The dawn of Darwinian fishery management

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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 (Figure 5.1). 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 or her 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 recognised for more than a century. Perhaps the earliest account can be credited to Cloudsley Rutter (1903), 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

Figure 5.1 The timing of maturation has a considerable influence on the size of females spawning for the first time (illustrated by the large fish above the growth curves) and

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 late 1970s that the issue of fisheries-induced evolutionary change started to attract serious attention. This was the time when life-history theory emerged as an independent branch of evolutionary ecology, recognising the power of mortality in shaping life histories (Stearns, 1977). A number of scientists noticed that exploited fish populations often showed life-history changes that were suggestive of mortality-induced evolution. For example, Handford *et al.* (1977) suggested that fisheries on lake whitefish (*Coregonus clupeaformis*) from Lesser Slave Lake, Canada, had favoured slower growth, and Borisov (1978) highlighted that intensive fishing of Northeast Arctic cod (*Gadus morhua*) could practically eliminate late-maturing genotypes from the population. Ricker (1981) analysed maturation data from several species of Pacific salmon and concluded that, at least for pink salmon (*Oncorhynchus gorbuscha*), the decreasing trend in length at maturation was likely to be a genetic response to selective fisheries. In a series of studies, Beacham (1983a, 1983b, 1983c, 1983d, 1983e, 1983f) reported large declines in age and length at maturation for a range of commercially important fish species in Canadian waters, but also noted that it was not possible to disentangle environmental and evolutionary influences in those changes. This challenge was taken up by Rijnsdorp (1993), who analysed changes in maturation, reproductive investment and growth in North Sea plaice (*Pleuronectes platessa*) in a first systematic attempt to quantify how much of the observed change in these life-history characteristics was caused by the environment and how much could be attributed to evolution. Amplifying concerns about the practical implications of fisheries-induced adaptations, Law and Grey (1989) used a theoretical model to show that maturation evolution in response to fishing could significantly reduce the productivity of fish populations.

Caption for Figure 5.1 (*cont.*) 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 and fishery mortalities (illustrated by gradients at the bottom and top of each panel). Top: 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. Centre: Fish that delay maturation end up trying to reproduce at ages when they are at high risk of having been fished. Bottom: Fish that reproduce early and invest their resources in reproduction instead of growth are favoured by fisheries-induced selection. For colour version, see plate section.

Efforts during the early years of Darwinian fisheries science culminated in the conference 'The exploitation of evolving resources' in 1991, resulting in an edited volume with the same title (Stokes *et al.*, 1993). The case for further consideration of the topic was clearly established. Since the early 1990s, fisheries-induced evolution has been discussed in several working groups of ICES, the International Council for the Exploration of the Sea, charged with providing scientific advice on fisheries in the Northeast Atlantic. Research activities have intensified since around 2000, resulting in dedicated theme sessions at the ICES Annual Science Conferences and in establishment of the ICES Study Group on Fisheries-Induced Adaptive Change. These fora, in turn, attracted more researchers to the field. Reviewing the evidence for fisheries-induced evolution and discussing its implications for fishery management, the ICES Study Group produced a Policy Forum article in the journal *Science* to call attention to the need for including evolutionary considerations in fishery management (Jørgensen *et al.*, 2007).

The main issues

The available evidence for fisheries-induced evolution stems from three different sources, which the next three sections will review in turn:

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

Support from field studies

The examples in Table 5.1 provide an overview of field-based observations suggestive of fisheries-induced evolution across species and stocks in both marine and freshwater systems across the world. While this overview comprises studies in which the original authors have highlighted fisheries-induced evolution as a plausible explanation for the reported changes or for interpopulation differences in life history and behaviour, this does not necessarily imply that fisheries-induced evolution was the most important or plausible explanation for the observed patterns.

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 example,

Table 5.1 Overview of case studies in which fisheries-induced evolution has been proposed as one factor explaining temporal changes in single populations subject to fishing, or differences between populations subject to contrasting fishing regimes. PMRN, probabilistic maturation reaction norm. Based on Jørgensen et al. (2007), with updates and modifications.

