

Fishing, selection, and phenotypic evolution

Richard Law



Law, R. 2000. Fishing, selection, and phenotypic evolution. – ICES Journal of Marine Science, 57: 659–669.

Large changes are taking place in yield-determining traits of commercially exploited fish, including traits such as size-at-age and age-at-maturation. The cause of these phenotypic changes is often not understood, and genetic change arising from the selective effects of fishing may be a contributory factor. Selection generated by fishing gear is strong in heavily exploited fish stocks, and the spatial location of fishing can also cause strong selection. The success of selective breeding in aquaculture indicates that significant amounts of genetic variation for production-related traits exist in fish populations. Fisheries managers should be alert to the evolutionary change caused by fishing, because such changes are likely to be hard to reverse and, if properly controlled, could bring about an evolutionary gain in yield.

© 2000 International Council for the Exploration of the Sea

Key words: age-at-maturation, evolutionary effects of fishing, growth rate, heritability, phenotypic evolution, selection caused by fishing, sustainable yield.

R. Law: Department of Biology, University of York, PO Box 373, York YO10 5YW, UK
[tel: +44 1904 432614; fax: +44 1904 432806; e-mail: RLI@york.ac.uk]

Introduction

Fishing is almost always non-random. Typically, gear is designed to remove some kinds of individuals in preference to others, usually individuals that are larger and, indirectly, older. The location of fishing is often non-random relative to spatial distributions of stocks, being concentrated where the harvestable biomass is greatest, or where fishes are most accessible, or both. Fishing mortality is therefore selective with respect both to species and to phenotypic variation within species (Stokes *et al.*, 1993; Jennings *et al.*, 1998). If some part of the phenotypic variation within species is due to genetic differences between individuals, then fishing causes evolutionary change. Of particular importance in this context are phenotypic traits related to yield, such as growth rate, length- and age-at-sexual maturation, and fecundity. Simply through the action of fishing, fishers generate selection, causing evolution that changes the sustainable yield.

These ideas about selection come originally from academic study of life-history evolution, from which specific predictions can be made about changes in life histories caused by mortality applied from outside (Roff, 1992; Stearns, 1992; Charlesworth, 1994). From the viewpoint of evolutionary biology, fisheries have a special interest as a world-wide experiment in life-history evolution comprising three groups of participants: (1) fishery managers setting the patterns of

selection, (2) fishers applying the mortality, and (3) the fish stocks themselves as recipients of the selective mortality. The argument that fishing could cause phenotypic evolution in fish stocks is quite widely known in general terms (Pitcher and Hart, 1982; Nelson and Soulé, 1985; Stokes *et al.*, 1993; Trippel, 1995), but it has yet to be internalized into thinking about fisheries management.

In an effort to raise consciousness of the issue, I review our current understanding of phenotypic evolution generated by fishing. First, the context is set by documenting some substantial changes in growth and maturation observed in heavily exploited stocks during the 20th century. Such changes are important for fisheries management and cannot always be explained satisfactorily by changes in the environment; in such cases, selection due to fishing may be a contributory factor. The next section outlines ways in which the strength of fishing-induced selection can be estimated, and shows that selection differentials can be large. Whether selection really matters for management purposes depends on the extent to which phenotypic variation is caused by genetic differences between individuals; the evidence gathered shows that genetic variation exists in significant quantities. The paper concludes with some suggestions about future research priorities that would help in reducing the uncertainties about evolution generated by fishing and would provide a foundation for management of evolution of fish stocks.

Table 1. Examples of phenotypic (W_a : weight-at-age; L_a : length-at-age; L_m : length-at-maturation; A_m : age-at-maturation) changes (I: increase; D: decrease) in commercial fish stocks over time.

Stock	Trait	Change	Comments	Source
North Sea sole	W_a , L_a	I	Associated with introduction of heavy beam trawls	de Veen, 1976; Millner and Whiting, 1996
Bristol Channel/Celtic Sea sole	W_a	I	Relaxation of intraspecific comp. unlikely to be cause	Horwood, 1993
North Sea cod	L_m	D		Oosthuizen and Daan, 1976; Rowell, 1993
NE Arctic cod	A_m	D		Borisov, 1979; Jørgensen, 1990
NW Atlantic Gadoids (3 spp.)	L_m , A_m	D	Substantial changes in most stocks since mid-1980s	Trippel <i>et al.</i> , 1997
NW Atlantic flatfish (4 spp.)	L_m , A_m	I, D	Changes in both associated with reduced abundance	Bowering and Brodie, 1991
North Sea plaice	L_m , A_m	D	To some extent thought to be genetic change	Rijnsdorp 1993
Halibut (northern Norway)	L_m , A_m	I, D	Interpreted as an environmental effect of fishing	Haug and Tjemsland, 1986
Pacific salmon (5 spp.)	Weight	D	Partly direct effect of fishing. Genetic change thought important in 2 spp.	Ricker 1981

