



Interim Report

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The dawn of Darwinian fishery management

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The Dawn of Darwinian Fishery Management

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The Dawn of Darwinian Fishery Management

Ulf Dieckmann, Mikko Heino, and Adriaan Rijnsdorp suggest we are incurring a “Darwinian debt” that will have to be repaid by future fishers and consumers.

Let us compare a livestock farmer and a fisher. The farmer selects and breeds individuals that exhibit the most desirable characteristics. This is good practice, because it increases the prevalence of these characteristics in the next generation of the stock. In contrast, the fisher catches large, fast-growing fish, so their desirable characteristics are less likely to be passed on to the next generation of the stock.

Fish that grow quickly tend to be caught sooner and therefore may produce fewer offspring. Fish that delay maturation tend to be caught before they have the chance to reproduce, so the fish that are left to breed are those that mature at a younger age. Fish that limit their current investment in reproduction in order to increase future reproductive success will often be harvested before such savings have a chance to pay dividends. The mortality imposed by fishing can therefore act as a selective force that favours slower growth, earlier maturation, and higher reproductive investment.

Clearly, the selections made by the farmer and the fisher work in opposite directions. The farmer selects desired characteristics that improve his stock, whereas the fisher selects characteristics that may inadvertently reduce a stock’s productivity and resilience. Therefore, fishery scientists need to incorporate both ecological processes and evolutionary processes in their research programmes in order to ensure the best scientific basis for fishery management.

The notion that fishing can affect the genetic composition of exploited populations has been recognized for a century. Perhaps the earliest account can be credited to Cloudsley Rutter (Rutter, 1904), a US salmon biologist, who warned more than a hundred years ago:

[A] stock-raiser would never think of selling his fine cattle and keeping only the runts to breed from. ... The salmon will certainly deteriorate in size if the medium and larger sizes are taken for the markets and only the smaller with a few of the medium allowed to breed.

Yet, it was not until the 1980s that decreasing trends in the age and size at maturation of Northeast Arctic cod and North Sea plaice renewed interest in this topic. In the UK, Richard Law explored the implications of fishery-induced evolution for fishery yields, demonstrating that maturation evolution in response to fishing could reduce productivity (Law and Grey, 1989). In the Netherlands, Adriaan Rijnsdorp (Rijnsdorp, 1993a) analysed changes in maturation, reproductive investment, and growth in North Sea plaice in an attempt to quantify how much of the observed changes in these life-history characteristics were caused by the environment and how much could be attributed to evolution.

In ICES, the topic was discussed at a meeting of the Long-term Management Working Group in 1993, chaired by Kevin Stokes. From 1995 onwards, various working groups were given the task of reviewing the literature in this field. Intensified research, conducted since around 2000, led to theme sessions at the ICES Annual Science Conferences in 2002 and 2006 and the establishment of the ICES Study Group on Fisheries-Induced Adaptive Change (SGFIAC) in 2006. These activities, in turn, attracted more researchers to the field. Reviewing the evidence for fishery-induced evolution and discussing its implications for fishery management,

the first SGFIAC report was summarized as a Policy Forum article in *Science* (Jørgensen *et al.*, 2007).

Observed trends suggestive of fishery-induced evolution. Based on Jørgensen *et al.* (2007) with modifications. Copyright: ICES Insight.



The evidence

The available evidence for fishery-induced evolution stems from three different sources:

- time-series analysis of long-term field data on maturation, reproductive investment, and growth,
- experiments in controlled laboratory environments,
- model-based studies.

The illustration on the first two pages of this article provides an overview of empirical findings suggestive of fishery-induced evolution across species and stocks (based on Jørgensen, *et al.* 2007 with modifications).

A challenge in the analysis of time-series of field data is that observable life-history characteristics are influenced by environment and genetics. It is well known that similar genotypes can give rise to a broad variety of phenotypes, depending on the environment that individuals experience. Trends caused by such phenotypic plasticity have to be taken into account before residual trends can be interpreted as being indicative of genetic changes.

For the process of maturation, therefore, a method has been developed to account for the impacts of growth-related phenotypic plasticity and survival changes (Heino *et al.*, 2002a; Dieckmann and Heino, 2007). In this manner, maturation schedules (called probabilistic maturation reaction norms, or PMRNs) can be estimated that describe the probability of an individual reaching maturation at a given age and size, provided it has grown and survived to that age and size. A shift in the PMRN, summarized by changes in the length-at-age at which the maturation probability reaches 50% (L_{p50}), means that observed maturation trends cannot be explained by growth-related phenotypic plasticity and survival changes alone. If such a change is in line with predictions of life-history evolution (adaptation towards earlier maturation under exploitation), it supports the hypothesis of fishery-induced evolution. Figure 1 shows the trend in L_{p50} for North Sea plaice females at the age of four years.