Species	Change	Population or area	Reference
Herrings (order Clupeiformes)			
Atlantic herring *Clupea harengus*	PMRN shift towards younger ages and smaller sizes, maturation at younger age and smaller size	Norwegian Sea, Newfoundland	Engelhard and Heino, 2004; Wheeler et al., 2009
Carps (order Cypriniformes)			
Common carp *Cyprinus carpio carpio*	Maturation at younger age, leaner body, higher viability, higher escapement	Aquaculture lineages, China and Europe	Wohlfarth et al., 1975
Marine smelts (order Argentiniformes)			
Larger argentine *Argentina silus*	Maturation at smaller size	Scotian Shelf, Northwest Atlantic	Beacham, 1983a
Salmons (order Salmoniformes)			
Lake whitefish *Coregonus clupeaformis*	Maturation at lower condition, reduced annual growth, decreased condition	Lesser Slave Lake, Alberta, Canada	Handford et al., 1977
Common whitefish *Coregonus lavaretus*	Reduced annual growth, increased reproductive effort	Lake Constance, Germany/ Switzerland/Austria	Thomas and Eckmann, 2007; Thomas et al., 2009
Alpine whitefish *Coregonus palaea*	Reduced annual growth	Lake Joux, Switzerland	Nusslé et al., 2009

Table 5.1 (cont.)

Species	Change	Population or area	Reference
Grayling *Thymallus thymallus*	Maturation at younger age and smaller size	Lakes in Norway	Haugen and Vøllestad, 2001
Atlantic salmon *Salmo salar*	Reduced annual growth, later smolting, lower sea age	Godbout River, Quebec, Canada; rivers in Spain	Bielak and Power, 1986; Consuegra et al., 2005; Saura et al., 2010
Brook trout *Salvelinus fontinalis*	Maturation at younger age, smaller size, and lower condition	Lakes in Canada	Magnan et al., 2005
Coho salmon *Oncorhynchus kisutch*	Maturation at smaller size, reduced annual growth	British Columbia, Canada	Ricker, 1981, 1995
Pink salmon *Oncorhynchus gorbuscha*	Maturation at smaller size, reduced annual growth	British Columbia, Canada	Ricker, 1981, 1995
Sockeye salmon *Oncorhynchus nerka*	Earlier run time	Bristol Bay, USA	Quinn et al., 2007
Chum salmon *Oncorhynchus keta*	PMRN shift towards smaller sizes	Hokkaido, Japan	Fukuwaka and Morita, 2008
Pikes (order Esociformes)			
Pike *Esox lucius*	Reduced annual growth	Lake Windermere, UK	Carlson et al., 2007; Edeline et al., 2007

Species	Observed changes	Location	References
Cods (order Gadiformes)			
Atlantic cod *Gadus morhua*	Maturation at younger age and smaller size, PMRN shift towards younger ages and smaller sizes, maturation at lower condition, reduced annual growth, increased reproductive effort	Baltic Sea, North Sea, west coast of Scotland, Barents Sea, Iceland, Northern cod, southern Grand Bank, St. Pierre Bank Scotian Shelf, southern Gulf of St Lawrence, Georges Bank, Gulf of Maine	Beacham, 1983c, 1983d; Jørgensen, 1990; Cardinale and Modin, 1999; Heino et al., 2002a; Barot et al., 2004; Olsen et al., 2004, 2005; Yoneda and Wright, 2004; Baulier, 2009; Pardoe et al., 2009; Vainikka et al., 2009; Swain, 2011
Haddock *Melanogrammus aeglefinus*	Maturation at younger age, PMRN shift towards smaller sizes, reduced adult size, increased reproductive effort	North Sea, southern Grand Bank, Scotian Shelf	Templeman et al., 1978; Beacham, 1983f; Wright et al., 2011; Neuheimer and Taggart, 2010
European hake *Merluccius merluccius*	Reduced annual growth	Balearic Islands	Hidalgo et al., 2009
Perches (order Perciformes)			
Bluegill *Lepomis macrochirus*	Maturation at younger age	Lakes in Minnesota, USA	Drake et al., 1997
Red porgy *Pagrus pagrus*	Maturation at younger age and smaller size	South Atlantic Bight	Harris and McGovern, 1997
Yellow croaker *Larimichthys polyactis*	Maturation at smaller size	Yellow Sea	Dieckmann et al., 2005
Flatfishes (order Pleuronectiformes)			
American plaice *Hippoglossoides platessoides*	Maturation at younger age and smaller size, PMRN shift towards younger ages and smaller sizes	Newfoundland–Labrador, St Pierre Bank, Grand Bank, southern Gulf of St Lawrence, Scotian Shelf	Beacham, 1983e; Barot et al., 2005

