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Fisheries-induced evolution

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Introduction

While fisheries management has traditionally focused on the maintenance of high sustainable yields, the ecological and evolutionary implications of fishing have received less attention. In particular, even though the earliest discussions about the possible evolutionary effects of fishing date back to the founding years of fisheries science, evolutionary thinking remained on the sidelines until very recently.

Harvesting often qualitatively changes the mortality regime to which a population had adapted in the past (**Figure 1**). For example, life-history theory predicts that, under most circumstances, increased mortality at ages and sizes at which fish can mature selects for earlier maturation (Law and Grey, 1989). Indeed, commercially exploited fish stocks often show trends towards earlier maturation (Trippel, 1995; Hutchings and Baum, 2005). However, another plausible explanation exists: earlier maturation may simply reflect demographic effects of fishing and phenotypic plasticity in response to fishing. Because of this ambiguity in disentangling the demographic, plastic, and evolutionary components of life-history changes, understanding the nature of phenotypic changes in exploited fish populations has been difficult, and plasticity has long been considered as a sufficient, or at least most parsimonious, explanation. This traditional view is now gradually changing. Careful analyses of field data are strengthening the case that fisheries-induced selection is actually quite common, and have received strong support from experimental studies and from quantitative models (Jørgensen *et al.*, 2007). Moreover, models and experiments suggest that evolutionary changes are likely to reduce sustainable yields, and that, once induced, such evolutionary changes are slow to reverse. There are thus sufficient scientific reasons to be concerned about the evolutionary effects of fishing. In consequence, a precautionary approach to fisheries management requires a better understanding of the nature and extent of fisheries-induced evolution in the wild, as well as of cost-effective measures for mitigating unwanted evolutionary changes.

<Figure 1 near here>

Evolutionary Challenges of Modern Fisheries Management

Fisheries management aims at ensuring that fishing activities are carried out so as to meet objectives set by society. Traditionally, the overarching objective has been to maintain high yields from the key target species. The last two decades have witnessed a broadening of the objectives of fisheries management, which presently are increasingly based on a more holistic perspective of benefits aquatic systems can provide to humans. Moreover, guidelines established in international agreements and declarations require the explicit consideration of risks and uncertainty. In particular, fisheries managers are expected to respect the precautionary principle, as formulated in the Convention on Biological Diversity: “Where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation” (UN, 1992). See also: 03252.

Theory and empirical evidence suggest that fisheries-induced evolution is negatively influencing both the quality and the quantity of fisheries yields, and that it may also alter biological diversity. Furthermore, models indicate that these changes are difficult to reverse. Under these conditions, managers adhering to the precautionary principle are obliged to take fisheries-induced evolution into

account, even before full scientific certainty is achieved as to how widespread and severe the consequences fisheries-induced evolution are.

Fisheries-induced Evolution

Fisheries-induced selection may take many forms, as harvesting is virtually always selective with regard to a great variety of heritable traits (**Table 1**). First, fishing gears are designed to capture individuals most efficiently within a certain range of sizes. Second, fishing regulations mandate size-selective fishing through minimum landing sizes and mesh size limits. Third, fish are not distributed randomly in space and time, so the choice to fish in a particular area at a particular time will usually cause differential exposure to fishing in dependence on individual characteristics. That evolutionary selection pressures arise from such selective fishing is obvious, since selective fishing alters which fish survive and reproduce.

It is less obvious, and often overlooked, that even mere changes in the overall mortality experienced by a population are powerful drivers of evolutionary selection. In other words, fisheries-induced evolution can occur even when fishing practices are entirely unselective and thus affect all individuals of a population alike. This is because increased overall mortality reduces life expectancy, so that the risks, and thus the costs, of all strategies involving waiting or saving are elevated. A prominent example of such a strategy is maturation: while delaying maturation, and thus growing to a larger size before first reproduction, is rewarded in terms of increased fecundity, the overall level of mortality determines whether this benefit outweighs the risk of dying before the benefit can be reaped. Overall mortality thus acts as a discounting factor for future benefits. When fishing increases this discounting factor, it inevitably favours fish that 'live fast and die young'.