It should be noted that analyses of long-term field data cannot provide definite proof of evolutionary change, because it is always possible that the observed residual trends may have been caused by additional environmental factors that were not considered. Nevertheless, the broad consistency of observed PMRN trends across a variety of different fish species, stocks, and ecosystems, and the agreement of these trends with the predictions of general life-history theory and of more specific models, makes an evolutionary interpretation likely. Empirical support for fishery-induced evolution in other life-history characteristics, such as reproductive investment and growth, is more ambiguous, partly because the disentangling of phenotypic plasticity and genetics is more complicated.

Definite proof that fishing mortality leads to evolutionary changes comes from studies that manipulated mortality in experimental populations. In the US, David Reznick and colleagues (Reznick *et al.*, 1993) demonstrated that differences in mortality led to differences in genetic life-history traits in guppies. David Conover and colleagues (Conover and Munch, 2002) exposed experimental laboratory populations of Atlantic silversides, a small pelagic species, to different types of size-dependent mortality and demonstrated a variety of genetic responses, as well as associated effects on yields.

Support from model-based studies

Further support for fishery-induced evolution stems from model-based studies. These range from simple age-structured models (e.g. Law and Grey, 1989), to age- and size-structured models that account for growth-related maturation plasticity (Ernande *et al.*, 2004), to eco-genetic models that combine the ecological processes of growth, maturation, reproduction, and survival with the quantitative genetics of the underlying life-history traits (Dunlop *et al.*, 2009).

Although simpler models can help to corroborate expected directions of evolutionary responses to fishing, reliably estimating the pace of such adaptations requires models that are more advanced. To be credible, such models need to do sufficient justice to the ecological and evolutionary complexities of natural stock dynamics, and they should be based as closely as possible on empirical measurements. Models accounting for these requirements can then be used to forecast the direction, speed, and outcome of future fishery-induced evolution, thus revealing the evolutionary implications of current management regimes. Studies of this kind have demonstrated that the selection patterns of current fisheries can indeed lead to fishery-induced evolution over a decadal time-scale and that such changes do affect the productivity of stocks.

The utility of models for studying fishery-induced evolution goes further.

First, models can help us to understand past fishery-induced evolution. In particular, they can provide a means of testing whether or not the observed life-history trends attributed to such adaptation are compatible with the selection pressures imposed by the life cycle of a stock and the fishing regime.

Second, fishery managers can use the information provided by models to support decisions regarding the prioritization of regulations and research. Specifically, a stock's evolutionary vulnerability differs with its current life history, the life-history trends that it may already have undergone, the amount of genetic variation that it currently harbours, and the detailed characteristics of its current fishing regime. These contingencies limit the value of one-size-fits-all models of fishery-induced evolution and, instead, underscore the importance of developing stock-specific models.

Third, and perhaps most importantly, models of fishery-induced evolution can assist fishery scientists and managers in the investigation of the evolutionary implications of alternative management scenarios. As changes in yield and sustainability depend on a complex interplay of life-history trends induced by fishing, responsible forecasts will often have to be model-based. In this regard, advanced models can be likened to flight simulators, allowing safe tinkering with a modelled stock, which would be far too costly or dangerous to implement without prior model-aided assessments.

The good news and bad news

Fishery-induced evolution is adaptation fishing, and the better adapted the fish, the more progeny it is likely to produce. This sounds positive, at least from the perspective of the fish, but it is not always the case.

An increased avoidance of fishing gear among fish can be regarded as an evolution-aided “escape” from fishing. The evolution of reduced adult body size can also be seen from this perspective because fish below the minimum legal landing size are typically less attractive fishing targets.

In contrast, fishery-induced evolution of traits such as maturation schedules can be interpreted as a means of coping with the inevitable: the primary effect of such changes is not a diminished exposure to fishing but the increased production of offspring under conditions of fishing.

In both cases, fish stocks that have adapted to fishing through evolution can be expected to be more resilient to fishing than those lacking such adaptations. This prediction is supported by recent model-based studies: fishery-induced adaptation allows populations to sustain greater fishing pressures than would be possible without such adaptation (see for example Heino, 1998; Enberg *et al.*, 2009).

The advantage of enhanced resilience, however, comes at a cost.

