SELECTIVE FISHING AND PHENOTYPIC EVOLUTION: 
PAST, PRESENT 
AND FUTURE 

Richard Law 

Biology Department, University of York, York, YO10 5YW, United Kingdom 

ABSTRACT 
There is accumulating evidence for genetic change caused by fishing. Selection differentials generated by fishing are detectable within year classes in certain major exploited stocks. Breeding experiments in the aquaculture industry demonstrate the existence of genetic variation in production-related traits. Genetic change in growth rates due to fishing has been found in experimental systems. There is evidence that changes in maturation taking place in fish stocks have a genetic component. This paper is therefore a call for action on the part of fisheries science to adopt a precautionary approach to fishing-induced evolutionary change, and to develop a Darwinian perspective to fisheries management. 

INTRODUCTION 
To an evolutionary biologist, fisheries around the world appear to be a theatre in which large scale selection experiments are being played out. The actors are first the fishery managers who set patterns of selection through regulations such as net mesh size and catch quotas, second the fishers who apply the selective mortality, and third the fish stocks that undergo genetic change due to selection caused by fishing. 

The selection experiment is well known to fisheries biologists (Pitcher and Hart 1982; Nelson and Soulé 1985; Stokes et al. 1993; Trippel 1995; Law 2000; Ratner and Lande 2001; Heino and Godø 2002). However, there are so many other urgent problems facing fisheries that evolutionary consequences of fishing have not been prioritised. Factors contributing to this low priority have been the relatively small amount of additive genetic variation associated with the phenotypic traits most likely to be under selection, and lack of information on the strength of selection that fishing can generate. Also it has been difficult to show beyond doubt that changes taking place in exploited fish stocks are genetic as opposed to compensatory changes (phenotypic plasticity) in growth due to fishing or changing abiotic conditions. 

However, evidence is accumulating that heavy exploitation of fish stocks causes them to undergo genetic change. The consequences of such change are important in the medium- and long-term because some of the traits under selection (e.g. growth and sexual maturation) are closely connected to productivity of fisheries. By ignoring genetic change, we run the risk of reducing productivity in ways that are not readily reversed in the future. Arguably the time has come to adopt the precautionary principle...
to try to ensure that these resources are left in a state that can be utilised as fully by future generations as by ourselves.

This paper is therefore a call to those who carry responsibility for fisheries to take action in preventing genetic erosion of the productivity of fish stocks. First I describe some of the evidence on which this call for action is based, and then discuss some steps that need to be taken in developing a Darwinian perspective on fisheries science.

**SELECTION DIFFERENTIALS**

How strong is selection generated by fishing? If a year class is monitored from its inception, how biased a sample does fishing make the surviving adults? It is important to answer this question because subsequent year classes are formed from these survivors and selection differentials caused by fishing thus guide the path of evolution. A number of phenotypic traits may be affected by selective fishing: below, growth and maturation are considered because of the important impact they have on productivity of fisheries.

Fishing-induced selection only becomes significant if fishing mortality is substantial: it is only then that average trait values of survivors can differ much from the values expected in the absence of fishing. Quite a lot of information is available on fishing mortality and, at a global level, the majority of fisheries are fully or over-exploited (FAO 1998). Fishing mortality in major fish stocks often exceeds natural mortality by a factor of two to three, and perhaps more, once a year class has been recruited into fishery. Clearly fishing mortality is not negligible.

For fishing-induced selection to be important, fishing mortality also needs to be non-random with respect to the trait values. Fishing gear is usually size selective (Myers and Hoenig 1997); thus size-at-age is likely to be under selection due to fishing. Less obvious, the stage in development at which fishing mortality is applied affects sexual maturation: removal of older individuals generates an advantage for early maturation because the older individuals are less likely to survive to reproduce at all; such phenomena are dealt with in the subject of life-history evolution (Roff 1992; Stearns 1992; Charlesworth 1994). Even the geographical location of fishing may generate selection on the life history: targeting the spawning grounds can put fish with delayed maturation (and greater growth before maturation) at an advantage.

