

Detecting and managing fisheries-induced evolution

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Exploitation of fish populations can induce evolutionary responses in life histories. For example, fisheries targeting large individuals are expected to select for early maturation at smaller sizes, leading to reduced fecundity and thus also reduced fisheries yield. These predicted phenotypic shifts have been observed in several fish stocks, but disentangling the environmental and genetic causes behind them has proved difficult. Here, we review recent studies investigating phenotypic shifts in exploited populations and strategies for minimizing fisheries-induced evolution. Responses to selective harvesting will depend on species-specific life-history traits, and on community-level and environmental processes. Therefore, the detection of fisheries-induced evolution and successful fish stock management requires routine population monitoring, and a good understanding of genetics, relevant ecological processes and changing environmental conditions.

Introduction

During the second half of the 20th century, the increasing harvest of natural fish stocks led to rapid and widespread population declines of several target [1–4] and nontarget fish species [5]. Although such population declines are themselves of concern [3], the effects of harvesting on individual life histories have received less attention but might be no less important. Most fisheries target large individuals, so that fisheries-induced mortality is typically highly size selective [6–8] (see Glossary). Therefore, fisheries are an important source of selective pressures favouring particular life histories, morphologies and behaviours. Harvesting of large individuals should select for maturation at a younger age and/or smaller size by reducing the proportion of old and/or large individuals in the spawning stock (for example, see Ref [9]). If individual phenotypic differences in the life-history traits under selection are heritable, then fisheries-induced selection could lead to evolutionary shifts towards lower maturing ages and/or sizes in exploited populations [10–12] (Box 1).

Decreasing age and size at maturation can induce cascading effects on population dynamics and even on community structures. For instance, somatic growth of mature individuals generally declines because energy is reallocated from growth to future reproduction. Because of a

positive correlation between body size and fecundity, reduction in the age at maturation thus reduces age-specific sizes of adult individuals and reproductive potential of the population [9,13]. If reduced average body size is not compensated for by increased population abundance, biomass and yield of the fish stock will decrease [9]. Changes in adult body size can also alter predator–prey interactions and affect food webs in fish communities [10]. Therefore, understanding fisheries-induced evolution is important not only for sustainable management of a particular fish stock, but also for conservation of entire marine and lake ecosystems.

During recent years much research has focused on detecting fisheries-induced evolution (for examples, see Refs [14–16]), but possible genetic effects of fisheries have been largely ignored in present-day fish-stock management practices. Here, we review recently published literature on fisheries-induced evolution, with particular emphasis on methods capable of identifying a genetic basis for observed phenotypic shifts in the age and size at maturation. We also discuss the prospects for future fish-stock management and strategies for minimizing the impacts of fisheries-induced selection. Current knowledge in these fields suggests that the detection of fisheries-induced evolution and successful fish stock management require routine population monitoring and a good understanding of genetics, relevant ecological processes and changing environmental conditions.

Glossary

Evolutionary response: a genetically based response to selection in a mean trait value of a population, that is, a change in genetic composition of the population.

Heritability (h^2): proportion of the variation in a quantitative character due to (additive) genetic causes.

Phenotypic change: a change in a trait value that can be due to either phenotypic plasticity or evolutionary response.

Phenotypic plasticity: ability of the same genotype to produce or express different phenotypes.

Plastic change or response: changes in phenotypes due to phenotypic plasticity.

Probabilistic maturation reaction norm: a function determining a size-specific probability of maturation for individuals of a given age.

Selection: nonrandom survival of phenotypes and/or genotypes.

Selection differential: a measure of intensity of selection on a quantitative character – the difference in the mean between the selected and the total population.

Size-at-age: the size of an individual at a given age; sizes at all ages together form the growth trajectory of an individual.

Size-selective fishing: fishing that does not remove fish randomly, but selects them – at least to some extent – according to size.

Size-selective mortality: probability of death depending on the size of an individual.

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Box 1. Quantitative genetic basis for fisheries-induced evolution

Quantitative genetics is a theory developed to study inheritance of continuously varying phenotypic traits and, in particular, to describe the impact of selection on these traits over generations [63]. Over a single generation, the expected evolutionary response (R) in a trait under fisheries-induced selection depends on the intensity of directional selection (S) acting on the trait and the heritability (h^2) of the trait. In a harvested fish population, S is simply the difference between the mean values of the trait for individuals that survive to reproduce (i.e. those not caught by fisheries) and for the entire cohort (i.e. those caught by fisheries plus those not caught by fisheries). Once S and h^2 are known, R can be obtained using the breeder's equation [Equation 1] [63]:

$$R = h^2 S \quad \text{[Equation 1]}$$

Strictly speaking, [Equation 1] applies only to nonoverlapping generations. However, predictions using [Equation 1] can still be applied, at least qualitatively, to populations with overlapping generations as well [9].

