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## Life-History Evolution, Human Impacts on

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### Glossary

**Adaptive landscape** Relationship between fitness and trait(s) under selection (= fitness landscape).

**Fitness** Individual contribution to the genetic pool of the next generation (= relative reproductive success).

**Response to selection** Change in mean trait value(s) in a population due to selection. Response to selection operates through the transmission of heritable information

(nucleic acids, hormones, knowledge...) from one generation to the next.

**Selection** The process through which environmental conditions generate fitness variation among individuals. Selection operates on different units of selection corresponding to the different levels of biological organization (genes, cells, individuals...).

### Introduction

The expansion of agriculture about 10 000 years ago allowed the settlement and growth of human populations, and from there the development of cities and of a social organization (civilization) that promoted technological innovations. Together, the human demographic expansion and technological improvements are the main drivers of so-called 'anthropogenic changes,' the perturbations brought about by human activities on natural systems.

Fundamentally, anthropogenic perturbations on natural systems simply arise from resource consumption by humans. However, its manifestations are multiple and interconnected, among which are often reported landscape alterations, soil deterioration, disruption of geochemical cycles, climate warming, or over-harvesting. All of these perturbations almost inevitably alter, directly or indirectly, the selective pressures acting on organisms.

Impacted populations must respond to these anthropogenic selective pressures by evolving life histories that are more fit to the newly selected, composite adaptive landscape that results from the combination of natural and anthropogenic selection. This response is the subject of the present article. If the response is too slow to track changes in the selective pressures, the population goes extinct. This failure to adapt is the underlying cause of the global biodiversity loss currently experienced by the earth ecosystems.

First, in this article, basic theory of selection and response to selection is recalled, then a specific focus on three major sources of anthropogenic selection (harvesting, habitat fragmentation, and temperature increase) is provided, and finally it is examined how rapid life-history evolution may change natural selection acting back on life histories, the so-called eco-evolutionary feedback loop.

### Selection and Response to Selection

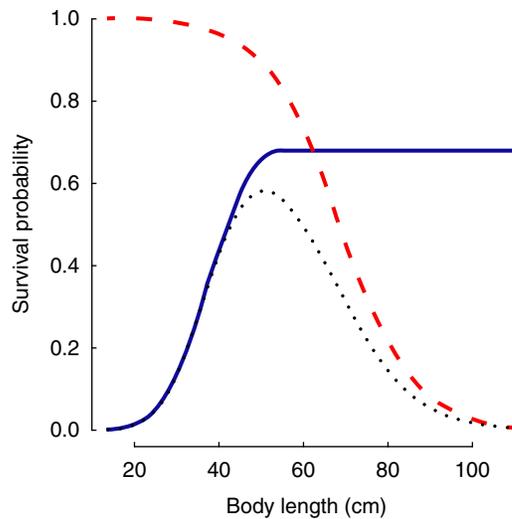
#### Natural and Anthropogenic Sources of Selection

In this article only selection acting on individuals transmitting genes to their offspring will be considered, because the

individual is the level of selection having received the most thorough treatment in the literature (for a broader perspective see [Wilson and Sober, 1994](#)), and because genes represent the most widespread 70 support of heredity (for non-genetic inheritance, see [Danchin, 2013](#)). Selection of individuals may be 'natural' or 'artificial' depending on whether it results from nonhuman or from anthropogenic factors, respectively. To illustrate this, let me consider the case of pike (*Esox lucius*) in Windermere, the largest natural lake in England.

In Windermere, scientists have conducted long-term mark-recapture experiments on pike ([Le Cren, 2001](#)). The resultant data has allowed the computation of a component of natural selection, namely the form of the relationship between survival and body size ([Haugen et al., 2007](#); [Carlson et al., 2007](#); [Vindenes et al., 2014](#)). This relationship shows that natural selection favors large-sized pike up to a body length of about 60 cm (blue solid line in [Figure 1](#)), after which survival is likely to remain constant ([Vindenes et al., 2014](#)). A larger size likely provides pike with access to more resources, increased protection against cannibals and other predators, and increased energy stores to survive to winter fasting ([Edeline et al., 2007](#); [Vindenes et al., 2014](#)). From this relationship, we may predict that there is a *directional natural selection* for rapidly reaching a body length of about 60 cm in Windermere pike.