Phenotypic changes associated with fisheries

There is a wealth of information demonstrating changes in growth and maturation in major commercial fish stocks over time (examples are given in Table 1). What is much less certain is why these changes are coming about.

The most obvious explanation is that exploitation, by reducing stock biomass, releases stocks from some pressures of intraspecific competition. The effects of release can feed through to the life history, enabling faster growth and earlier maturation if maturation is size dependent. Plasticity in life-history traits, i.e., a tendency of these traits to take different values depending on the current environmental conditions, is well documented (Reznick, 1993).

For several reasons, the explanation above needs to be evaluated carefully on a case-by-case basis, rather than being used as a general blanket explanation. Some stocks have been heavily depleted for long periods, and yet are still undergoing phenotypic changes. Horwood (1993), for instance, noted an increase in weight-at-age of sole (*Solea solea*) in the Bristol Channel and Celtic Sea from 1971 to 1990. Although adult biomass declined to some extent during this period, the stock was already much depleted by 1971; a fishing mortality rate of 0.2 yr^{-1} , lower than the rate that typically applies, would itself give a reduction in spawning-stock biomass of 75% according to ICES (1992). With this in mind, Horwood argued that the change in growth of adults is unlikely to be due to relaxation of intraspecific competition; recent work implicates regulation in the plankton

(Horwood, 1999). Another reason for caution is Bromley's (1989) observation that the apparent density-dependent growth in North Sea gadoids is predominantly an area effect: some areas have larger numbers of smaller fish than others. This could come about for a variety of reasons apart from density-dependent growth, such as temperature, interspecific competition, or size-dependent migration.

The effects of fishing, of course, go far beyond simply releasing a single target stock from intraspecific competition. Other stocks are most likely being harvested at the same time, and these species, which may be competitors, predators or prey of the target species, also change in biomass. How such effects feed through the marine community to affect growth and maturation of the target stock is far from obvious. Some kinds of bottom fishing gear may have major impacts on benthic communities, and this can have its own effects on fish growth. For instance, the weight-at-age of mature female North Sea sole nearly doubled in the late 1960s, around the time when heavy beam trawls became widely used; bottom trawls cause substantial disturbance to the sea-bed and are likely to have left more food available for the sole (de Veen, 1976; Millner and Whiting, 1996).

Superimposed on all these direct effects of fishing are other changes in the physical and biotic environment. Weight-at-age of different cod (*Gadus morhua*) stocks, for instance, is closely correlated with water temperature (Brander, 1995), and one might expect fluctuations in such an environmental factor to leave their mark on time series of phenotypic traits. But the causal web linking the environment to the phenotype is complex. These complexities are illustrated by Northeast Arctic

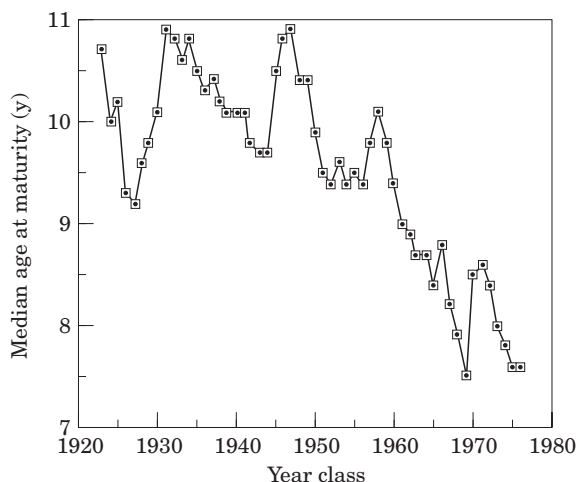


Figure 1. Median age-at-maturation (sexes combined) of Northeast Arctic cod based on spawning zones in otoliths (from Jørgensen, 1990).