Size-selective fishing targeting large individuals removes proportionally more large fish from a population than small fish [9]. The effect of this is reflected in a negative value of S with respect to size, and, if the size at maturation is heritable (i.e. $h^2 > 0$) results in the evolution towards lower size at maturation [Equation 1]. Even high fishing mortality *per se* can render S negative [12]. This is because fish that mature as young as possible are most likely to survive for reproduction, whereas if maturation is delayed, then survival until reproduction becomes very unlikely. As age and size at maturation are typically strongly correlated [17,38], selection on either trait is likely to lead to a correlated evolutionary response in the other.

Recently, selection differentials on body size have been estimated to assess the magnitude of fisheries-induced selection, for example for populations of Atlantic salmon [66] and Atlantic cod [50]. However, heritability estimates of life-history traits in fish are scarce, and usually they are obtained under artificial conditions, which limit their applicability in the wild [64]. Nevertheless, most phenotypic traits in fish, including traits known to be under fisheries-induced selection, are typically at least moderately heritable ($h^2 \sim 0.2\text{--}0.3$) (for example, see Refs [6,7]). Hence, evolutionary responses to fisheries-induced selection should be common.

Distinguishing evolutionary responses from phenotypic plasticity

In fish, about 20–30% of the variation in life-history traits, such as age and size at maturation, is heritable [6,7]. Exploitation of fish stocks is typically so intense that in exploited stocks adult fish are more likely to die as a result of being fished than of natural causes [6,7]. For example, 60–80% exploitation rates have been reported for several commercially important Atlantic cod *Gadus morhua* stocks [9]. Thus, evolutionary responses in life-history traits subject to fisheries-induced selection can be expected to be seen on a decadal time scale [6,8].

The expected evolutionary responses to size-selective harvesting have recently been demonstrated experimentally. For guppies *Poecilia reticulata*, increased predation has been shown to select for earlier maturation at smaller sizes [17]. Similarly, harvesting of the largest individuals leads to decreased average body size in Atlantic silversides *Menidia menidia* [18]. These findings, albeit observed in simplified experimental settings, suggest that similar evolutionary responses are also occurring in natural fish populations that are subject to size-selective harvesting.

Phenotypic plasticity in growth can also affect the timing and size at maturation in an exploited population.

Harvesting reduces population density, which increases the amount of resources available per capita and reduces competition among individuals. These changes might increase individual growth rates and lead to early maturation, possibly at smaller sizes [6,15,19–24]. However, growth and the timing of maturation might also be affected by environmental trends, such as increasing water temperatures [6,8,19–22], so that causal processes can be difficult to disentangle.

Whether life-history changes induced by fisheries are of a plastic or genetic origin is important to the management of fish stocks. Plastic changes in, for example, growth rates are only temporary, because they are not transferred to subsequent generations. By contrast, evolutionary responses in life histories alter genotype frequencies in a population and can even lead to the loss of genetic variability (for example, see Ref. [25]). Reversing such changes can be slow or even impossible [6,26,27]. Hence, for conservation and management purposes, it is important to detect evolutionary responses in harvested populations and separate them clearly from possible plastic changes in life histories [12,15,21,28,29].

From phenotypic observations to modelling of adaptation

The Atlantic cod in the north-west Atlantic Ocean is a well-known example in which a decrease in the age and size at maturation has been linked to heavy exploitation by fisheries [16,21] (Box 2). Changes in the age and size at maturation or in age-specific sizes have also been reported for several other exploited species and populations (for a review, see Ref [19]) (Table 1), for example five species of Pacific salmon [30] and Atlantic salmon *Salmo salar* [31]. Detecting the relative roles of plastic changes and evolutionary responses in any of these observed phenotypic patterns has been and still is challenging [6–8,12,21,28,32]. A population of orange roughy *Hoplostethus atlanticus* is a rare case in which a decreasing trend in the genetic diversity of the population has been directly detected during the exploitation [25]. By contrast, in most exploited populations the available data comprise observational time series of life-history traits and estimates of cohort sizes but no information about possible changes in genotype frequencies is available. Indirect methods are, therefore, needed to explore the possible genetic basis of these changes in life histories.