In parallel with mark-recapture experiments, scientists have also submitted pike to gillnet fishing since the early 1940s ([Le Cren, 2001](#)). All pike captured in the gillnet fishery are killed, measured for several biological variables, and their opercular bones are removed. These bones record the age of each fish in the form of annuli (like in a tree trunk), and the radius of these annuli are proportional to individual body length, thus allowing the back calculation of length-at-age. From this information, it was possible to model the link between body length and the probability for a fish to be captured in the fishery. This relationship is depicted in [Figure 1](#) (red dashed line), which shows that the probability for a pike to be caught in the gillnet fishery suddenly increases after a body length of 50 cm. Hence, we predict that there is a *directional anthropogenic selection* for growing slowly so as to remain smaller than about 50 cm in Windermere pike.



**Figure 1** Size-dependent survival probability of Windermere pike (*Esox lucius*) through the directional components of natural selection (blue solid line) and the gillnet fishery (red dashed line). The resultant composite survival curve (the product of the two functions) is represented with the black dotted line and shows stabilizing selection around an adaptive peak at about 50 cm. The natural survival function was computed following [Vindenes et al. \(2014\)](#).

Combining these two (natural and anthropogenic) sources of selection acting on the body size of Windermere pike reveals the composite adaptive landscape, which reflects the truly experienced selective regime (black dotted line in [Figure 1](#)). We see that this composite landscape is very different from the naturally selected landscape. Anthropogenic selection decreases the overall area below the curves, i.e., it decreased overall survival probability of pike. This is predicted to induce an evolutionary response toward faster life histories in the pike population (see section Non-phenotypically Selective Harvesting of this article).

However, this increase in mortality is nonrandom, but instead biased toward large-sized pike, thus further reinforcing directional selection toward smaller sizes and faster life histories (see section Phenotypically selective harvesting of this article). This biased mortality is visible in that anthropogenic selection generates an adaptive peak (i.e., stabilizing selection) around a body length of 50 cm. Let us now more closely examine how response to these sources of selection may be qualitatively predicted.

### Response to Directional Selection

Predicting response to selection is the central purpose of quantitative genetics theory ([Lynch and Walsh, 1998](#)). This theory predicts that dynamic response to selection of a single trait having negligible genetic covariance with other fitness traits obeys the equation:

$$\bar{\chi}_{t+1} = \bar{\chi}_t + R_\chi \quad [1a]$$

where  $\bar{\chi}_{t+1}$  = mean value of trait  $x$  in the population at generation  $t + 1$ ,  $\bar{\chi}_t$  = mean value of trait  $x$  in the population at generation  $t$ , and  $R_\chi$  = response to selection in trait  $\chi$ , that may

be recast as:

$$R_\chi = H_\chi S_\chi = \frac{Va_\chi}{Vp_\chi} S_\chi = Va_\chi \frac{\partial w_\chi}{\partial \chi} \quad [1b]$$

where  $H_\chi = Va_\chi / Vp_\chi$  = narrow-sense heritability for the trait where  $Va_\chi$  = additive genetic variance and  $Vp_\chi$  = phenotypic variance (with  $Vp_\chi \geq Va_\chi$ ), and  $S_\chi = \bar{\chi}_a - \bar{\chi}_b$  = net directional selection differential where  $\bar{\chi}_a$  = mean trait value in the population after selection and  $\bar{\chi}_b$  = mean trait value in the population before selection. Here, following [Lande and Arnold \(1983\)](#) the equation is rearranged to obtain the directional selection gradient  $(\bar{\chi}_a - \bar{\chi}_b) / Vp_\chi = \partial w_\chi / \partial \chi$ , where  $w_\chi$  = relative fitness of an individual with trait  $x$ .

Note that eqn [1b] makes the assumption that  $Va_\chi$  is independent of  $S_\chi$ , which is not true if directional selection drives allelic frequencies toward 0 or 1 in the population (see section Evolvability of this article). In such a case, eqn [1b] can be used only to predict short-term response to selection. Additionally, eqn [1b] is often used by considering  $S_\chi$  as a constant, which may be true when one considers artificial selection only, but which is wrong when trait change alters natural selection acting on that trait – the so-called eco-evolutionary feedback loop (see section Change in the naturally selected adaptive landscape of this article).