For evolution to take place, selection pressures must affect traits that are heritable. Breeding programs carried out to improve yield from aquaculture species show that life-history traits in fish are heritable to a similar degree as observed for other taxa (Law, 2000). In addition, experimental harvesting of fish has confirmed that harvesting, especially when it is size-selective, can cause significant selection responses within just a few generations (Jørgensen *et al.*, 2007). In general, it is therefore largely inevitable that fisheries are driving evolution in exploited species. Yet there are still many open questions: which traits are most likely to evolve significantly in response to fishing, which species and stocks are most vulnerable to fisheries-induced evolution, which fishing practices are most likely to induce evolutionary responses, and how are all these factors affecting the expected pace of fisheries-induced evolution?

Table 1 Examples of fisheries-induced selection pressures and of costs associated with the corresponding adaptations to fishing. A more comprehensive discussion is provided by Heino and Godø (2002).

Trait group	**Trait**	**Possible fisheries-induced selection pressure**	**Possible costs of the corresponding adaptations to fishing**
Life-history traits	Maturation schedule	Increased mortality among adults and late juveniles	Smaller body size, and accordingly reduced fecundity, at maturation and

		favours earlier maturation	later in life
	Reproductive effort	Increased mortality among adults favours increased reproductive effort	Smaller body size after maturation and later in life; reduced burst swimming speed resulting from larger gonads
	Growth rate	Positively size-selective fishing mortality favours remaining small for longer	Diminished fecundity
		High fishing mortality may favour faster growth to maturation size	Increased natural mortality resulting from elevated energy allocation to growth
Behavioural traits	Vigilance and avoidance behaviour	Some fishing gears may favour increased vigilance and avoidance behaviour	Compromised foraging efficiency
		Higher reproductive effort earlier in life and faster growth may necessitate decreased vigilance and avoidance behaviour	Higher predation mortality
	Timing of spawning migration	Fishery targeting peak spawning times favours off-peak spawning	Sub-optimal mating opportunities and conditions for eggs and larvae
Morphological traits	Body shape	Net fishing may favour more elongated body shapes that allow slipping through meshes	Contracted room for gonads; reduced burst swimming speed
Physiological traits	Burst swimming speed	Mobile fishing gears such as trawls may favour faster burst swimming speed	Increased natural mortality and diminished fecundity resulting from physiological tradeoffs

Identifying Fisheries-induced Evolution

Conclusively proving that fisheries-induced evolution has taken place in a phenotypic trait requires addressing two logically independent questions (Dieckmann and Heino, 2007). The first question concerns the nature of the change: since phenotypes are determined by genotypes in conjunction with the environment, changes in phenotypes may be caused by changes in the environment alone.

The second question concerns the causes of the observed phenotypic change: is fishing among the drivers?

Do observed phenotypic changes have a genetic basis?

The seemingly easiest way of identifying a genetic basis of phenotypic changes is to circumvent the problem altogether, by shifting the level of investigation from the phenotypic level to the genetic level and demonstrating changes in the genes underlying the phenotypic trait in question.

Unfortunately, the genetic basis of relevant phenotypic traits in fish is not yet sufficiently well known, so that at the present state a purely genetic approach is essentially infeasible. Based on the rapid improvement and spread of suitable sequencing techniques and of relevant insights into the interpretation of sequence data, this situation is likely to change in the medium term. However, the direct demonstration of genetic changes requires not only suitable techniques and insights, but also suitable tissue samples. For many stocks that have been under fisheries-induced selection pressures for decades, sufficiently old and yet properly well preserved tissue samples will often be difficult to find.

Alternatively, when control populations exist that are of common ancestry with an exploited population but have not been exploited themselves, one could try to detect genetic changes by standardizing environmental influences, as done in common-garden experiments. Conducting such experiments on long-lived species can be laborious and costly. Furthermore, the phenotypic differences established in common-garden experiments may not be representative of differences in the wild, owing to the difficulty of recreating natural environmental conditions in such experiments.

While the aforementioned methods would enable conclusive demonstrations of evolutionary changes, their practical applicability is yet severely limited. It is therefore crucial to make best use of the wealth of phenotypic data that has been collected for decades from exploited fish populations for purposes of research and monitoring. Without knowledge about genetic changes and without control over all environmental factors, such data are inherently weaker for demonstrating evolution, as the possibility that an unaccounted environmental factor explains a phenotypic pattern can never be fully excluded.