One of the earliest studies focusing on the origin of phenotypic changes was by Rijnsdorp [14]. He used traditional statistical analyses to show that the decreasing trend in the age and size at maturation in European plaice *Pleuronectes platessa* could not be explained solely by changes in growth and that observed life-history changes matched well with the adaptive changes expected under fisheries-induced selection. Although this study generally supports the hypothesis of evolutionary adaptation of life histories, it is not possible to rule out environmentally induced effects (e.g. owing to changes in temperature and population density) [14]. Therefore, new modelling approaches have been introduced for detecting evolutionary responses in the age and/or size at maturation and in correlated traits (Table 2).

Box 2. The collapse of cod

The northern cod stock, comprising the populations of Atlantic cod *Gadus morhua* (Figure 1) in the north-west Atlantic Ocean, has been supporting fisheries for hundreds of years [16,67]. Since the late 1980s, the yields of the populations gradually declined and reached historically low levels by the mid-1990s [21]. For example, the estimated biomass of the George bank cod population decreased from 91 000t in 1980 to 31 000t in 1994. Correspondingly, the spawning stock biomass of the population declined from 83 000t to 25 000t during the same period [68].

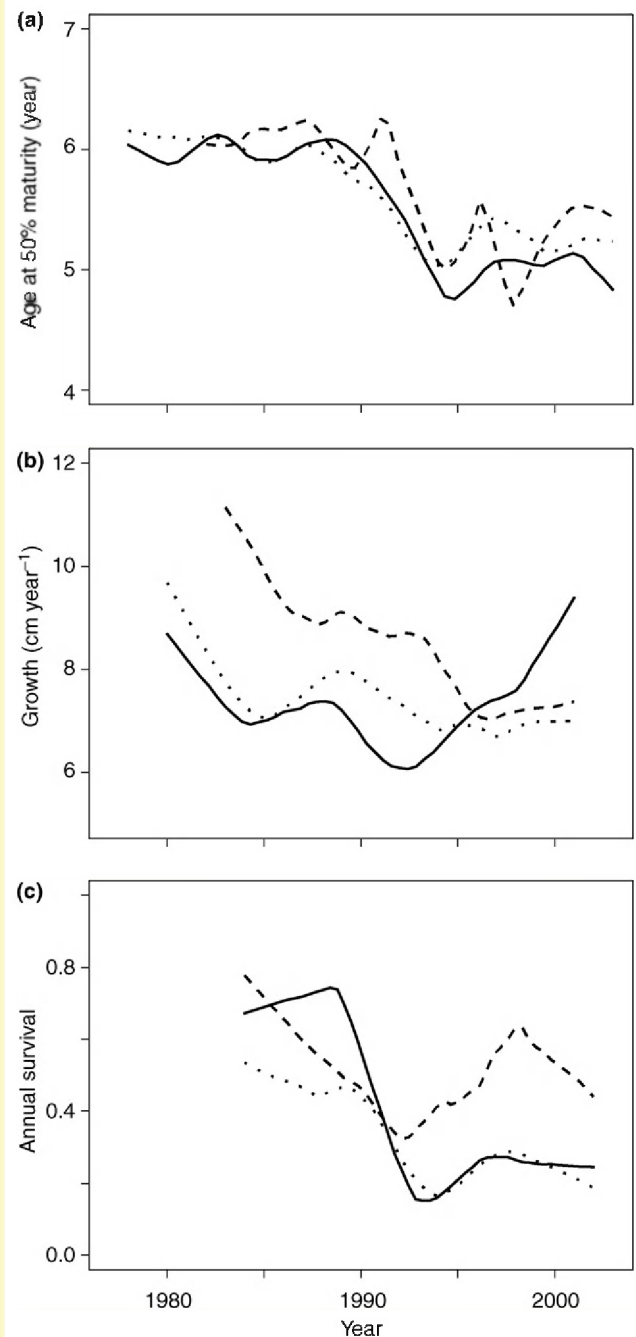
The collapse of the northern cod stock was assumed to be caused by intensive exploitation of the cod stock during the second half of the 20th century, and the cod fishery in the area was closed in July 1992. Before the collapse of the stock, age and size at maturation were observed to decrease dramatically [16,21,67] (Figure 11). These traits have still not recovered to the state preceding the collapse (Figure 11a), despite very little fishing of the stock for more than a decade. This finding is seen as an indication that the changes in the age and size at maturation were evolutionary and were inherited by subsequent generations, rather than being a plastic phenotypic response to the prevailing levels of fishing mortality [16].