However, despite these shortcomings, eqn [1b] remains conceptually very useful in that it clearly shows that evolution of a life-history trait requires that both  $Va_\chi > 0$  and  $\partial w_\chi / \partial \chi \neq 0$ , and that the speed of evolution is proportional to the values of these two components. Generally,  $Va_\chi > 0$  for life-history and morphological traits ([Mousseau and Roff, 1987](#)), which are thus highly susceptible to respond to anthropogenic directional selection. Let us now concentrate on reviewing some of the current knowledge on such responses.

### Evolutionary Response to Harvesting

Humans have harvested wild plant and animal species since they appeared on earth. Hunting by human populations is thought to have played a role in the late Pleistocene (15 000 years ago) extinctions of large terrestrial mammals in Australia, North America, and South America ([Barnosky et al., 2004](#)). The development of agriculture has made humans less dependent upon wild plant and animal resources, but the parallel rise in the human population and progress in harvesting technologies has also tremendously increased the pressure on those populations that remain exploited. The overexploitation problem is mostly documented in fish and mammals, but it may arise in any animal or plant population. Here, we will consider separately the effects of non-phenotypically selective and phenotypically selective harvesting.

#### Non-Phenotypically Selective Harvesting

Non-phenotypically selective harvesting adds a mortality component to the natural mortality background uniformly in all age or size classes, and thus provides a gain in relative fitness to early-maturing individuals which have a higher

probability to reproduce before being killed (Abrams and Rowe, 1996).

If maturation (and reproductive allocation) conflicts with somatic growth due to physiological or ecological trade-offs, then harvesting also induces a decrease in somatic growth rates. Similarly, trade-offs may occur between reproduction and somatic maintenance, so that we may expect to also observe increased senescence in exploited populations. Accordingly, a number of studies have demonstrated that reproduction incurs a cost in terms of somatic growth (Roff, 1992), predation risk (Magnhagen, 1991), or immune capacity (Zuk and Stoehr, 2002). A cost of reproduction in terms of senescence (Williams, 1957) has received more contrasted support (Reznick *et al.*, 2004).

### Phenotypically Selective Harvesting

Harvesting is almost always phenotypically selective. Harvesters often target larger and older individuals due to their higher market or trophy values, and/or due to regulatory rules that impose a minimum size limit to the catch. Compared to non-size-selective harvesting, this biased mortality further strengthens the relative advantage for an early maturation, and also directly selects for slower somatic growth because larger individuals are often faster growers (Biro and Post, 2008). In line with this theoretical prediction, earlier maturation and/or smaller body size in response to harvesting have been documented in a variety of wild, exploited populations.

Size-related trait change in exploited populations are on average 3 times faster than in unexploited populations, and results in 20% smaller traits on average (Darimont *et al.*, 2009). For instance, in the snow lotus (*Saussurea laniceps*), plant cropping for medicine has induced a decrease in mean plant size from about 30 cm in 1900 to about 20 cm in the 2000s (Law and Salick, 2005). In the bighorn sheep (*Ovis canadensis*), mean body weight of rams has declined from 85 to 65 kg from 1975 to 2005 due to trophy hunting, while mean horn sizes have decreased from about 70 to 50 cm (Coltman *et al.*, 2003). In the pink salmon (*Oncorhynchus gorbuscha*), weight at spawning (age 2) has decreased by up to 34% from the 1950s to the 1990s (McAllister *et al.*, 1992). In the Canadian Atlantic cod, female length at 50% maturation probability dwindled from about 65 cm (and 7 years of age) in the early 1950s to about 40 cm (and 4.5 years of age) in the early 1990s, and remained at this low level up to the early 2000s (Olsen *et al.*, 2004; Swain, 2011). On longer time scales, decrease in mean body size may be even larger. Archeological records of skeletal parts suggest that mean body size of cod in the Gulf of Maine (USA) has decreased from 100 to 30 cm due to overfishing (Jackson *et al.*, 2001).