First, stocks that become better adapted to fishing usually do so at the expense of becoming less well adapted to their “natural” environment. In particular, populations may become less resilient to long-term variations in their environment. For example, a long lifespan is usually interpreted as an adaptation to unpredictable variations in recruitment success, but fisheries favour individuals that live fast and die young, as illustrated in Figure 2.

Second, theoretical and empirical studies suggest that the effects of fishery-induced evolution on fishing yields are largely negative. Total biomass yield usually declines when fish redirect the investment of energy from body growth into reproduction. Consequently, a greater proportion of the catch will consist of small, and therefore less valuable, fish.

Third, fish that are forced to reproduce early in life often do so less successfully than their older conspecifics, making the same spawning stock size less valuable in terms of the stock’s reproduction. For these reasons, fishery managers will often want to minimize fishery-induced evolution.

Turning it around

What options are there for slowing or reversing unwanted fishery-induced evolution? Possible solutions fall into two categories.

First, reducing fishing effort, while keeping its selectivity unchanged, will almost certainly help to slow the pace of fishery-induced evolution. If the reduction is large enough, and conditions are especially favourable, the unwanted evolution might even be reversed. A reduction in fishing effort is often compatible with more traditional management goals: many fish stocks are overexploited, so, in the long term, reduced exploitation is likely to generate higher yields with lower costs and emissions and reduced ecosystem effects.

Second, changing the selectivity of fishing mortality is more likely to stop or reverse fishery-induced evolution, because – in principle – it allows fishery managers to fine-tune selection

pressures so as to achieve this. Models are currently being developed to support fishery scientists and managers in accomplishing this task.

A conceptually straightforward approach would be to make the size selectivity of fishing mortality similar to that of natural mortality. However, this simple strategy usually has two disadvantages.

First, when the size selectivity of fishing mortality matches that of natural mortality, the extra mortality resulting from fishing will continue to cause fishery-induced evolution. (At this point, it is helpful to recall that fully size-independent mortality still induces selection pressures, because such uniform mortality still devalues reproduction late in life.)

Second, as natural mortality is typically much greater for small fish than large fish, changing fishing selectivity to match such a pattern is liable to cause recruitment overfishing, which undermines yields.

Therefore, fishery managers need to adjust fishing selectivity in order to minimize fishery-induced evolution for traits that are considered important without sacrificing too much yield. How best to achieve this must be evaluated on a case-by-case basis, which will usually require the investigation of stock-specific models.

As long as some sacrifices are made, slowing down unwanted fishery-induced evolution is relatively straightforward. Reversing it is another matter. This is because reverse evolution would often have to rely on natural selection. Law and Grey (1989) have already suggested that natural selection for delayed maturation is relatively weaker than fishery-induced selection for earlier maturation.

This idea was corroborated by recent, more realistic models (Dunlop *et al.*, 2009; Enberg *et al.*, 2009), which demonstrate that the rate of evolutionary recovery is much lower than the rate of fishery-induced evolution. In other words, evolutionary “damage” usually occurs much faster than it can be repaired. Model results suggest that, for each year during which current exploitation patterns continue, several years of evolutionary recovery, under the best of conditions, may be required; this implies the build-up of a “Darwinian debt” that will have to be repaid by future fishers and consumers.

Given the social and political difficulties encountered when trying to implement major changes to current exploitation patterns, fishery-induced evolution could essentially be irreversible on time-scales that are of interest to fishery management (from years to a few decades). It seems self-evident that this observation should trigger the attention of managers subscribing to the precautionary approach to fisheries.

Looking forward

Despite the fact that evolutionary theory has been the cornerstone of biology since the publication of *On the Origin of Species* 150 years ago, the implications of Darwin’s dangerous idea for fishery science have sparked a lively debate (Hilborn, 2006; Marshall and Browman, 2007; Kuparinen and Merilä, 2008). This debate does not so much question whether or not fishery-induced evolution occurs, but focuses on the strength of the empirical evidence and on the expected rate of fishery-induced evolution.

Although there may be some residual scepticism within the community of fishery scientists, and although the practical implications of fishery-induced evolution have yet to be examined more closely, the evidence supporting the likely and widespread occurrence of fishery-induced evolution has become sufficiently strong that fishery scientists and managers can no longer ignore the evolutionary dimension of fisheries.

This conclusion agrees with the precautionary approach to fisheries (FAO, 1995), which prescribes the exercise of

...prudent foresight to avoid unacceptable or undesirable situations, taking into account that changes in fisheries systems are only slowly reversible, difficult to control, not well understood, and subject to change in the environment and human values.