Analysis of the probabilistic reaction norms for age and size at maturation (Box 3) suggested that the observed phenotypic changes might be of genetic origin [16,67]. However, opposing views have also been expressed [8,69]. An evident increase in the age and size at maturity within only 3 years after the fishing moratorium (Figure 11a) suggests that pre-existing cohorts were responding in some way to the absence of exploitation [8]. In addition, decrease in the age and size at maturation in northern cod occurred simultaneously with a decline in sea-water temperature and an increase in sea-ice cover [69]. Such prevailing environmental trends might have induced plastic changes in the age and size at maturation. Thus, it is difficult to base conclusions on the evolution of life histories on purely phenotypic observations [70].



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Figure 1. The Atlantic cod *Gadus morhua*. Reproduced with the permission of Lauri Urho.



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Figure 11. Time series of life-history traits estimated in northern cod stock. The stock collapsed between the late 1980s and early 1990s, and a fishing moratorium of the stock was introduced in 1992. Life-history traits are from Northwest Atlantic Fisheries Organization (NAFO) Division 2J (solid lines), 3K (dotted lines) and 3L (dashed lines). (a) Time series of the ages at which 50% of female cod were mature show how age at maturity rapidly decreased in the late 1980s and early 1990s. After introduction of the fishing moratorium, age at 50% maturity increased slightly, but it did not recover to the level preceding the stock collapse. Annual length increments for female cod and annual, non-sex-specific survival probabilities are shown in (b) and (c), respectively. Length increments and survival probabilities are arithmetic and geometric averages for 5-year-old and 6-year-old fish, respectively. During the stock collapse, both growth and survival declined considerably, but since 1992 they have partly recovered. Reproduced with permission from Ref. [16].

Table 1. Examples of recent empirical investigations of the genetic basis of observed phenotypic changes in harvested fish populations

Species	Investigated phenotypic change ^a			Time frame	Method ^b	Conclusion ^c	Refs
	AM	SM	SA				
Grayling <i>Thymallus thymallus</i>	—	—	na	1903–1998	Statistical analyses and simulations	ER	[49]
European plaice <i>Pleuronectes platessa</i>	—	—	na	~1900,1960–1990	Statistical analyses and simulations	ER	[14]
Herring <i>Clupea harengus</i>	—	+	na	1955–1995	2D- and 3D-PMRN	ER	[15,44]
Atlantic cod <i>Gadus morhua</i>	—	—	na	1935–2000	PMRN	PC	[40]
	—	—	na	1977–2002	PMRN	ER	[16,67]
	—	—	na	~1970–2000	PMRN	ER	[39]
	na	na	—	1970–2004	Quantitative genetics	ER	[50]
Smallmouth bass <i>Micropterus dolomieu</i>	—	—/+	na	~past 100 years	PMRN	PC	[41]
American plaice <i>Hippoglossoides platessoides</i>	—	—	na	~1970–2000	PMRN	ER or PC	[38]
Chum salmon <i>Oncorhynchus keta</i>	+	—	na	~past 25 years	PMRN and simulations	PC	[48]

^aAbbreviations: AM, age at maturation; SM, size at maturation; SA, size-at-age. Change in trait: +, increase; —, decrease; na, change unknown or not investigated.

^bPMRN, probabilistic maturation reaction norm.

^cType of change in phenotypic trait: ER, evolutionary response; PC, plastic change.

Probabilistic maturation reaction norms

The reaction norm for age and size at maturation is a well-established method for describing the optimal age and size for maturation for a range of growth rates [33,34]. More recently, an analogous stochastic interpretation, the probabilistic reaction norm (PMRN) has been developed [35–37] (Box 3). PMRN has rapidly become a very popular and widely applied method for detecting fisheries-induced evolution [19].