Given the high levels of fishing mortality and the selectivity of fishing, there should be a signal of selection, detectable within year classes. Sinclair et al. (2002a, b) recently described a technique to search for this signal in length-at-age and applied it to Atlantic cod (Gadus morhua) in the Gulf of St. Lawrence. The technique entails backcalculating length at an earlier age (using otoliths) to estimate the mean length at the earlier age among fish still alive when older. The backcalculated mean length is then compared with the mean length of fish alive at the earlier age; a value larger than the backcalculated one implies selective loss of larger fish in the intervening period. Their results showed a switch from selection favouring greater length-at-age in the 1970s to one favouring lower length-at-age in the 1980s and 1990s. Backcalculation does not separate fishing mortality from natural mortality; in this context it is notable that a large decline in selection occurred following closure of the fishery in 1993 – it would be surprising if this was coincidental. The selection differential is of the same order as that from a rather different technique applied to 1980s year classes of North Sea cod (Law
and Rowell 1993), although Huse and Johansen (2001) obtained much more variable results in a recent study on Greenland halibut (*Reinhardtius hippoglossus*).

Life-history models can give insight into the strength of selection on length and age at maturation generated by fishing. Rowell (1993) estimated lifetime’s egg production of North Sea cod maturing at different ages under several patterns of fishing mortality using a von Bertalanffy growth equation. With the levels of mortality that applied in the 1980s there was a strong advantage to early maturation: delay in maturation was very disadvantageous because survival to reproduce in the following year was unlikely under such high fishing mortality.

The message is that the intensity and distribution of fishing mortality is great enough to generate substantial selection differentials on size-at-age and maturation in major fish stocks.

**GENETIC VARIATION**

It would not matter whether fishing generates strong directional selection if there was little genetic variation in the traits under selection: selection could be applied generation after generation without a corresponding change in the selected traits. It is therefore important to establish if there is genetic variation of a kind that can be selected. A statistic widely used for this purpose in quantitative genetics is heritability: the additive genetic variance in a trait expressed as a proportion of the trait’s total phenotypic variance (Falconer and MacKay 1996).

The development of aquaculture in the last twenty years has been accompanied by selective breeding programmes in which knowledge of heritability plays an important part. As a result, there is now a large literature on fish breeding containing information on heritabilities of size-at-age and to a lesser extent on maturation. A review of the literature (Law 2000) gave heritability distributions for weight-at-age with a mean of 0.24 (standard deviation 0.15; 28 studies) and for age at maturation a mean of 0.31 (standard deviation 0.19; 8 studies). A more extensive review by Friars and Smith (2002) gave similar results for traits related to growth, but a wide spread of heritabilities for maturation. Average values in the region of 0.2 to 0.3 are much as expected for life-history traits (Mousseau and Roff 1987) which, being under directional selection, tend to lose genetic variation relatively fast.

Heritabilities measured under controlled experimental conditions may not be a good guide to those that operate at sea, where environmental variability could be greater, inflating phenotypic variance. It is much harder to estimate heritabilities in the wild and, with one notable exception, such information is not available. The exception is an estimate of heritability of body weight of Atlantic salmon (*Salmo salar*) obtained by Jónasson et al. (1997) as part of a study on the potential of this species for sea ranching. Tagged parr of known parentage were released and the body weights of survivors measured after one winter at sea; the resulting heritability of body weight was 0.36, similar to that found in experimental farms. The similarity of heritability in the wild and in controlled experiments is surprising at first sight, but is in keeping with findings in other systems (Weigensberg and Roff 1996). In the absence of better information, heritabilities from aquaculture can give some indication of the values that apply in the wild.
The heritabilities are relatively small, but this does not mean they should be ignored. The success of selective breeding for aquaculture bears witness to the fact that there is genetic variation and that selection can be applied to achieve rapid improvement in yields. What the heritabilities do mean, in conjunction with estimated strength of selective fishing, is that the time scale on which genetic change is detectable is likely to be over decades rather than over years.

**RESPONSE TO SELECTION**

The raw material for evolution – selection differentials and genetic variation – evidently exists. Is it possible to detect genetic change taking place due to fishing? Evidence of two kinds is available: laboratory experiments and phenotypic changes in fish stocks.