cod (Fig. 1), in which there has been a strong trend towards earlier maturation through the 20th century (Borisov, 1979; Jørgensen, 1990; but see also Marshall *et al.*, 1998). One might think that the change in age-at-maturation is primarily a compensatory response to the large fall in stock biomass known to have taken place (Jørgensen, 1990), leaving more food for the survivors with the result that they grow faster and mature earlier (see Godø and Moksness, 1987). But, as well as a decline in cod biomass, there have been major changes in the abundance of young Norwegian spring-spawning herring (*Clupea harengus*) and capelin (*Mallotus villosus*), the main sources of food of the cod in the Barents Sea. Herring declined during the 1960s when there was a fall in temperature in the East Icelandic Current (Blindheim and Skjoldal, 1993); the introduction of purse seines about then was another contributory factor. In addition, herring and capelin are themselves interdependent, because predation by young herring on capelin larvae can have a deleterious effect on the capelin stock (Bogstad *et al.*, 1997). To some extent, climatic forcing acts on the system, as year classes of cod tend to be larger at times when conditions are relatively warm (Loeng, 1989; Øiestad, 1994). Changes in the environment are linked to changes in body length, there being evidence that length increases faster when capelin is abundant relative to the cod, and when water temperature is relatively high (Jørgensen, 1992). The message to take from this is the obvious point that other things do not necessarily remain equal when stock biomass is fished down: compensatory responses need to be evaluated in the light of other physical and biotic changes taking place in the ecosystem.

Rijnsdorp (1992, 1993) carried out a study to disentangle the causes of a major phenotypic change in

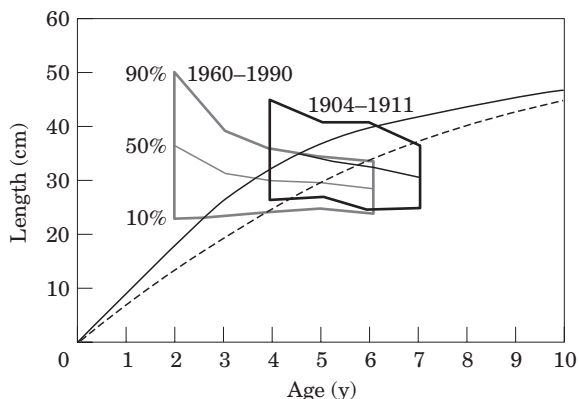


Figure 2. Length-at-age of female North Sea plaice, 1904–1911 (dashed line) and 1960–1990 (drawn line), and the envelopes of 10%, 50% and 90% mature fish at each length and age for the two periods (from Rijnsdorp, 1993).

maturation of North Sea plaice (*Pleuronectes platessa*) from the early to late 20th century (Fig. 2). In the Southern Bight, females were mostly maturing at 5 and 6 years old and at a length of 32–35 cm at the start of the century, and even later and larger further north, whereas they are now maturing about 2 years earlier and at substantially smaller sizes (Rijnsdorp, 1989, 1992). They are also growing faster. Large stock sizes in the 1940s and 1960s were associated with slower growth, and it can reasonably be argued that compensatory growth underlies the change in maturation. But Rijnsdorp (1993) showed that such compensation was not sufficient to account for all the change in maturation; at the very least it left about 2.4 cm of the 5.8 cm reduction in length-at-maturation of 4-year-olds unaccounted for. There has also been a small increase in sea temperature (approximately 1°C), but this accounted only for a further 0.7 cm. A substantial part of the change in maturation remains unexplained, and is consistent with genetic change caused by fishing (Rijnsdorp, 1993).

Ricker's (1981) study of changes in weight of Pacific salmon species is particularly enlightening. There is evidence for a decline in body weight in all five species from the 1950s onwards. The pink salmon (*Oncorhynchus gorbuscha*) is relatively straightforward to interpret because this species almost always returns to spawn at the end of its second year of life, and has decreased in adult body weight by up to 34% (McAllister *et al.*, 1992). Fishing is mostly by gillnets, seine nets, and by trolling as the fish return to spawn, and thus concentrates on individuals of a similar age. Ricker argued that the source of the change in weight-at-age was a change in the market place in the late 1940s: fish became sold by weight rather than by piece, and it was advantageous for fishers to increase the mesh size of gillnets to catch larger individuals. Thus, the observed change was interpreted as a genetic change due to the size-selective fishery giving

Table 2. Data on selection on body length of North Sea cod generated by fishing (from Law and Rowell, 1993).