PMRNs have recently been used for investigating changes in the age and size at maturation in, for example, exploited populations of European plaice and American plaice *Hippoglossoides platessoides* [15,38], Atlantic cod [16,39], Atlantic herring *Clupea harengus* [40] and Smallmouth bass *Micropterus dolomieu* [41] (Table 1). For cod and plaice, the PMRNs suggested evolution towards early maturation at smaller sizes [15,16,39], whereas phenotypic trends in the herring and bass populations (Table 1) were considered to be predominantly plastic [40,41]. For herring

and bass, the PMRN was estimated using back-calculations of size-at-age based on scale growth rings [40,41], whereas, for cod and plaice, growth of individuals was modelled by assuming common growth rates for mature and immature individuals of the same age and cohort. Such an assumption cannot be considered realistic [6,15] and, therefore, there is a degree of uncertainty related to the estimation of the reaction norms for cod and plaice. By contrast, the estimation of the PMRN has been considered robust for the description of growth trajectories [36,37].

The most pronounced problem related to PMRNs is that the ‘decision’ to mature is modelled only through the age and size at maturation. In reality, this decision is usually made before maturation, and past growth has been shown to be a better predictor of the probability of maturation than present size [42] (Box 3). Maturation can also be based on physiological factors, such as energy status or biochemical thresholds at a given period [43]. In addition, PMRNs have commonly been estimated by accounting only

Table 2. Modelling tools for investigating fisheries-induced evolution

Modelling approach	Description	Advantages	Disadvantages	Example Refs
Probabilistic maturation reaction norms (PMRN)	Estimates the probability of maturation based on age and body size.	Required data are easy to obtain. The method is simple to use.	Maturation can depend on factors other than age and body size. PMRN cannot detect evolution of growth rates.	[16]
Multidimensional probabilistic maturation reaction norms	Estimates the probability of maturation based on age, body size and any other relevant covariate affecting it.	The method allows the incorporation of information on physiological and environmental factors that affect the process of maturation.	Obtaining data on the relevant covariates can be impossible. Multidimensional PMRN cannot detect evolution of growth rates.	[44]
Quantitative genetics	Estimates to what extent observed phenotypic changes due to fisheries-induced selection are genetically based.	Quantitatively links selection differentials and heritability to phenotypic changes.	Disentangling genetic changes from plastic changes can be difficult if environmental conditions have changed during selection.	[50]
Statistical regression and time-series analyses	Estimates to what extent variation in phenotypes can be explained by variation in known biotic and abiotic factors over the investigated period.	Simple method for investigating correlations between life-history traits and observed physiological and environmental processes, and for investigating whether a population exhibits significant changes in life histories.	The approaches do not include any mechanistic description of the evolution of life histories and therefore cannot assess evolutionary processes directly.	[14]
Simulations of adaptive population dynamics	Predicts evolutionary and plastic changes in life histories by using process-based simulation models.	Provides comprehensive insights into the processes underlying phenotypic changes and estimates the fitness of alternative life-history strategies under different rates of exploitation.	Models can be complex and difficult to parameterize. Models predict rather than assess observed phenotypic changes.	[48]

Box 3. Probabilistic reaction norms for the age and size at maturation

At birth, most species are immature, and their chances of maturation increase with increasing age and body size. The process of maturation can be described through probabilities of maturation that depend on the current age and size of an individual. These probabilities are given by the probabilistic reaction norm (PMRN) for the age and size at maturation (Figure 1), and they can be estimated using a logistic regression model [35–37]. If the probability of maturation at age a is denoted by p_a , then it can be linked to the size-at-age of an individual by [35] (Equation I):

$$\log\left(\frac{p_a(s)}{1 - p_a(s)}\right) = \alpha_a + \beta_a s \quad [\text{Equation I}]$$

where α_a and β_a are the age-specific shape parameters and s is the size of an individual at age a [31–33].

Once growth histories and the timing of maturation are known for a range of individuals, the shape parameters of a PMRN can be estimated by maximizing the likelihood (Equation III)

$$L = \prod_{n=1}^N p_a(s_n)^{I_n} (1 - p_a(s_n))^{1-I_n} \quad [\text{Equation III}]$$

where s_n is the size of an individual at age a and I_n indicates whether the individual matured ($I_n = 1$) or not ($I_n = 0$) at age a . N is the total number of observed individuals.

Estimated in the way described above, the PMRN determines the probability of maturing at a given age and size, on condition that the individual has survived up to this age and size and is still immature. Because of depending only on the current size of an individual, the probability of maturation is insensitive to variation in growth trajectories (Figure 1c). For this reason, the PMRN should distinguish variation in growth rates from changes in the age- and size-specific probabilities of maturation [35]. However, if the 'decision' to mature is made before maturation, then size at maturation is no longer directly connected to the probability of maturation. Morita and Fukuwaka [42] recently demonstrated that past growth of an individual can better predict the probability of maturation than the current size of the individual. If a PMRN is regressed against the sizes before the moment at which their maturation 'decisions' are recorded (Equation II), then the PMRN is no longer insensitive to variation in growth.