Harvest-induced evolution is sometimes (maybe abusively) termed 'maladaptive,' because it may drive the population far from its naturally selected adaptive peak (i.e., evolution is maladaptive relative to natural selection acting alone). This 'maladaptive' evolution simply reflects a severe reduction in fitness due to anthropogenic selection. For instance, in Atlantic cod (*Gadus morhua*), earlier maturation at a smaller size in response to fishing is expected to increase the mortality cost of reproduction. A reduction of age at maturity from 6 to 4 years

projects into a 25–30% decrease in population growth rate (Hutchings, 2005). This decrease in fitness may be linked to increased reproductive mortality (Hutchings, 2005; Swain, 2011), as well as changes in traits correlated with body size. For instance, selection against a large body size in Atlantic silverside (*Menidia menidia*) depresses fecundity, egg volume, larval size at hatch, larval viability, larval growth rates, food consumption rate, and conversion efficiency (Walsh *et al.*, 2006).

### Evolutionary Response to Habitat Loss and Fragmentation

Habitat loss and fragmentation often result from 'modern' agricultural practices, road building or, more dramatically, from urbanization. Habitat loss is a primary cause of species extinction, indicating that the generated selective pressures are so strong that many populations can simply not adapt. Habitat fragmentation, in contrast, may allow species to persist, but tend to change large homogeneous populations into metapopulations, i.e., a population of populations between which individuals may disperse (Levins, 1969; Pulliam, 1988). Here, I consider how anthropogenic habitat fragmentation may affect life histories through selection acting on body size and on dispersal ability.

### Size-Dependent Selection

Although many studies have linked a large body size with an increased extinction risk in response to anthropogenic perturbations (Purvis *et al.*, 2000; Cardillo *et al.*, 2005; Van Allen *et al.*, 2012), the link between body size and sensitivity to habitat perturbation is not clear (Henle *et al.*, 2004). This lack of evidence for size-dependent selection might come from conflicting selective pressures.

Large animals have large home ranges (Peters, 1983; Jetz *et al.*, 2004), and are thus more likely to be impacted by the fragmentation and loss of their vital habitat. For instance, carnivores in protected areas primarily die from 'edge effects,' i.e., due to conflicts with humans on reserve borders (Woodroffe and Ginsberg, 1998). In the Amazonian forest, fragmentation-induced edge effects magnify the negative impact of hunting on medium-sized and large vertebrates (Peres, 2001). Additionally, a large body size is associated with small population sizes (Woodward *et al.*, 2005). Hence, in a context of reduced habitat availability, large-bodied species may rapidly reach population sizes at which demographic stochasticity elevates extinction risk. Finally, because habitat perturbation imposes so strong selective pressures, population persistence critically depends on the capacity of the population to adapt (or disperse, see below). However, a large body size requires a long development time (i.e., long generation time), and thus imposes slow life histories and slow rates of adaptive evolution. In parallel with selection against a large body size, habitat perturbation may also select against a *small* body size. A small size is associated with a narrower range of prey sizes, reduced trophic generalism (Woodward *et al.*, 2005), and possibly also with an increased habitat specialization.

Accordingly, this link between a small body size, habitat specialization, and increased sensitivity to habitat loss was found in birds (Owens and Bennett, 2000) and freshwater fish (Olden *et al.*, 2007), but the underlying drivers remain unclear. Therefore, the net overall effect of habitat fragmentation might be to select against both small and large body sizes, ultimately favoring medium-sized individuals and species. More research is needed to test this hypothesis.

### Dispersal-Dependent Selection

Dispersal generally brings a selective advantage in heterogeneous environments, where the environment is understood in terms of the ecological niche (Hutchinson, 1957). Hence, anthropogenic selection for increased dispersal propensity occurs when habitat fragmentation increases habitat heterogeneity in space and time. In particular, smaller patch sizes are likely to amplify population fluctuations due to increased demographic stochasticity (from smaller population sizes), elevate the temporal heterogeneity of the environment, and ultimately result in increased selection for dispersal (Parvinen *et al.*, 2004).

In turn, dispersal-dependent selection may induce the evolution of life-history traits correlated with dispersal (Roff and Fairbairn, 2001). For instance, the sand cricket (*Gryllus firmus*) shows a genetically based trade off between flight allocation and reproductive allocation (King *et al.*, 2011), indicating that selection for dispersal will also induce evolution towards reduced reproductive investment. In insects and fish, an increased ability for long-distance dispersal is often positively associated with a large body size, because a larger size increases the energetic efficiency of movement (Roff, 1991). Hence, anthropogenic selection for increased long-distance dispersal may indirectly select for a large body size, and is thus expected to interact with direct size-dependent selection (see previous section).