Table 5.1 (cont.)

| Species	Change	Population or area	Reference
Plaice *Pleuronectes platessa*	Maturation at younger age and smaller size, PMRN shift towards younger ages and smaller sizes, increased reproductive effort	North Sea	Rijnsdorp, 1989, 1991, 1993; Grift *et al.*, 2003, 2007; Rijnsdorp *et al.*, 2005; van Walraven *et al.*, 2010
Witch flounder *Glyptocephalus cynoglossus*	Maturation at younger age and smaller size	Southern Gulf of St Lawrence, Scotian Shelf	Beacham, 1983b
Yellowtail flounder *Limanda ferruginea*	Maturation at younger age and smaller size	Southern Gulf of St Lawrence, Scotian Shelf	Beacham, 1983e
Sole *Solea solea*	PMRN shift towards younger ages and smaller sizes	North Sea	Mollet *et al.*, 2007
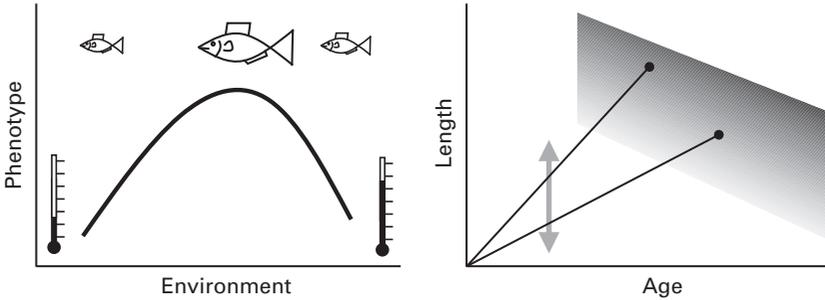
Figure 5.2 Reaction norms describe how a single genotype can give rise to different phenotypes, depending on the environment. The left panel illustrates a typical univariate reaction norm describing how the expressed phenotype varies as a function of the environment it experiences, here adult body size as a function of ambient temperature. The right panel shows a probabilistic maturation reaction norm (PMRN). A PMRN describes an individual's probability to mature as a function of its age and size; it may also account for additional explanatory variables (Heino *et al.*, 2002b). Increasing maturation probability is depicted by darkening shades of grey. Individuals will typically mature once their growth trajectories 'hit' the PMRN, i.e. when their combination of age and size confers a significant maturation probability. In PMRNs, the environment does not vary along the horizontal axis; instead, different growth environments result in different sizes at a given age (as indicated by the vertical grey arrow: a good growth environment implies faster growth, and therefore a larger size at a given age).

while fishing usually favours evolution towards earlier maturation, a number of other mechanisms may produce similar trends. First, fishing may induce a phenotypically plastic change in maturation. When fishing causes population size to decline, individual growth often accelerates, because the remaining individuals have more resources to feed on. Faster growth, in turn, enables earlier maturation. Second, increased mortality will cause a population's mean age at maturation to decline as a direct demographic response, simply because fewer old fish can be sampled when surveying the stock. Thus, fishing can result in earlier maturation through three different mechanisms: demographic, plastic and evolutionary.

To disentangle the contributions of demographic response, phenotypic plasticity, and evolutionary change, 'reaction norms' play a central role. A reaction norm describes the pattern of phenotypic expression of a single genotype, or of a population of genotypes, across a range of environments. Typically, a reaction norm is presented as a graph where the environment varies along the horizontal axis and the corresponding phenotypic values are shown on the vertical axis (Figure 5.2). For describing plasticity in the process of maturation, however, a different representation is often more useful: the reaction norm for age and size at maturation describes the combinations of

ages and sizes at which an individual will become mature, with variability in size at a given age reflecting environmentally induced variability in growth (Figure 5.2). Therefore, maturation reaction norms account for the majority of growth-induced variations in maturation and therefore help disentangle environmental and genetic influences on maturation (Stearns and Crandall, 1984; Heino *et al.*, 2002b; Dieckmann and Heino, 2007).