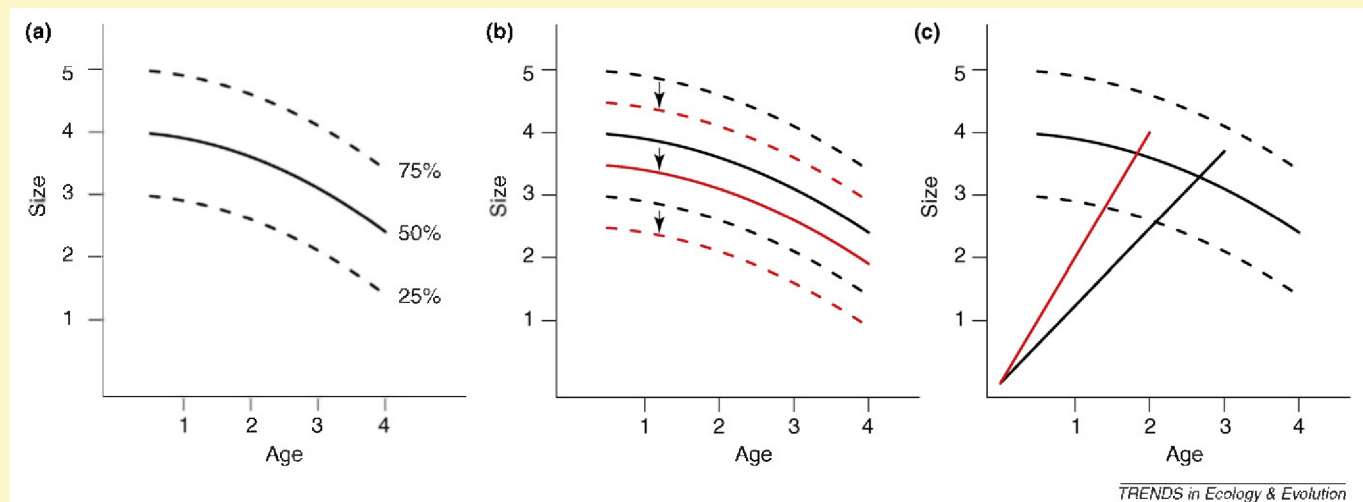


Figure 1. Analysis of the probabilistic maturation reaction norm. (a) A probabilistic reaction norm is commonly described by the age-specific sizes at which 25%, 50% and 75% of the individuals mature. (b) An evolutionary decrease in the age and size at maturation is shown by a downward shift of the probabilistic reaction norm. This is because if average age and size at maturation decrease in a population, then the probabilities of maturing at lower ages and sizes increase. In (b) the evolutionary shift of the reaction norm is indicated with downward arrows from old reaction norm (black) to new reaction norm (red). As in (a) the solid line indicates 50% probability of maturation and the upper and the lower broken lines denote 75% and 25% probabilities of maturation, respectively. (c) The probabilistic reaction norm describes the probability of maturing at a given age and size, on condition that the individual has survived up to this age and size and is still immature. Because of this, only current age and size of an individual affect the probability of maturation. Changes in growth rates therefore only affect the growth trajectories of individuals [in (c) a shift from black to red growth trajectory], but the age and size specific probabilities of maturation (i.e. the probabilistic reaction norm) remain unchanged. Units of the age and size in (a–c) are arbitrary.

for the environmental variation that is reflected in growth histories, and other factors that may directly affect maturation, such as temperature, feeding conditions or the social structure of the population, have not been considered [20,32]. For example, similar shifts in PMRNs have been found in three populations of American plaice under different fishing pressures [38], which suggests that a common environmental trend, rather than fisheries, caused phenotypic changes in the populations.

Multidimensional PMRNs with one or more explanatory variables in addition to the age and size at maturation have been introduced to overcome some of these uncertainties [44]. When this approach was used, body condition was found to be significantly correlated with the probability of maturation for a population of European plaice, but no considerable improvements in the estimation of PMRNs were seen. In general, the concept of PMRNs

enables information to be incorporated from as many covariates as necessary [19]. Thus, for increasing the realism of PMRNs, the timing of the maturation decision should be known and the main factors affecting it should be identified, measured and incorporated to the estimation of the PMRNs [32,43].