One option, then, is to quantify and isolate the effects of confounding environmental factors through well-established regression methods (e.g., Rijnsdorp, 1993). This approach naturally presumes that the relevant environmental variables were recorded. Furthermore, these explanatory variables must not be strongly correlated, either with time or among each other, if interpretations of regression analyses are not to be compromised. Sometimes, regression analyses may result in strong support in favour of a particular interpretation of the data relative to all other interpretations. However, when analyzing historic data collected for purposes different from addressing a contemporary research question, one has to work with whatever happens to be available, and one will thus often have to rely on suboptimal data that do not lend themselves to reaching incontrovertible conclusions.

A potentially more robust approach is to analyze traits that are intrinsically less affected—or ‘contaminated’—by confounding environmental factors. This can, at least in principle, be achieved by focusing on reaction norms as phenotypic traits. Environmental variability is then not merely a nuisance that confounds the observed trait but instead serves as the very prerequisite for its observation. However, observational field data are not necessarily suitable for estimating reaction

norms. Fortunately, there is one important exception: reaction norms for life-history transitions, most notably reaction norms for age and size at maturation, can often be estimated from the kind of data typically available through field observations. The reason is that maturation patterns are critically influenced by growth patterns, so that growth needs to be treated as an important environmental cause of phenotypic plasticity in maturation. Since growth patterns can often be inferred from observational field data—through back-calculations based on scales or otoliths, and from direct measurements of size at age—it is frequently feasible to disentangle plastic effects of growth on maturation from other impacts on maturation.

A reaction norm for age and size at maturation describes how variable conditions for survival and growth, reflected by variations in distributions of size at age, influence maturation. A probabilistic maturation reaction norm measures the probability with which an immature individual that has reached a certain age and size matures during a given time interval (Heino *et al.*, 2002). Importantly, this probability is conditional on the individual's having reached the considered combination of age and size: it has to survive until, and grow to, this age and size. Through this definition, probabilistic maturation reaction norms allow considering the maturation process separately from survival and growth effects (see Dieckmann and Heino, 2007, for a review). Main sources of environmentally triggered maturation plasticity can thus be removed from an analysis of the underlying maturation schedules. Other sources of maturation plasticity will remain, unless they are included as explanatory variables, in addition to age and size, in the definition and estimation of the probabilistic maturation reaction norm. Unaccounted sources of maturation plasticity pose a challenge to identifying evolutionary changes only when they display a trend that parallels the observed maturation trend – otherwise, they merely add noise around the trend.

Are observed phenotypic changes caused by fishing?

The unambiguous identification of fishing as a driver of changes in fished populations – be they demographic, plastic, or evolutionary – requires an experimental set-up. Studies based on fisheries data, without controls or true replication, are far from this ideal. Nevertheless, the credibility of fisheries-induced selection as a driver of observed changes, relative to other potential drivers, can often be increased (Dieckmann and Heino, 2007). First, alternative hypotheses can be evaluated independently, using the best available knowledge about factors affecting the trait in question. Second, while true replicates are not available, numerous fish stocks have been subjected to a similar 'treatment' of increased mortality through fishing. Third, one can construct dynamic models to examine which selective forces can explain the observed changes.

In conclusion, while it must be kept in mind that incontrovertible demonstrations of fisheries-induced evolution based on observational field data are virtually impossible to establish, one or another interpretation of observed phenotypic changes will often emerge as the most credible, or at least most parsimonious, explanation.

Evidence for Fisheries-induced Evolution

Evidence for fisheries-induced evolution is strongest for life-history traits, and in particular for maturation (Jørgensen *et al.*, 2007). There are three reasons for this. First, for most traits, we lack historic knowledge against which fisheries-induced evolutionary changes could be evaluated. By contrast, data on maturity have been collected for decades for the purpose of stock assessments.

Second, disentangling demographic, plastic, and evolutionary effects is always challenging. At present, a widely applicable solution to this challenge is only available for estimating maturation schedules. Third, models suggest that, relative to other traits, fisheries-induced selection on maturation schedules is particularly strong. This is not entirely surprising: a fish that delays maturation for too long under conditions of heavy fishing is unlikely to leave any offspring at all, resulting in a strong selection pressure towards early maturation.

The introduction of probabilistic maturation reaction norms (Heino *et al.*, 2002) has opened the way for a large range of case studies on fisheries-induced evolution in wild fish populations (**Table 2**). While only certain confounding effects are accounted for (survival-related and growth-related maturation plasticity, together with the demographic effects of fishing), the consistency of findings throughout these case studies strongly supports the hypothesis that fisheries-induced evolution towards earlier maturation is commonplace. Remarkably, the pace of fisheries-induced maturation evolution can be very high, leading to detectable changes within just a few generations.