However, anthropogenic habitat fragmentation may also increase dispersal mortality and select against dispersal traits. Hence, the counteracting effects of landscape fragmentation on the evolution of dispersal and life histories may give rise to complex evolutionary dynamics when realistic ecological complexity is accounted for (Parvinen *et al.*, 2004). This complexity might be responsible for an often reported absence of a link between dispersal-dependent selection and life-history evolution (Ronce and Clobert, 2012).

### Evolutionary Response to Climate Warming

Temperature determines the rate of metabolic reactions and is a key driver of individual physiology (Brown *et al.*, 2004). Warmer ambient temperatures have been repeatedly reported to favor smaller body sizes and faster life histories in both endotherms and ectotherms (Angilletta, 2009), a phenomenon dubbed 'Bergmann's Rule' (BR) in endotherms and temperature-size rule (TSR) in ectotherms (Atkinson, 1994).

BR posits that heat loss of an endotherm organism is proportional to its body surface-to-volume ratio. Because body volume increases faster than body surface area with increasing

body size, there is a selective advantage to a small body size (higher body surface-to-volume ratio and easy heat loss) in warm areas, and conversely to a large body size in colder climates (lower body surface-to-volume ratio and reduced heat loss).

The thermodynamic argument proposed by Bergmann for endotherms does not hold for ectotherms, and the underlying drivers of the TSR remain far from clear (Angilletta, 2009). Proximate mechanisms so far proposed to explain the TSR include a higher thermal sensitivity of gonad growth rate than body growth rate, resulting in an increased fraction of energy allocated to gonads under warmer temperatures (Van der Have and de Jong, 1996; Zuo *et al.*, 2011), and/or smaller sizes of cells and genome at higher temperature (Partridge *et al.*, 1994; Hessen *et al.*, 2013), and/or limitation of oxygen path length at higher body sizes (Pörtner and Knust, 2007; Forster *et al.*, 2012). Ultimate (adaptive) mechanisms include increased mortality and/or higher population rate of increase at higher temperatures (Sibly and Atkinson, 1994).

However, none of these mechanisms has yet been shown to be universal. Recently, however, there has emerged the idea that different thermal sensitivities of ingestion and maintenance rates may drive a competition-mediated selective advantage for small-bodied individuals under warm conditions (Ohlberger *et al.*, 2011; Reuman *et al.*, 2014; Edeline *et al.*, 2013). To understand the arguments it is necessary to start from the  $R^*$  theory of exploitative competition (Tilman, 1982), adapted to account for the size-dependency of resource consumption and metabolic rates (Persson *et al.*, 1998; De Roos *et al.*, 2003).

In this framework, resource-dependent variations in individual body mass  $dB/dt$  are given by:

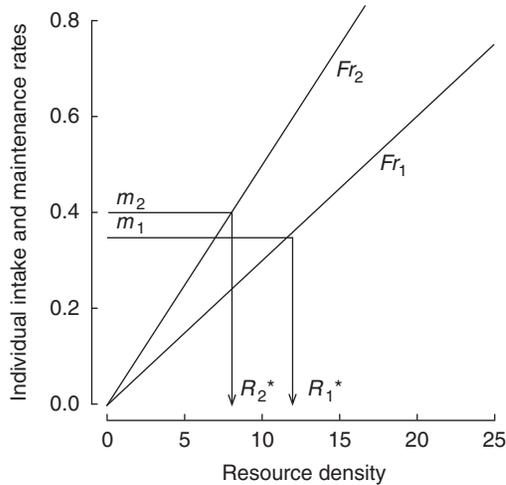
$$\frac{dB}{dt} = Fr(R) - m = aR - m \quad [2]$$

where  $dB/dt$  is also equivalent to individual fitness since mass gain can be invested in reproduction,  $a$  = attack or intake rate in a Holling's type I functional response, and  $m$  = maintenance metabolic rate. Equilibrium, i.e., null fitness, occurs at  $R=R^*$  such that  $R^*=m/a$ , i.e., where resource density makes  $aR^*$  equal to  $m$  (Figure 2). Just as in Tilman's (1982) theory, the individual having the lowest  $R^*$  wins the competition and excludes the others that starve to death (Persson *et al.*, 1998).