Evolutionary responses in growth rates are problematic in the PMRN analysis. Selection induced by fisheries can act on growth strategies rather than age and size at maturation or these traits can be genetically correlated [8,20,38,45]. PMRNs are generally unable to disentangle genetic from plastic changes in growth. Consequently, PMRN analyses can lead to the rejection of the hypothesis of fisheries-induced evolution even if it is true [20]. The risk of this depends on the extent to which species-specific growth strategies are under genetic control.

Comprehensive perspectives on life-history adaptation

Evolutionary responses occurring over a few decades are influenced by interactions among the environment, population demography, genetic variability and selection [46]. For example, an increase in fishing effort is expected if stock abundance and size of harvested individuals decline. This, in turn, alters the selective pressures on the population [47]. Consequently, comprehensive modelling approaches integrating evolutionary and ecological processes have been called for, to realistically assess the evolutionary responses to harvesting [11,21,29].

Recently, life-history changes have been investigated by simulating the dynamics of the harvested populations with models that describe the impacts of changing population density, energy trade-offs and natural mortality. By combining PMRNs with such simulations Morita *et al.* [48] showed that declining growth rate was sufficient to explain increasing age and decreasing size at maturation in chum salmon *Oncorhynchus keta*. As the variation in the growth of chum salmon is considered predominantly environmental [48], phenotypic changes were considered to be plastic responses to changing environmental conditions. By contrast, high rates of evolutionary divergence in the age and size at maturation have been observed in grayling *Thymallus thymallus* [49]. In this case, the study [49] further demonstrated that such evolutionary responses were expected under the prevailing harvesting strategies. These modelling approaches can be used to address some of the questions that could not be considered in the analyses of PMRNs. However, the link between the observations and life-history responses still remains circumstantial. As Law [8] pointed out, 'Quantitative analysis of whether rates of change are consistent with likely heritabilities and selection differentials caused by fishing, allowing for change in the environment, is a critical issue needing more research.'

Using a quantitative genetics-based model (Box 1), Swain *et al.* [50] made connections among selection differentials, heritability and a declining trend in the body size of Atlantic cod. In addition to evolutionary adaptation, they investigated the roles of density- and temperature-dependent growth in the observed phenotypic changes. Within-population variation in growth was accounted for by estimating individual growth trajectories from otolith (small ear bone) formations. The size-at-age of cod was correlated with the nongenetic factors investigated but, after controlling for these effects, the observed phenotypic changes were still positively correlated with the selection differentials, and the estimated heritability of the size-at-age was high [50]. Although these findings strengthen the evidence of fisheries-induced evolution of Atlantic cod, the plausibility of the results depends on how reliably heritability was estimated. If the size-at-age of cod was affected by changes in environmental factors other than population density and temperature, the heritability estimate might have been upwardly biased [51].

Management strategies for preventing fisheries-induced evolution

Concerns arising from trends towards lower maturing ages and/or sizes in exploited fish stocks were rapidly addressed

by theoretical investigations of the adaptive dynamics of harvested populations [9,26,52]. Fisheries-induced evolution was found to be not only possible but also likely under realistic rates of exploitation and size selectivity of fisheries [9,26,52]. This finding created a demand for management practices that would minimize the evolutionary impacts of fisheries.

Two main forces that affect the rate of evolution in an exploited stock are the size selectivity of fisheries and the intensity of harvesting [6,12,53]. Heavy exploitation of a stock can induce an evolutionary shift towards early maturation, even in the absence of size selection [12] (Box 1). By contrast, fisheries targeting only mature individuals should favour late maturation at large sizes [29,53]. In practice, declines in the age and/or size at maturation can, therefore, be prevented by considerably reducing harvesting rates, and by setting a minimum size of harvested fish so that most immature individuals remain below the limit [29] or by harvesting only on spatially isolated spawning grounds [53]. If evolutionary shifts have already taken place, they can be reversed if complete fishing moratoria are introduced quickly enough, whereas belated or partial fishing moratoria might not reverse the changes, because of the lack of selection towards late maturation [23].

Setting a maximum size of harvested fish is a tempting possibility to control the evolutionary impacts of fisheries [18], particularly because large, old individuals constitute an important reservoir of genetic variability [25] and reproductive potential [54] of the population. However, in a population that has already evolved towards lower maturing ages and/or size it is very difficult to find the optimal maximum size limit that would reverse the direction of selection, because the fitness benefit of large individuals is very sensitive to the level of natural mortality [53].