Table 2 Studies in which probabilistic maturation reaction norms have been used to facilitate the interpretation of maturation trends in exploited populations and stocks of wild fish. For details, see Heino and Dieckmann (2008).

Species	**Population or stock**	**Time span**	**Results indicative of evolutionary change?**
Atlantic cod *Gadus morhua*	Northeast Arctic	1932–2006	Yes
	Eastern Baltic	1991–2005	Yes
	Georges Bank	1970–1998	Yes
	Gulf of Maine	1970–1998	Yes
	Northern (2J3KL)	(1977–) 1981–2002	Yes
	Southern Grand Bank (3NO)	1971–2002	Yes
	St. Pierre Bank (3Ps)	1972–2002	Yes
Haddock *Melanogrammus aeglefinus*	Georges Bank	1968–2002	Yes
	North Sea	1977–1999	Yes
Plaice *Pleuronectes platessa*	North Sea	1957–2001	Yes
American plaice *Hippoglossoides platessoides*	Labrador–NE Newfoundland (2J3K)	1973–1999	Yes
	Grand Bank (3LNO)	1969–2000	Yes
	St. Pierre Bank (3Ps)	1972–1999	Yes

Sole *Solea solea*	Southern North Sea	1958–2000	Yes
Atlantic herring *Clupea harengus*	Norwegian spring-spawning	1935–2000	Yes, weak
	North Sea	1990–2006	Yes, weak
Small yellow croaker *Pseudosciaena polyactis*	Yellow Sea	1985–2001	Yes
Chum salmon *Oncorhynchus keta*	Shari River, Hokkaido, Japan	1992–1997	No
Grayling *Thymallus thymallus*	Lake Lesjaskogsvatnet, Norway	1903–2000	Yes
Smallmouth bass *Micropterus dolomieu*	Opeongo Lake, Ontario, Canada	1936–2002	No

Evidence for fisheries-induced evolution in traits other than maturation is more scattered (Jørgensen *et al.*, 2007). A number of studies suggest changes towards slower growth and increased reproductive effort. While these changes are in line with theoretical predictions, disentangling demographic, plastic, and evolutionary effects in these traits is inherently more difficult than for maturation.

Management Implications of Fisheries-induced Evolution

The current drive towards an ecosystem approach to fisheries management recognizes a broader range of values and services of aquatic ecosystems than the classic yield-focused management paradigm. In this context, the implications of ecological and evolutionary effects of fishing are receiving increasing attention. This begs the question whether, based on such considerations of values and services, fisheries-induced evolution should always be avoided.

Fisheries-induced evolution is adaptation to fishing. Sometimes, fisheries-induced evolution can be envisaged as an evolutionary attempt to escape fishing. Evolutionary changes in vigilance, gear avoidance, or swimming speed are the most obvious examples, but also evolution of reduced adult body size can be seen from this angle. By contrast, fisheries-induced evolution in other traits such as maturation schedules can be interpreted as coping with the inevitable: the primary effect of such changes is not a diminished exposure to fishing, but the elevated production of offspring under conditions of fishing. Fisheries-induced evolution may thus be viewed as having a positive side: fish stocks that have evolutionarily adapted to fishing are likely to be more resilient to fishing than those lacking such adaptations.

This upside, however, comes at a cost. First, adaptation to fishing usually implies that individuals become less well adapted to their ‘natural’ environment. Worryingly, this may make populations less resilient to long-term variations in the environment. For example, a long lifespan is usually seen as an insurance against unpredictable variations in recruitment success, but fisheries favour individuals that live fast and die young. Second, theoretical and empirical studies suggest that the effects of fisheries-induced evolution on the quantity and quality of fishing yields are largely negative. Thus,

there are good reasons to expect that fisheries managers will mostly want to minimize fisheries-induced evolution.

There are two kinds of solutions. First, reducing fishing pressure will almost certainly help to slow the pace of fisheries-induced evolution, and if the reduction is large enough, stop or even reverse it. This approach is often compatible with more traditional management goals: many fish stocks are over-exploited, so reduced exploitation would in the long run generate higher yields with lower costs. Reducing fishing pressures also diminishes negative effects that fishing may have on non-target species and on the habitat.