Biological rates usually follow power allometric exponents (Peters, 1983; Brown *et al.*, 2004), such that the relationship between  $R^*$  and body size can be written:

$$R^* = \frac{m}{a} = \frac{\mu B^\gamma}{\alpha B^\delta} = \frac{\mu}{\alpha} B^{\gamma-\delta} \quad [3]$$

where  $\mu$ ,  $\alpha$ ,  $\gamma$ , and  $\delta$  are positive constants. Equation [3] shows that whether  $R^*$  increases or decreases with an increasing body mass,  $B$  depends on the sign of the  $\gamma - \delta$  difference. If maintenance metabolic rate increases faster with increasing body mass than intake rate, i.e., if  $\gamma > \delta$ , then  $R^*$  increases with increasing body mass, small individuals dominate large individuals in exploitative competition (Persson *et al.*, 1998; De Roos *et al.*, 2003; Persson and De Roos, 2006), and low resources select for smaller body sizes. Resource-poor environments select for reduced somatic growth rates (i.e., select for smaller body sizes) in a variety of taxa (Arendt, 1997), suggesting that an increase of  $R^*$  with body size is common.



**Figure 2** The  $R^*$  rule for two individual consumers competing for the same resource  $R$ . Resource intake rate is represented by a Holling's type I functional response  $F_r$ , while maintenance rate  $m$  is resource-independent. Zero growth (equivalent to null fitness in eqn 2) occurs where  $R=R^*$ . The individual having the lowest  $R^*$  (here individual 2) wins the competition. Reproduced from Tilman, D., 1982. Resource Competition and Community Structure. Princeton, NJ: Princeton University Press.

However,  $R^*$  decreases with body size in waterflies *Daphnia* sp. (Gliwicz, 1990), suggesting that filter-feeding organisms – and maybe generally organisms having a Holling's type I functional response – might constitute an exception. More research is needed to clarify this question.

Biological rates are in fact not just size- but also temperature-dependent (Gillooly *et al.*, 2001). The effects of temperature on intake and maintenance rates included in eqn [3], and thus on and its size dependency, are poorly understood. It was shown in a physiologically-structured model tailored for Eurasian perch *Perca fluviatilis* that higher temperatures may increase the advantage of small against large individuals in exploitative competition (Ohlberger *et al.*, 2011). Hence, climate warming seems to increase in large individuals relative to small individuals. Reuman *et al.* (2014) and Edeline *et al.* (2013) came to a similar conclusion in unicellular phytoplankton and river fish communities (52 species), respectively. Finally, Vindenes *et al.* (2014) showed in Windermere pike that this temperature-dependent  $R^*$  selection translated into accelerated juvenile growth and decreased survival of large individuals, such that the proportion of medium-sized individuals increased in the population. More details about warming-induced selective pressures acting on life-history traits may be found in the chapter An Age- and Length-Structured Life History Model for Pike, a Top Predator in Freshwater Ecosystems (00094) by Yngvild Vindenes. Taken together, these results call for an increased focus on size-dependent exploitative competition in climate-warming research.

### Reversibility of Trait Changes and Population Recovery

A natural management response to human-induced ecological problems is to relax the source of perturbation, so that the

ecosystem may return to its initial state. However, not all sources of perturbation are easily relaxed. In case of habitat loss and fragmentation, backward re-naturalization of urbanized or agricultural habitats requires will power and investments that often go beyond the capacities of local managers. This problem is even more insurmountable when it comes to reversing the global trend toward increased production of greenhouse gas and the parallel global warming.

Hence, most examples of relaxed anthropogenic forcing on life histories come from harvested systems. In particular, fisheries provide us with reassuring examples of systems that return to their initial state (rebound) after fishery relaxation or closure, but also with the worrying cases of systems that do not recover (stasis). Let us here concentrate on the possible causes of stasis (for rebounds, see Edeline *et al.*, 2007; Edeline *et al.*, 2009; Conover *et al.*, 2009 and Frank *et al.*, 2011). Evolutionary stasis has two possible sources: a loss of evolvability for life-history traits and/or a change in the natural selective pressures acting on life histories.