Marine protection areas (MPAs) with little or no fishing have been suggested as a method for controlling the evolutionary impacts of harvesting [55]. The effectiveness and optimal structure of MPAs depend on the dispersal distances of individuals. However, in general, MPAs reduce the declining trend in the size at maturation and prevent the populations from collapsing, even in the presence of very intensive harvesting outside the MPA.

Evolutionary and plastic responses to harvesting appear to be affected by more complex processes than those considered in any single-species model. Namely, fisheries can also have impacts at the community level: they not only remove large individuals of all target species, but also decrease the relative abundances of species with the capability to grow to large sizes [10]. Changes in species abundance can affect interspecific processes, such as predator-prey interactions, and alter natural mortality rates [7,12]. This is particularly relevant given that the strength and selectivity of natural mortality can determine the direction in which size at maturation evolves in a population, especially in the presence of low harvest rates [56,57]. Targeting only small individuals to reverse evolutionary responses induced by fishing might even lead to further decreases in the size at maturation instead of the desired increase. This is because survival up to the sizes that are no longer targeted can be so low that early

reproduction still might be a more beneficial strategy [57]. To this end, an ecosystem-level approach is required for successful fisheries management [13,58].

Challenges for future management and research

Even in the absence of concrete evidence for fisheries-induced evolution, rapid evolutionary responses have been considered so likely that they should be accounted for in management and conservation strategies [6,11,17,27,46,50]. Thus, interactions between ecological and evolutionary processes should be considered in the assessment of the population dynamics and when predicting future yields [11,17,23]. Present harvesting regulations, such as minimum sizes and fishing seasons, should also be re-evaluated [18,59]. Particular attention should focus on establishing practices minimizing the selective pressures on harvested populations [23,29] and preventing loss of genetic diversity (e.g. introduction of MPAs [55] and preservation of large, old individuals [18,25,54]).

Slow-growing, late-maturing species (e.g. Atlantic cod) [10,60] and populations with low natural mortality [29] are particularly vulnerable to fisheries-induced evolution, because they are least adapted to incurring high adult mortality. Even species that are not at a particular risk or even not targeted by fisheries can suffer indirect effects of harvesting [17,56]. A better understanding of species interactions and food webs in the exploited populations is urgently needed to account for such ecosystem-level impacts of fisheries [57].

Continuous monitoring of key life-history traits will be essential for the proper management of fish stocks. Conservation actions taken promptly after suspicion of evolutionary responses are expected to be successful in restoring the population [23], whereas delays can lead to a permanent loss of adaptive genetic variability. This is because observed phenotypic changes in harvested populations have often been associated with steep declines in population size [16,21]. Population bottlenecks, genetic drift and inbreeding in small populations will then reduce genetic diversity and make recovery difficult or even impossible [9,27,61].

Until now, the potential evolutionary effects of fisheries have not been taken into account in management because researchers have found it difficult to convince the authorities that the changes observed are indeed genetic [6,46]. For this reason, solid evidence for fisheries-induced genetic shifts in exploited stocks is needed. To this end, in parallel with the monitoring of phenotypes in harvested fish populations, more rigorous genetic approaches are also needed. There are, in principle, two main possibilities for this. The first relies on traditional quantitative genetic analyses (Box 1) that require either breeding experiments in captivity or monitoring of individually marked (or genetically tagged [62]) relatives in the wild [63]. These approaches are unlikely to be useful for practical monitoring, because heritabilities estimated in captivity can be misleading [64], and the sampling effort required for mark-recapture studies would be enormous. A second way to monitor genetic changes in exploited populations is based on genetic markers linked to genomic regions

under fisheries-induced selection. This type of approach, although demanding to establish, provides perhaps the most promising and realistic expectation for future monitoring [65].

Concluding comments

Theory, phenotypic observations and modelling studies all suggest that fisheries are capable of inducing evolutionary changes in life histories in harvested populations. These changes can cause a permanent loss of adaptive genetic variation and decrease future yield. Consequently, fish-stock management strategies should be adjusted to prevent or decrease the evolutionary impacts of harvesting. In practice, this requires stock-specific information on life histories, demography, environmental conditions and species interactions. Identifying the genetic basis of the phenotypic changes requires tools for investigating genetic responses to fisheries-induced selection. Therefore, establishment of practices for the routine monitoring and sampling of harvested fish populations is vital for the detection of fisheries-induced evolution and successful fish stock management.

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