Second, changing the selectivity of fishing mortality may help to slow the pace of fisheries-induced evolution. The devil here is in the details, and at the present stage of scientific understanding just a few general insights can be offered. Basically, there are two alternative directions. One is to make fishing less selective, such that the size dependence of fishing mortality more closely resembles that of natural mortality (Figure 1). The other is to carefully craft the size dependence of fishing mortality such that fisheries-induced evolution is minimized for those traits that are considered most important. These may be the traits that respond most rapidly to fishing or that have the largest impact on yield. There is at least one situation in which such a solution may be both helpful and feasible: if mature and immature fish are spatially segregated for some part of the year, shifting harvesting pressure from immature to mature individuals reduces the selection pressure towards early maturation, and may even favour delayed maturation. Other traits may then of course still be subject to undesired fisheries-induced effects. It is therefore necessary to evaluate the consequences of alternative fishing practices with the help of dynamic quantitative models. These have to be carefully parameterized for a specific stock, adequately reflect the complexity of its ecological embedding, and include the relevant heritable traits.

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Key concepts

Fisheries management — Management of fish resources for the common good, typically by restricting the quantity and quality (e.g., size) of fish captured directly or indirectly, by restrictions to fishing methods and areas and times when fishing is permitted.

Precautionary principle — A principle according to which uncertainty should not be used as a reason for postponing mitigating management measures when the absence of such measures would risk severe and unrecoverable damage to the environment or human well-being.

Life-history theory — Evolutionary theory predicting how life histories are expected to be shaped by the ambient environment. Predictions often focus on key life-history traits such as maturation, growth, and reproductive investment, and thus on the main determinants of an individual's expected reproductive success.

Fisheries-induced evolution — Genetic change of the population-level distribution of heritable characteristics of individuals, with mortality caused by fishing as the selective agent driving the change.

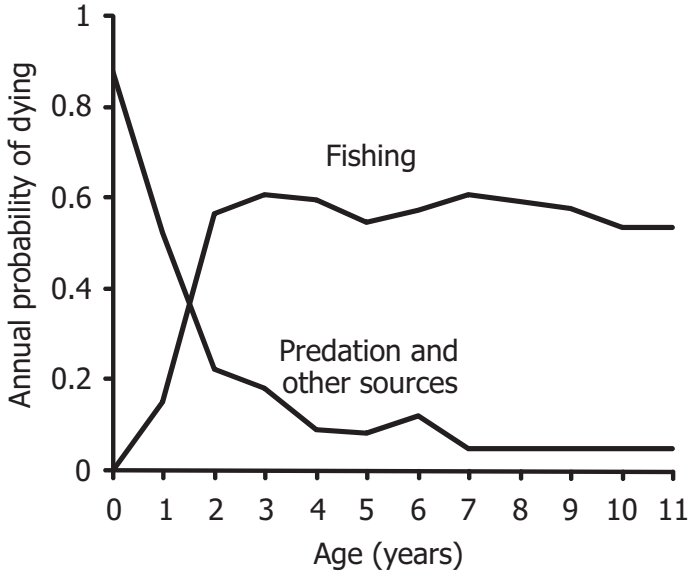
Fisheries-induced adaptive change — Change of the population-level distribution of phenotypic characteristics of individuals, caused by fishing and reflecting both genetic changes and changes due to adaptive phenotypic plasticity.

Phenotypic change — Change of the population-level distribution of phenotypic characteristics of individuals. While such changes are often observed readily and unambiguously, the challenge is to disentangle genetic changes from other changes and fisheries-induced causes from other causes.

Probabilistic maturation reaction norm — A conceptual and statistical tool accounting for the effects of growth conditions on maturation. This tool has helped to establish that maturation changes widely observed in exploited fish stocks can usually not be explained by changes in growth conditions alone. Once this major component of maturation plasticity has thus been isolated from the total phenotypic change in maturation, potentially remaining maturation changes must have other explanations, among which fisheries-induced evolution often appears as being the most parsimonious.

Figure Captions

Figure 1 Estimated age-dependent profiles of mortality for Atlantic cod (*Gadus morhua*) in the North Sea from fishing, in comparison to predation and other natural causes. Adding fishing mortality implies that the probability of surviving from age 3 years to age 12 years is 0.02%. Without fishing, that survival probability would be 47%. Data from ICES (1997).


Annual probability of dying
1
0.8
0.6
0.4
0.2
0
Fishing
Predation and
other sources
0 1 2 3 4 5 6 7 8 9 10 11
Age (years)