This approach also requires managers of over-utilized fisheries to

...take immediate short-term action even on the basis of circumstantial evidence about the effectiveness of a particular measure.

In the long term, evidence for fishery-induced evolution is likely to be strengthened by modern genetic techniques based on the extraction and analysis of DNA sequences from historical otoliths or scales. Such approaches can document and quantify changes in gene frequencies over periods of several decades. In particular, changes in genes that are linked to life-history processes, such as growth, maturation, and reproduction, will be of interest. This does not mean, however, that we can expect to obtain definite proof of fishery-induced evolution by applying such techniques, because changes in gene frequencies may be caused either by fishery selection or by selection that is the result of other environmental factors, such as climate change.

Accordingly, the conclusive attribution of causal interpretations to correlative evidence is practically impossible for uncontrolled field observations, such as those obtained from fisheries. In addition, current knowledge of the full genetic underpinning of complex life-history processes, such as maturation, remains woefully incomplete. Therefore, for most species and stocks, it seems safe to assume that fishery scientists and managers must continue to rely on correlative phenotypic evidence for fishery-induced evolution for the next decade, if not longer. Mitigating actions cannot be postponed that long.

Reflecting on the considerations above, we propose three courses of action.

First, the monitoring of salient life-history characteristics, such as growth rates, maturation schedules, and reproductive investments, should be integrated into routine stock assessments.

Second, stock-specific models need to be developed and calibrated that take into account the genetics as well as the ecological processes involved in the dynamics of the stock under exploitation.

Third, such calibrated stock-specific models should be used to explore and evaluate the implications of alternative patterns of fishery selection on the life history, productivity, and resilience of stocks.

This calls for close collaboration between life-history modellers and fishery scientists who assemble data and give management advice. We expect that case studies integrating the three components recommended here – life-history monitoring, model calibration, and strategy evaluation – will provide useful examples of how fishery management can develop its long overlooked evolutionary dimension.

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Box 1: Effects of fishery-induced evolution on reference points

Biological reference points quantify limits between desirable and undesirable states in fishery systems. Typically, reference points describe either the status of a stock (e.g. spawning-stock biomass) or the pressure exerted on it (e.g. fishing mortality). To account for uncertainty, reference points are often set on a precautionary basis. Good reference points are insensitive to short-term variability of a fishery system, but may require adjustment when long-term changes in a fish stock or its fishery are occurring, e.g. as a result of climate change.

The ICES Study Group on Fisheries-Induced Adaptive Change (SGFIAC) is preparing an article titled “Can fisheries-induced evolution shift reference points for fisheries management?”, which explores the different routes through which fishery-induced evolution may affect reference points: by biasing the estimation of indicators on which reference points are based (e.g. by biasing SSB estimates) and/or by changing a stock’s dynamics (e.g. by changing the SSB–recruitment relationship). As a result of changes along either route, a reference point might become more precautionary than intended – a safe mistake. More troubling, fishery-induced evolution might also covertly shift a reference point in the direction of danger, thereby causing a false sense of safety. Which outcome is more likely depends on the considered reference point and on particulars of the fish stock and its fishery.

Box 2: Evolutionary impact assessment

Fishery-induced evolution may change the utility of fish stocks, e.g. by altering utility components such as fishery yields, stock stability, recovery potential, trophic interactions, geographical distributions, genetic diversity, touristic benefits, and the intrinsic values of species and ecosystems. Such changes modify the ecosystem services through which living aquatic

resources provide value to society. Therefore, quantifying and characterizing the evolutionary effects of fishing is important for both economic and ecological reasons.

The ICES Study Group on Fishery-Induced Adaptive Change (SGFIAC) is preparing an article titled “Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fishery management”, which describes evolutionary impact assessment (EvoIA; Jørgensen *et al.* 2007) as a set of methods for assessing the evolutionary consequences of fishing and for evaluating the merits of alternative management options. EvoIAs (i) contribute to the ecosystem approach to fishery management by clarifying how evolution alters stock properties and ecological relations, (ii) support the precautionary approach to fishery management by addressing a previously overlooked source of uncertainty and risk, and (iii) help realize the Johannesburg summit’s commitment to the restoration of sustainable fisheries by assisting fishery managers to cope with the evolutionary implications of fishing.