### Evolvability

Equation [1b] assumes for simplicity that additive genetic variance (evolvability) and selection differentials are independent, such that the trait can endlessly evolve. However, in theory evolvability and selection are not independent because intense directional selection should exhaust additive genetic variance and impair reversibility of trait changes, unless genetic variation is constantly renewed (Crow, 2008). This gave rise to concern about a potential loss of evolvability in heavily exploited populations (Hutchings and Fraser, 2008), and might explain why some fish stocks have problems to recover even after the relaxation of exploitation rates (Hutchings and Reynolds, 2004; Frank *et al.*, 2005; Swain, 2011). In these stocks, relaxation of fishing would reestablish the naturally selected phenotypic optimum (i.e.,  $\delta w_x / \delta x \neq 0$  in eqn [1b]), but traits could not follow due to lack of genetic variability (i.e.,  $V a_x \rightarrow 0$  in eqn [1b]). Is this a credible hypothesis?

The tremendous phenotypic diversity of formerly wild, now domestic animals (e.g., dogs, pigeons, chicken, ...) or plants (roses, cereals, ...) suggests that genetic diversity hardly limits the range of possible phenotypes under captive conditions. For instance, maize (*Zea mays*) still responds to strong bidirectional selection on oil and protein concentration in grains since more than 100 generations (Moose *et al.*, 2004). Similarly, white Plymouth Rock chickens continued to respond to bidirectional selection on body weight at 8 weeks of age since 54 generations (Dunnington *et al.*, 2013). At generation 54, males weighted on average 2 kg in the high-selected lines versus 0.173 kg in the low-selected lines, respectively (1.380 vs. 0.129 kg in females). These examples from domestic populations suggest that additive genetic variance often persists, even under severe directional selection (Crow, 2008). But what about wild populations?

A fundamental difference between captive and wild conditions is natural selection. If anthropogenic and natural selection act in opposition (Figure 1), then overall selective pressures are no longer directional but stabilizing, and stabilizing selection may erode trait genetic variance even more

rapidly than directional selection. However, in Windermere pike, the overall form of fishing-induced selection was in fact not directional (as presented for simplicity in Figure 1) but disruptive (Carlson *et al.*, 2007), which is typical for gillnets (Lagler, 1968). Consequently, scientific gillnet fishing for pike in Windermere, whose intensity was mild (mean exploitation rate was 6.5% per year  $\pm$  4.7 SD (Langangen *et al.*, 2011)), was associated with an increased variability for length-at-age in the population, and thus presumably increased genetic variance for body size in the pike population (Edeline *et al.*, 2009).

In contrast with scientific fishing, commercial fishing may impose very high exploitation rates (Hutchings (2000) reports reductions of 45–99% in reproductive biomass), in which case medium-sized individuals probably have no chance to reach a large size, even if harvest-induced selection is disruptive. Hence, in many situations anthropogenic selection likely generates strong directional selection acting in opposition with natural selection (Figure 1), and resulting in magnified stabilizing selection with a great potential for eroded genetic variance in body size and associated traits. To date, no empirical study has specifically explored the effects of commercial harvest on the genetic variability of fitness-related traits (for neutral genetic markers see for instance Allendorf *et al.*, 2008; Pinsky and Palumbi, 2014), and this obviously represents an important gap in our knowledge.

### Change in the Naturally Selected Adaptive Landscape

If a loss of adaptive genetic variability for body size and correlated traits is not involved (i.e.,  $V_{a_x} > 0$  in eqn [1b]), impediment to the recovery of exploited populations necessarily results from a change in natural selection (i.e.,  $\delta w_x / \delta x \rightarrow 0$  in eqn [1b]). It has been argued that natural selection toward the phenotypic optimum is likely to be much weaker than harvest-induced selection away from it (Law, 2000; Enberg *et al.*, 2009). However, weak natural selection is incompatible with the fact that harvest-induced evolution incurs severe fitness costs (see above). Instead, as a population phenotype evolves away from the naturally selected optimum, the strength of natural selection toward the optimum should increase. A more likely hypothesis to explain impediment to recovery involves a fishing-induced change in the naturally selected optimum itself.