	1984	1986	1988	1990
Legal min. mesh size (mm)	80	80	85	90
Legal min. landing size (cm)	30	30	30	35
Discards (%)	44	61	15	29
1-group: mean length (cm)				
Landings	34.36	33.39	34.14	38.00
Landings + discards	29.19	28.68	31.27	33.60
Stock before fishing	24.39	25.10	28.75	30.27
Stock after fishing	24.15	24.90	28.54	29.97
Selection differential	-0.24	-0.20	-0.21	-0.30
2-group: mean length (cm)				
Landings	40.58	36.14	40.03	43.72
Landings + discards	40.58	36.14	40.03	43.36
Stock before fishing	40.41	35.76	39.16	42.68
Stock after fishing	40.36	35.67	38.95	42.51
Selection differential	-0.05	-0.09	-0.21	-0.17

individuals of low body weight more chance of survival than those of greater weight.

In support of Ricker's (1981) interpretation is the existence of additive genetic variation in body size (Beacham and Murray, 1988), and his observation that the decline in body weight occurred fastest in areas where most of the catch was taken by gillnets and by trolling (trolling also takes larger individuals, whereas seine nets are relatively unselective). The weight change is unlikely to come from a release from intraspecific competition because this should lead to greater rather than lower weight, although growth has been correlated with food availability in the sea more recently (Peterman, 1987). Ricker (1981) could not find a consistent relationship between body weight and environmental variables such as ocean temperature or salinity (but see McAllister *et al.*, 1992).

In sum, there are many well-documented cases of change in growth and maturation of commercial fish stocks over time. Undoubtedly these changes are often immediate consequences of shifts in the physical environment, the biotic environment, and the prevailing patterns of fishing. But not all changes can be accounted for as direct effects of the environment. Fishing may have effects on stocks that are not readily reversed, through selection on genetic variation in phenotypic traits.

Strength of selection generated by fishing

How large are the selection differentials generated by fishing? To put it another way, suppose you know the mean value of some phenotypic trait in a stock before the fishing fleets leave harbour one week: how much has the mean value of the trait in the stock changed due to fishing when the fleets return at the end of the week? The difference between the value before and after fishing is

the selection differential, and is crucial to understanding the potential for evolution caused by fishing. Various traits could be under selection; this section is concerned with some of those most closely related to yield, namely length-at-age and age-at-maturation.

Selection on length-at-age due to fishing gear

Fishing gear can clearly be selective with respect to fish size (Myers and Hoenig, 1997). Indeed fishing gear is usually designed to be so, mesh sizes being an important tool for controlling age-at-entry into fisheries. Here I give an estimate of the selection differential on length-at-age of cod in part of the North Sea from 1984 to 1990 (Law and Rowell, 1993). The estimate comes from an area off the east coast of northern England and southern Scotland, and the traits involved are body lengths in the third quarter of the year for individuals aged 1 and 2 years. This quarter was chosen because a ground-fish survey covering the area at this time of year provided a non-selective sample over the size range needed for obtaining the selection differential. During the 1980s, the catch was mostly taken by bottom and pair trawls, and in the absence of more precise information it is assumed that nets had the minimum legal mesh, and minimum landing size regulations were enforced.

The main results are given in Table 2. Fishing and individual growth are of course continuous through time, and it is perhaps easiest to think of the selection differential below as the change that would apply if all fishing mortality were concentrated at a single point in time, the midpoint of the third quarter.

- (1) The starting point is the length-at-age distribution of the landings taken from catch statistics routinely

collected at English ports; this enables the mean length of 1- and 2-group individuals in the landings to be estimated.

- (2) Landings represent only part of the total catch, because fish below legal minimum landing size are also caught, but cannot be brought into port. Because discards can be a large part of the catch, we made an allowance for these by extending the length distribution of the catch back to 15 cm using the length distribution from the groundfish survey. Once discards are allowed for, the mean length of 1-group in the catch is reduced by several centimetres.
- (3) With the length distribution of the catch in place, the length distribution, and mean length-at-age, in the stock before fishing can be reconstructed by allowing for gear selectivity, assuming the selection ogive corresponding to the legal minimum mesh size.
- (4) The next step is to construct the length-at-age distribution of the stock after fishing has taken place. This obviously depends on the mortality rate due to fishing. Results from virtual population analysis indicate a high fishing mortality rate F of about 1 yr^{-1} in the 1980s. We used a quarter of that value for fully recruited fish during the 3-month period. The mean length-at-age in the stock after fishing can then be obtained from the length-at-age distributions before fishing after allowing for fishing mortality and gear selectivity.
- (5) The selection differential is the difference between the mean length-at-age in the stock before and after fishing (Table 2). Selection differentials were between -2 and -3 mm for 1-group throughout the period. For 2-group, they were less than -1 mm in the mid-1980s, but increased to -2 mm in 1987, when the legal minimum mesh size was increased to 85 mm.

