the
 1374 highest fitness potential. *Proc. Natl. Acad. Sci.* **109**(51): 20960–20965.
 1375 doi:10.1073/pnas.1212536109.
- 1376 Swain, D.P., Benoît, H.P., Hammill, M.O., McClelland, G., and Aubry, É. 2011. Alternative
 1377 hypotheses for causes of the elevated natural mortality of cod (*Gadus morhua*) in the
 1378 southern Gulf of St. Lawrence: the weight of evidence. *DFO Can. Sci. Advis. Sec. Res.*
 1379 *Doc.* 2011/036.
- 1380 Terribile, L.C., and Diniz-Filho, J.A.F. 2009. Spatial patterns of species richness in New
 1381 World coral snakes and the metabolic theory of ecology. *Acta Oecologica* **35**(2): 163–
 1382 173. doi:10.1016/j.actao.2008.09.006.

- Therkildsen, N.O., Nielsen, E.E., Swain, D.P., and Pedersen, J.S. 2010. Large effective population size and temporal genetic stability in Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* **67**(10): 1585–1595. doi:10.1139/F10-084.
- Therkildsen, N.O., Wilder, A.P., Conover, D.O., Munch, S.B., Baumann, H., and Palumbi, S.R. 2019. Contrasting genomic shifts underlie parallel phenotypic evolution in response to fishing. *Science*. **365**: 487–490. doi:10.1126/science.aaw7271.
- Thresher, R.E., Koslow, J.A., Morison, A.K., and Smith, D.C. 2007. Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proc. Natl. Acad. Sci.* **104**(18): 7461–7465. doi:10.1073/pnas.0610546104.
- Uriarte, A., Ibaibarriaga, L., Pawlowski, L., Massé, J., Petitgas, P., and Santos, M. 2016. Assessing natural mortality of Bay of Biscay anchovy from survey population and biomass estimates. **73**(2): 216–234. doi:10.1139/cjfas-2015-0096.
- Uusi-Heikkilä, S., Sävilammi, T., Leder, E., Arlinghaus, R., and Primmer, C.R. 2017. Rapid, broad-scale gene expression evolution in experimentally harvested fish populations. *Mol. Ecol.* **26**(15): 3954–3967. doi:10.1111/mec.14179.
- Uusi-Heikkilä, S., Whiteley, A.R., Kuparinen, A., Matsumura, S., Venturelli, P.A., Wolter, C., Slate, J., Primmer, C.R., Meinelt, T., Killen, S.S., Bierbach, D., Polverino, G., Ludwig, A., and Arlinghaus, R. 2015. The evolutionary legacy of size-selective harvesting extends from genes to populations. *Evol. Appl.* **8**(6): 597–620. doi:10.1111/eva.12268.
- Uusi-Heikkilä, S., Wolter, C., Klefoth, T., and Arlinghaus, R. 2008. A behavioural perspective on fishing-induced evolution. *Trends Ecol. Evol.* **23**(8): 416–419. doi:10.1016/j.tree.2008.04.011.

- 1407 Verberk, W.C.E.P., Bilton, D.T., Calosi, P., and Spicer, J.I. 2011. Oxygen supply in aquatic
1408 ectotherms: Partial pressure and solubility together explain biodiversity and size
1409 patterns. *Ecology* **92**(8): 1565–1572. doi:10.1890/10-2369.1
- 1410 Verberk, W.C.E.P., Durance, I., Vaughan, I.P., and Ormerod, S.J. 2016. Field and laboratory
1411 studies reveal interacting effects of stream oxygenation and warming on aquatic
1412 ectotherms. *Glob. Chang. Biol.* **22**(5): 1769–1778. doi:10.1111/gcb.13240.
- 1413 Walsh, M.R., Munch, S.B., Chiba, S., and Conover, D.O. 2006. Maladaptive changes in
1414 multiple traits caused by fishing: Impediments to population recovery. *Ecol. Lett.* **9**(2):
1415 142–148. doi:10.1111/j.1461-0248.2005.00858.x.
- 1416 Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-
1417 structured populations. *Annu. Rev. Ecol. Syst.* **15**: 393–425.
- 1418 West, G.B., and Brown, J.H. 2005. The origin of allometric scaling laws in biology from
1419 genomes to ecosystems: towards a quantitative unifying theory of biological structure
1420 and organization. *J. Exp. Biol.* **208**(9): 1575–1592. doi:10.1242/jeb.01589.
- 1421 West, G.B., Brown, J.H., and Enquist, B.J. 1997. A general model for the origin of allometric
1422 scaling laws in biology. *Science* **276**(5309): 122–6. doi:
1423 doi:10.1126/science.276.5309.122.
- 1424 White, J.R., Meekan, M.G., McCormick, M.I., and Ferrari, M.C.O. 2013. A comparison of
1425 measures of boldness and their relationships to survival in young fish. *PLoS One* **8**(7).
1426 doi:10.1371/journal.pone.0068900.
- 1427 White, R.S.A., Mchugh, P.A., Glover, C.N., and McIntosh, A.R. 2017. Metabolism drives
1428 distribution and abundance in extremophile fish. *PLoS One* **12**(11): e0187597.
1429 doi:10.1371/journal.pone.0187597.

1430 van Wijk, S.J., Taylor, M.I., Creer, S., Dreyer, C., Rodrigues, F.M., Ramnarine, I.W., Van
1431 Oosterhout, C., and Carvalho, G.R. 2013. Experimental harvesting of fish populations
1432 drives genetically based shifts in body size and maturation. *Front. Ecol. Environ.* **11**(4):
1433 181–187. doi:10.1890/120229.

1434 Wood, J.L.A., Yates, M.C., and Fraser, D.J. 2016. Are heritability and selection related to
1435 population size in nature? Meta-analysis and conservation implications. *Evol. Appl.* **9**:
1436 640–67. doi:10.1111/eva.12375.

1437 Yates, M.C., Bowles, E., and Fraser, D.J. 2019. Small population size and low genomic
1438 diversity have no effect on fitness in experimental translocations of a wild fish. *Proc. R.*
1439 *Soc. B Biol. Sci.* **286**(1916). doi:10.1098/rspb.2019.1989.

Draft

1440
1441
1442
1443
1444
1445
1446
1447
1448
1449
1450

Figure 1. 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.

Figure 2.

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.

1474
1475
1476
1477
1478

Draft

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) James1970; 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.

338x190mm (96 x 96 DPI)