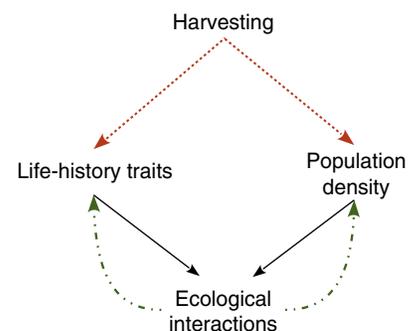
This idea is well illustrated by a study by Douglas Swain on cod (*Gadus Morhua*) in the southern Gulf of Saint Lawrence (Swain, 2011). This cod stock, like several other Canadian cod stocks, has collapsed during the early 1990s in parallel with a rapid decrease in age and size at maturity, which presumably represented a response to fishing-induced selection (Olsen *et al.*, 2004). However, despite severe reductions in the fishing pressure, age and size at maturity remained low in this stock and apparently did so because of an increase in natural mortality (Swain, 2011). Hence, the fishery seems to have changed the ecological conditions, shifting the naturally selected adaptive landscape of cod such that a faster life history is now the new adaptive optimum. This important result requires that we now examine what ecological changes may cause this shift in the naturally selected adaptive landscape.

Swain (2011) points to potential candidate mechanisms for increased natural mortality in southern Gulf of St. Lawrence

cod. First, increased reproductive investment (as initially favoured by a high fishing mortality), together with low food conditions (Shelton *et al.*, 2006), might have caused an increase in reproductive mortality. This hypothesis is supported by the fact that post-fishery increase in natural mortality mainly affected cod older than 5 years, i.e., reproductively active cod (Swain, 2011). Second, cod collapse was paralleled by an increase in the number of gray seals (*Halichoerus grypus*), which are predators for cod. However, seals tend to prey on juvenile cod, while the increased natural mortality effectively affected mainly adult cod (Chouinard *et al.*, 2005), suggesting that predation from seals might not be a major cause of the now high natural mortality in adult cod.

We may propose additional mechanisms for increased mortality in adult cod. Cod and seals might in fact interact through intraguild predation (IGP), a type of interaction in which predators and prey also compete for common food sources (Holt and Polis, 1997). Hence, increased seal numbers might thus participate in depleting food resources for adult cod, and thus favor starvation during energy-demanding reproductive periods. Other species probably interact with cod through IGP. For instance, in the North Sea, herring (*Clupea harengus*) – a prey for cod – inhibits cod recruitment through competition with juvenile cod for zooplankton, but also through predation on cod eggs and larvae (Fauchald, 2010). In the southern Gulf of St. Lawrence cod, increased adult cod mortality possibly operated through exploitative competition from smaller-sized (i.e., lower  $R$ -starred) fish species that may also be prey for cod. Hence fishing for cod might have pushed an initially cod-abundant system to a new, stable but cod-sparse system in which selection favors smaller-sized cod (Abrams, 2011).

The cod example highlights the potential for eco-evolutionary feedback loops in human-perturbed ecosystems (Figure 3). These feedback loops act through density- or frequency-dependent natural selection, and are of crucial importance if one wants to correctly manage natural populations



**Figure 3** Density-dependent feedback loops arising from harvesting wild populations. Harvest-induced selection (dashed red arrows) favor in parallel faster life histories and reduced population density, which both potentially alter the strength or even nature of intra- and interspecific interactions (solid black arrows). Ultimately, natural selection acting through these ecological interactions (dotted and dashed green arrows) may feedback on life histories and population densities to either oppose (stabilizing eco-evolutionary feedback loop) or reinforce (runaway eco-evolutionary feedback loop) the effects of anthropogenic selection.

(Dieckmann and Ferriere, 2004). A natural selection opposing the effects of anthropogenic selection results in a stabilizing feedback loop, helps in maintaining the system under control, and fosters recovery when the perturbation has ceased. However, in some cases (e.g., cod) natural selection may instead reinforce anthropogenic selection, accelerate change to a new population or ecosystem state, and impede reversal to the initial state. Hence, eco-evolutionary feedback loops stress the need to fully integrate food–web interactions and life-history theory in the next generation conservation plans.

*See also:* Evolvability, Quantitative Genetics of. Life History: Pike. Natural Selection, Measuring. Responses to Climate Change, Evolution and

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