Methods have been developed to estimate maturation reaction norms from data that are routinely collected for many commercial fish stocks (summarised in Heino and Dieckmann, 2008). These methods acknowledge that the maturation process is not fully deterministic, and therefore results in the estimation of probabilistic maturation reaction norms (PMRNs; Heino *et al.*, 2002b). A PMRN describes the probability of an individual maturing at a given age and size, provided it has grown and survived to that age and size. A shift in the PMRN is often summarised by changes in the length at which the maturation probability reaches 50% at a given age (with such a length being referred to as the reaction-norm midpoint, L_{p50}, for that age). A PMRN shift means that observed maturation trends cannot be explained by growth-related phenotypic plasticity and survival changes alone. Furthermore, if such a residual change is in line with predictions of life-history evolution (adaptation towards earlier maturation under exploitation), it supports the hypothesis of fisheries-induced evolution. Figure 5.3 shows the trend in the reaction-norm midpoint for female North Sea plaice (*Pleuronectes platessa*) at the age of four years.

We emphasise 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 environmental factors that were not considered. For example, the maturation process will often be influenced also by other factors, such as temperature. Hence, the maturation probability of two fish that are identical in their PMRNs and growth trajectories, but have experienced different temperature environments, will likely be different. While, data permitting, the PMRN approach can readily be extended by including other environmental variables (e.g. Grift *et al.*, 2007), one can never be sure that all relevant environmental variables have been included. 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 increasingly plausible (Heino and Dieckmann, 2008). Empirical support for fisheries-induced evolution in other life-history characteristics, such as reproductive investment and growth, is more ambiguous, in large part because disentangling of phenotypic plasticity and evolutionary changes is more complicated for these traits, as techniques analogous to PMRN estimation are not yet widely applied.
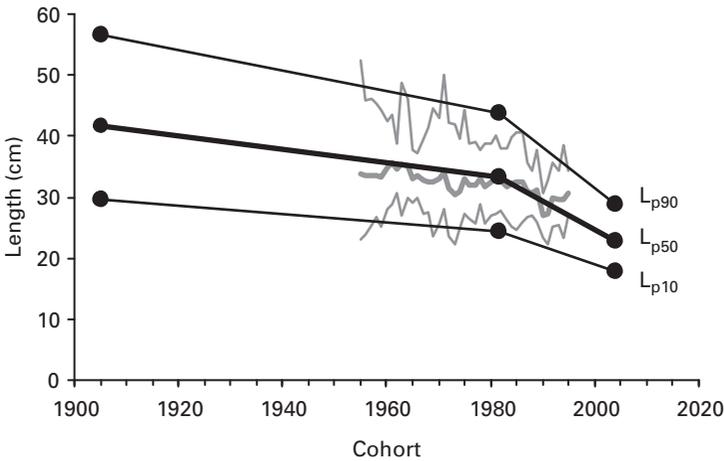
Figure 5.3 Changes in the probabilistic maturation reaction norm (PMRN) of female North Sea plaice at the age of 4 years. The figure shows how the body lengths at which female plaice of this age mature have dropped precipitously throughout the twentieth century. The thick curves indicate the length at which maturation probability is 50% (the reaction norm midpoint, L_{p50}), and the thin curves show the maturation envelope (between L_{p10} and L_{p90}) in which maturation probability increases from 10 to 90%. Based on Grift *et al.* (2003; grey curves) and van Walraven *et al.* (2010; black curves).

Support from laboratory studies

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 and Bryga, 1987; Reznick *et al.*, 1990) demonstrated that differences in mortality led to differences in genetic life-history traits in guppies (*Poecilia reticulata*): introductions of guppies from sites with high predation on adults into sites with low predation on adults led to rapid evolution towards later maturation, and common-garden experiments could confirm that these changes were genetic. David Conover and colleagues (Conover and Munch, 2002; Walsh *et al.*, 2006) exposed experimental laboratory populations of Atlantic silversides (*Menidia menidia*), a small coastal species, to different types of size-dependent mortality and demonstrated a variety of genetic responses, as well as associated effects on yields. Importantly, Conover and Munch (2002) could show that harvesting the largest silversides (akin to the commercial fisheries of many stocks) led to marked reductions in genetic growth rates within just four generations, and that this change was associated with significant decreases in the size of harvested fish and their total biomass.