Most remarkable is an experiment by Conover and Munch (2002) on several populations of Atlantic silverside (*Menidia menidia*). They kept the populations under contrasting patterns of size-selective harvesting, removing large, small or random individuals, and leaving a small proportion of individuals as parents for the next generation. At the start a greater harvest was obtained from removing large individuals; but this rapidly changed and, by the fourth generation, removing the small individuals was giving nearly twice the yield of the large-harvested populations. There are two reasons for this. First, because the adults were larger in size when small individuals were harvested, these populations had a greater reproductive potential. Second, genetic change in growth rate caused by harvesting was taking place, removal of small individuals selecting for fast growth (heritability for size at 190 days was approximately 0.2).

The genetic change in growth observed by Conover and Munch (2002) matches results of an experiment on water fleas (*Daphnia magna*), similar in many respects but involving age-structured populations harvested repeatedly over time (Edley and Law 1988). There was genetic change in growth of the water fleas, the phenotypes selected being those that did not linger in the vulnerable stages, as expected from life-history theory (Williams 1966:89). The decline in yield when harvesting large sizes found by Conover and Munch (2002) was also evident in the water fleas. An increase in yield when harvesting small individuals was not found in the case of water fleas, but this may be because harvest was measured by number of individuals rather than by biomass (Edley and Law 1988).

It has proved much harder to get unequivocal evidence for genetic change of traits in fish stocks caused by harvesting. Although there are many examples of changes in size-at-age and maturation consistent with expectations from evolutionary theory, the traits involved are plastic and also change as a result of factors such as population density, food availability and water temperature (reviewed by Law 2000). A single genotype is thus expressed as a set of phenotypes dependent on the environment, the set being known as the reaction norm (Stearns 1992:41). Separating the environmental and genetic components of change in time series of traits such as maturation is not straightforward. Until recently the only information available on the relative importance of environment and genotype was a study by Rijnsdorp (1993) on the decreasing age at maturation of North Sea plaice (*Pleuronectes platessa*) during the 20th Century. Rijnsdorp found a substantial reduction in age at maturation remained after allowing for
compensatory growth and changes in water temperature; this remainder was taken to be genetic change.

A technique has now been devised to separate environment-dependent changes in maturation from more fundamental changes in the reaction norm itself (Heino et al. 2002a, b). So far the technique has been applied to the Northeast Arctic cod. This stock has a special interest because age at maturation has been decreasing since the development of a fishery on its feeding grounds in the Barents Sea in the 1930s (Jørgensen 1990); up to this time there had only been a fishery on the spawning grounds near the coast of Norway. Such a decline in age at maturation is consistent with fishing-induced selection for early maturation because late maturers became more likely to be caught before they could spawn once the Barents Sea fishery was opened (Borisov 1978; Law and Grey 1989); it is also consistent with compensatory growth through more food becoming available as the stock biomass decreased. New results indicate that, after removing the immediate effects of compensatory growth, the reaction norm itself has been changing, such that maturation now occurs at earlier ages (Heino et al. 2002c).

The message is that genetic change takes place due to size-selective harvesting at a rate which is detectable over fairly small numbers of generations, and that this can impact on the productivity of a fishery. There is much to be learnt about the phenotypic changes taking place in wild fish stocks and, in the next few years, there should be progress in separating effects of compensatory changes in growth on maturation from underlying changes in reaction norms. The early indications are that reaction norms are changing as well as individual growth rates.

**DOES GENETIC CHANGE MATTER?**

The evidence above provides support for the case that exploitation of fish stocks is causing genetic change in phenotypic traits of the fish. Is such evolution of any importance in management of fisheries?

Whether genetic change matters is partly a matter of the time scale of change. If the time scale of genetic change is centuries, it is obviously less pressing to deal with it than if the time scale is years. In fact the evidence suggests that selection pressures are large enough for substantial change to occur on a time scale of decades, even though heritabilities of the traits are small on average. Such change is clearly less urgent to deal with than year-to-year matters of ensuring survival of fish stocks, but it raises important issues about the health of the fisheries we pass on to our descendants.