A feature not taken into account in these calculations is the existence of phenotypic correlations between lengths at different ages: fish that are large at age 1 are also likely to be large at age 2, etc. This has the effect, paradoxical at first sight, that mean phenotypic values change under selection even when they are not being expressed. To allow for this further change, a phenotypic covariance matrix has to be constructed from the growth trajectory of individual fish (Law, 1991). For this purpose, we used age 3 cod from the groundfish survey and estimated their lengths at age 1, 2, and 3 from the otoliths. The accumulated selection differential due to fishing in the third quarter was approximately -4 mm, once the phenotypic correlations had been taken into account.

These calculations apply only to one quarter of the year, and comparable data for other quarters are not available. However, taking the whole period during

which a year class is entering the fishery, the selection differential that accumulates is probably roughly -1 cm. In other words, the mean length of a cohort surviving once it is fully recruited into the fishery, given the fishing patterns that prevailed in the 1980s, would be about 1 cm less than it would have been in the absence of fishing, all other things being equal.

Selection on age-at-maturation due to age-at-entry into the fishery

Quite apart from direct selective effects of fishing gear on body length, fisheries generate selection on life-history traits simply because they catch more individuals of some ages than of others (Law, 1979; Michod, 1979; Charlesworth, 1994). This is intuitive: think of a stock in which fish reach sexual maturity over an age range of, say, 2 to 8 years, and a fishery that catches fish of age 4 and older; other things being equal, early-maturing fishes leave more offspring to future generations than do late-maturing ones and are selected for.

The strength of selection acting on age-at-maturation under a given regime of fishing can be determined from the expected lifetime's egg production (R_0) of females maturing at different ages. Although this does not provide a selection differential in the sense used in quantitative genetics (Lynch and Walsh, 1998), R_0 is a direct measure of the contribution to future generations made by different phenotypes in an age-structured population that is constant in size, and ratios between phenotypes that depart substantially from unity indicate strong selection.

Rowell (1993) estimated the strength of selection on age-at-maturation of North Sea cod stock off the east coast of northern England and southern Scotland, given the level of fishing in recent years (Macer and Easey, 1988). The estimate was derived from a growth model for cod in which reproduction and growth compete for resources, early maturation incurring a cost in terms of lower somatic growth subsequently. The model was based on the von Bertalanffy growth equation, using body weight at each age as a surrogate for egg output because of a well-established relationship between weight and egg production (Oosthuizen and Daan, 1974). From the product of egg output at age and rate of survival up to that age (incorporating both natural and fishing mortality), and summing the product over all ages, the value of R_0 for a female maturing at a given age is obtained.

Figure 3a shows, as one would expect, that late-maturing fish are at a strong disadvantage relative to early-maturing fish under the current high levels of exploitation. More generally, selection for early maturation is likely to be quite common, in view of the widespread tendency of fisheries to remove larger (and older) fish. Such selection is consistent with many of the