Support from model-based studies

Further support for fisheries-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 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 fisheries-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 fisheries-induced evolution over a decadal time scale and that such changes do affect the productivity of stocks. For example, Dunlop *et al.* (2009) developed a model for Atlantic cod (*Gadus morhua*) showing that intensive harvesting could lead to large changes in the population's life history within just a few generations. These changes were most striking for maturation, followed by body growth, whereas reproductive effort changed only a little.

The utility of models for studying fisheries-induced evolution goes further. First, models can help us to understand past fisheries-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 prioritisation of regulations and research. Specifically, a stock's evolutionary vulnerability depends on 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 fisheries-induced evolution and, instead, underscore the importance of developing stock-specific models. Third, and perhaps most importantly, models of fisheries-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.

Northeast Arctic cod has been a test bed for model-based assessments of fisheries-induced evolution and its management. Law and Grey (1989) pointed out that the change in exploitation from a spawner fishery in the first half of the twentieth century to a predominantly feeder fishery in the second half of the century has led to a dramatic change in selection pressures on the timing of maturation. While the historical fishing pattern favoured delayed maturation, modern fishing favours early maturation, in qualitative agreement with the maturation trends observed for this stock. Later studies have tried to evaluate whether the observed rate of change in maturation reaction norms is compatible with the stock's exploitation history (Eikeset, 2010; Eikeset *et al.*, in prep.). In addition, Jørgensen *et al.* (2009) have assessed how different gear types influence evolutionary change, concluding that gillnets with bell-shaped size-selection might offer a more robust way than trawls of maintaining relatively high yields without causing too much evolution.

Resilience and productivity

Fisheries-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 important to recognise that such adaptations do not necessarily, or even typically, lead to enhanced resilience and productivity. For example, an increased awareness and avoidance of fishing gear among fish can be regarded as an evolution-aided 'escape' from fishing and implies reduced productivity. The evolution of reduced adult body size can also be interpreted from this perspective: fish below a stock's minimum legal landing size are less attractive fishing targets, again reducing the stock's productivity. In contrast, fisheries-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 off-spring under conditions of fishing. Whether fisheries-induced maturation evolution leads to enhanced or diminished fishing yields, therefore, is an open question that can only be addressed by examining specific stocks.

Independently of whether evolutionary adaptations serve to enable fish to escape or cope with fishing, 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: fisheries-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). For example, Northeast Arctic cod currently spawn for the first time at the age of about 7 years, whereas during the 1930s the first spawning occurred at the age of 9–10 years (Heino *et al.*, 2002a). During recent decades, less than 10% of 7-year-old cod survive until the age of 10 years, and it is therefore likely that the stock would have collapsed in the absence of the fisheries-induced evolution that has presumably occurred during the past 70 years.

However, the advantage of enhanced resilience to fishing 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 environmental conditions. For example, a long lifespan is usually interpreted as an adaptation to unpredictable variations in recruitment success (Longhurst, 2002), but fisheries favour individuals that live fast and die young, as illustrated in Figure 5.1. Second, theoretical and empirical studies suggest that the effects of fisheries-induced evolution on fishing yields are largely negative. The total fished biomass usually declines when fish redirect their investment of energy from body growth to 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 minimise fisheries-induced evolution.

Mitigating fisheries-induced evolution

What options are available for slowing or reversing unwanted fisheries-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 fisheries-induced evolution. If the reduction is large enough, and conditions are otherwise favourable, the unwanted evolution might even be reversed. Importantly, 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 can potentially generate higher yields – with lower costs and emissions, as well as reduced ecosystem effects.

Second, the selectivity of fishing mortality could be changed in order to stop or reverse fisheries-induced evolution. In principle, fishery managers could regulate the permitted fishing methods and gears so as to fine-tune

selection pressures to achieve this. For example, if selectively fishing the largest fish was the main culprit for unwanted life-history evolution, protecting the largest fish (at the expense of medium-sized ones) could mitigate the problem. However, the possibilities for tinkering with fishing selectivity are limitless, and it is usually impossible to see *a priori* which solutions would be most practical and effective. Stock-specific models are needed to address such challenges, and are currently being developed to help fishery scientists and managers accomplish this task.