Whether genetic change matters is also partly a matter of the kind of traits that change. Change in some traits may be relatively unimportant, for instance morphological ones selected by nets. However, other traits such as individual growth rate and age- and size-at-maturation are critical to the productivity of fisheries. The evolutionary decline in yield found in experimental studies when removing large individuals (Edley and Law 1988; Conover and Munch 2002) is especially thought provoking because this is the kind of harvesting typically used in practice. The effect of evolution on yield has the potential to be large: some simple calculations on the life history of Northeast Arctic cod suggested that the effect could be as great as a factor of two, depending on the levels of fishing mortality applied on the spawning and feeding grounds (Law and Grey 1989).
Whether genetic change matters also depends on how easily it can be reversed. In the case of ecological over-exploitation, the damage can often be undone by dropping fishing mortality rates; such recovery was seen in the North Sea herring after closure of the fishery in 1977 (Cushing 1988:101). Matters are not so straightforward if genetic change is to be reversed. Quite apart from the practical problems of how to change the selection pressure, selection in the reverse direction may have to be much weaker. This problem arises in the Northeast Arctic cod. Calculations on the life history of this stock suggest that the ancestral fishery on the spawning grounds, which gives a large yield after evolution, selected weakly for late maturation; in contrast, the current fishery selects strongly for early maturation, and gives a smaller yield after evolution (Law and Grey 1989). If the management tools for guiding evolution are the rates of fishing mortality on the feeding and spawning grounds, these calculations suggest it is much easier to move the stock along an evolutionary path towards low yield than towards high yield. It is therefore important not to assume that evolution caused by fishing can be readily reversed.

Clearly the first priority has to be short-term management of fish stocks from one year to the next. However, the precautionary principle places responsibility on us to leave our resources in a state that can be utilised as fully by our descendants as by ourselves. The evidence is that fish stocks are changing over the decades in a way that is deleterious for those who may need them in the future. To deal with this an evolutionary perspective to management – a Darwinian fishery science (Conover 2000) – is needed.

**DARWINIAN FISHERY SCIENCE**

A Darwinian fishery science deals explicitly with the patterns of selection caused by fishing and the phenotypic evolution that follows from this. To develop this science, knowledge is needed the genetic architecture of the traits under selection, including the genetic correlations between them. It is quite feasible to obtain this information – the intellectual tools from quantitative genetics are all in place. Knowledge of the selection differentials is also needed. The raw material for estimating selection differentials caused by current patterns of fishing is already sitting in the archives of fisheries institutes, and various methods can be devised to estimate the selection (Law and Rowell 1993; Sinclair et al. 2002a, b). Armed with this knowledge, Darwinian fishery science is in a position to determine genetic change taking place and to evaluate management options for the future.

The main management options are where and how fishing mortality should be applied. For instance, marine reserves could provide a source free from evolution caused by fishing, although their effectiveness depends on there being little gene flow back from areas in which selection is taking place. Fishing on spawning grounds needs careful consideration, because there is a conflict between the short-term deleterious effects on recruitment and possible longer-term beneficial effects through selection for body growth rather than early maturation. In the case of the Northeast arctic cod, calculations on the life history suggest that the ancestral fishery on the spawning grounds was beneficial to the yield in the long term (Law and Grey 1989).

How to distribute fishing mortality over fish of different sizes also needs careful thought. The limited evidence available suggests that if there is a lower limit and no upper limit on size of fish that can be landed, selection for slow growth takes place, and
that this leads to evolution of lower yields. A nice solution to this problem is to manage fisheries in such a way that large fish are unlikely to be caught (Conover and Munch 2002). This both fulfils the short-term needs of increasing spawning stock biomass and, other things being equal, also puts in place long-term selection for faster growth in the size range liable to be harvested. (But note that other things might not be equal because of genetic correlations with and selection on maturation; this is one reason why knowledge of the genetic architecture would be useful.) There are various management tools that, if adopted, would increase the chance of survival of large individuals; such tools include controls on gear and the power of fishing boats.

CONCLUSION

The evidence is that genetic change caused by fishing is taking place and that this has serious consequences for the productivity of major stocks in the medium and long term. Arguably, a Darwinian fishery science is needed that can deal with evolutionary effects of fishing. There needs now to be a willingness to put this science in place, and to rethink – perhaps quite radically – the way in which fish stocks are exploited.

REFERENCES


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