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Figures

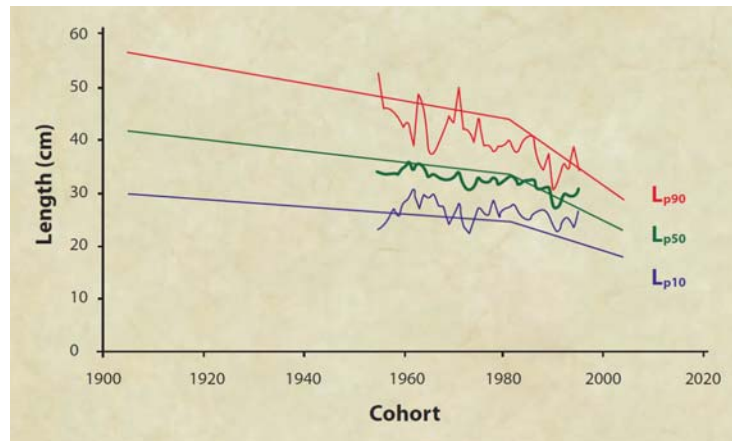


Figure 1. Changes in the probabilistic maturation reaction norm (PMRN) of female North Sea plaice at the age of 4 years. The figure shows how the body lengths at which female plaice of this age mature have dropped precipitously throughout the 20th century (blue curves, 10% probability; green curves, 50% probability; red curves, 90% probability). Based on Grift *et al.* (2003; jagged curves) and van Walraven *et al.* (2009; straight curves). Copyright: *ICES Insight*.

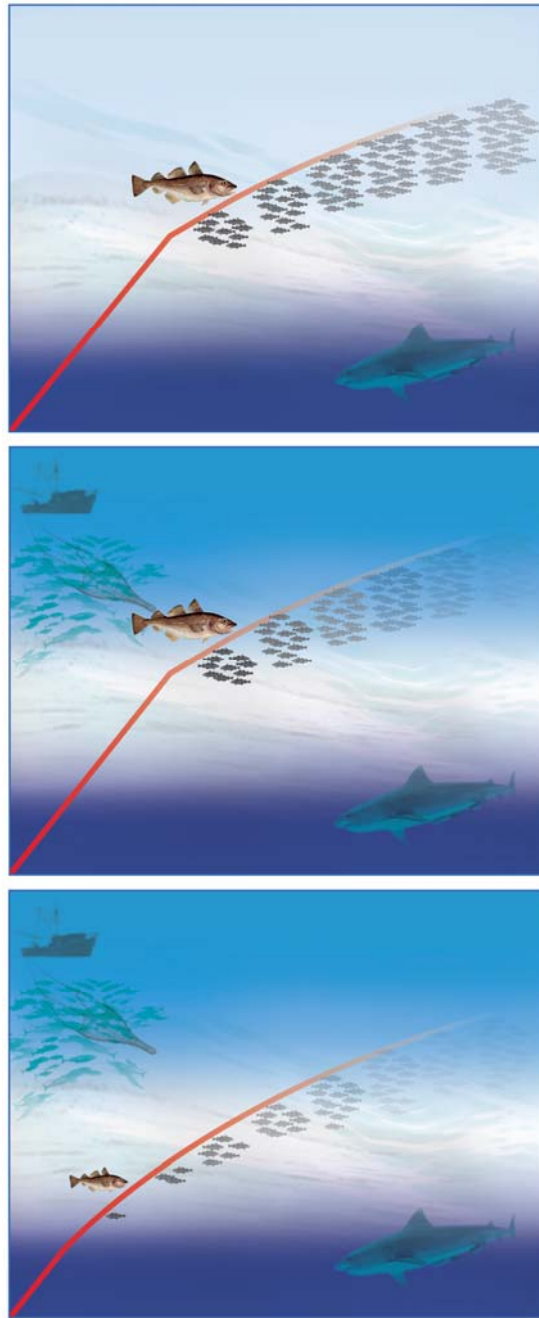


Figure 2. The timing of maturation has a large influence on the size of females spawning for the first time (illustrated by the large fish above the red growth curves) and their expected reproductive success. The latter is determined by two components, relative clutch size (illustrated by clutches becoming larger as females grow) and probability of surviving to produce a clutch (illustrated by the fading colour of clutches). Which maturation age is evolutionarily favoured depends on natural mortalities and fisheries mortalities (illustrated by gradients at the bottom and top of each panel). (a) In the absence of fishing, large fish face little mortality. Under such conditions, delayed maturation and growth to a large size are advantageous. Fishing turns this situation around by targeting large fish. (b) Fish that delay maturation end up trying to reproduce at ages when they are at high risk of having been fished. (c) Fish that reproduce early and invest their resources into reproduction instead of growth are favoured by fisheries-induced selection.