A conceptually straightforward approach would be to make the size selectivity of fishing mortality similar to that of natural mortality (Etnier and Fowler, 2010). 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 fisheries-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 smaller fish than for larger fish, changing fishing selectivity to match such a pattern is liable to cause recruitment overfishing, which undermines fishing yields. Therefore, fishery managers need to adjust fishing selectivity in order to minimise fisheries-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 sufficient sacrifices are made, slowing down unwanted fisheries-induced evolution is relatively straightforward.

Reversing unwanted fisheries-induced evolution is another matter. This is because reverse evolution would often have to rely on natural selection. Law and Grey (1989) had suggested that natural selection for delayed maturation is relatively weaker than fisheries-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 fisheries-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, fisheries-induced evolution could essentially be irreversible on timescales 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; Browman *et al.*, 2008; Kuparinen and Merilä, 2008; Andersen and Brander, 2009). This debate does not so much question whether fisheries-induced evolution occurs, but focuses on the strength of the empirical evidence and on the expected rate of fisheries-induced evolution. Although there may be some residual scepticism within the community of fishery scientists, and although the practical implications of fisheries-induced evolution have yet to be examined more closely, the evidence supporting the likely and widespread occurrence of fisheries-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, 1996), 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-utilised fisheries to 'take immediate short-term action even on the basis of circumstantial evidence about the effectiveness of a particular measure'.

Evidence for fisheries-induced evolution is soon 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 fisheries-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 fisheries-induced evolution for years to come. Mitigating actions cannot be postponed that long.

Conclusions

Fisheries-induced evolution is likely to be widespread and can negatively impact the utility of fish populations for humans. The first step in reducing unwanted fisheries-induced evolution can be remarkably simple: fishing less will almost always reduce unwanted evolution. Often such action is fully compatible even with fishery management that is blind to evolution: overfished stocks can produce higher yields at lower costs if they are allowed to recover, and fishing less will moreover reduce the unwanted ecological side-effects of fishing.

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

- First, we encourage fishery managers to maintain fishing pressures at precautionary levels, or whenever applicable, reduce fishing pressure to such levels.
- Second, the monitoring of salient life-history characteristics, such as growth rates, maturation schedules and reproductive investments, should be integrated into routine stock assessments.
- Third, 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. Such calibrated stock-specific models should then be used to carry out evolutionary impact assessments (Box 5.1) to explore and evaluate the implications of alternative patterns of fishery selection on the life history, resilience and productivity 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.

Acknowledgements

Box 5.1 Evolutionary impact assessment

Fisheries-induced evolution may change the utility of fish stocks, by altering utility components such as fishing yields, stock stability, recovery potential, trophic interactions, geographical distributions, genetic diversity, benefits to tourism, and the intrinsic values of species and ecosystems (Jørgensen *et al.*, 2007). Such changes modify the ecosystem services through which living aquatic resources provide value to society. Therefore, quantifying and characterising the evolutionary effects of fishing are important for both economic and ecological reasons.

Evolutionary impact assessment (EvoIA; Jørgensen *et al.*, 2007) is a set of methods for assessing the evolutionary consequences of fishing and for evaluating the merits of alternative management options. Evolutionary impacts must always be assessed against some baseline levels. In a retrospective (or backward-looking) EvoIA, this baseline would ideally be the pristine stock, before its characteristics were changed by fisheries-induced evolution (if such evolution has occurred). However, usually data are insufficient to describe pristine stocks, so that the assessment would instead need to start from whenever systematic data collection started, hopefully during the early stages of exploitation. The goal will be to assess how life-history characteristics, fishing yields and other utility components have been changed by fisheries-induced evolution.

A prospective (or forward-looking) EvoIA will usually compare alternative management actions. Such an analysis will typically proceed in two main steps. The first describes how alternative management actions lead to trait changes. The considered management actions will usually include, as a baseline, those conditions that are implied by 'business as usual', i.e. that result from not changing the current management regime. The second step addresses how trait changes affect the stock's utility to society, e.g. in terms of sustainable fishing yields. Carrying out a forward-looking EvoIA requires predicting future evolution, which is possible only with relatively complex models that have been calibrated to specific stocks. Eco-genetic models (Dunlop *et al.*, 2009) have been designed to offer a suitable framework for such tasks.

Research. Figure 5.3 is reproduced from van Walraven *et al.* (2010), Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (*Pleuronectes platessa* L.). *Journal of Sea Research* **64**:85–93, with kind permission from Elsevier.

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