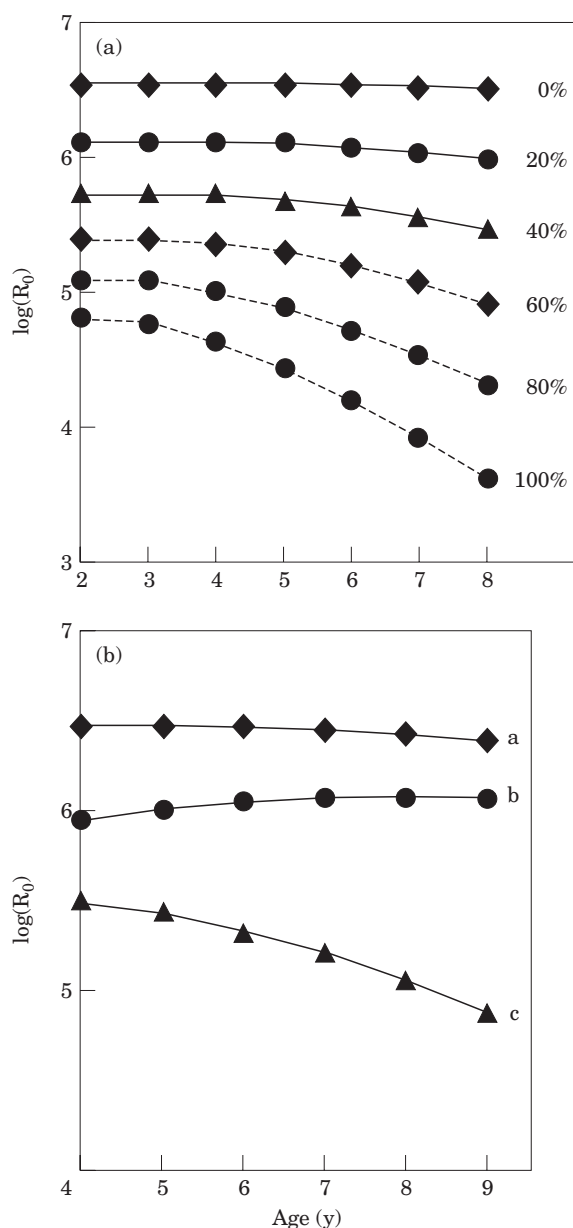


Figure 3. Expected lifetime's production of eggs R_0 , as an index of strength of selection, in relation to age-at-maturation and at varying levels of exploitation: (a). North Sea cod – for fishing mortality rates ranging from 0 (no fishing) to 100% of the current level at 20% intervals (redrawn from Rowell, 1992). (b) Northeast Arctic cod – for contrasting rates of fishing mortality rates (yr^{-1}) on the spawning grounds F_1 , and on the feeding grounds F_2 (fishing assumed to start at age 4): (a) No fishing – $F_1=0, F_2=0$; (b) fishing only on the spawning grounds – $F_1=0.2, F_2=0$; (c) fishing on the spawning and on the feeding grounds: $F_1=0.2, F_2=0.4$. (Drawn from data in Law and Grey, 1989).

observed phenotypic changes (Table 1), although the cause of these changes is still a matter of current debate.

Fishing does not inevitably select for early maturation, however; the location of fishing could reverse this (see below).

Notice also that, in the absence of fishing, age-at-maturation has rather little effect on lifetime's expected production of eggs (Fig. 3a). The loss in egg production by later maturation is roughly balanced by the greater gain in body weight allowed for by delayed maturation, and the greater production of eggs that results once maturation has occurred. This points to an important asymmetry. Current patterns of fishing generate strong selection for early maturation and, given appropriate genetic variation, substantial genetic change can be expected. But, if one were to try to reverse the process by closing the fishery, selection for later maturation would be weak. In other words, it could be hard to undo the effects of inadvertent selection caused by fishing.

Selection on age-at-maturation due to location of fishing

Fish stocks are not randomly distributed over space, and neither are fishing fleets. In addition to direct selection caused by fishing gear and indirect selection through age-dependent fishing mortality, selection is caused simply by where fishing takes place.

Some spatial effects of fishing are well illustrated by Northeast Arctic cod (Law and Grey, 1989). The main feeding grounds of this stock are in the Barents Sea, whereas the spawning grounds are close to the Norwegian coast, for the most part in the vicinity of the Lofoten Islands. Once the fish have reached sexual maturity, they undertake annual spawning migrations from the northern waters to the Norwegian coast. For many centuries, there has been a major fishery on the spawning grounds, and it was not until the early part of the 20th century, with the advent of deep-sea trawlers, that exploitation of the stock on the feeding grounds began. There are in effect two spatially separated fisheries operating: a feeder and a spawner fishery.

What selective pressures do the feeder and spawner fisheries generate? This depends on the trait in question and the fishing mortalities applied in the two areas. For age-at-maturation, estimates of the expected lifetime's production of eggs R_0 , obtained from a growth model (like the North Sea cod model above), give an indication of the strength of selection (Fig. 3b). In the absence of fishing, maturation at different ages has little effect on R_0 , as in the case of North Sea cod (Fig. 3a). Selection is therefore weak, although there is a slight advantage to early maturation. Fishing confined to the spawning grounds, as applied until the 20th century, gives an advantage to late maturation. This is because the extra mortality due to fishing on the spawning grounds makes it advantageous to grow for longer before maturation and thereby to produce more eggs when risking a visit to

the spawning grounds. This is an instance in which fishing mortality actually selects for delayed maturation: it differs from the North Sea cod because spawners alone are the target of fishing. If fishing mortality on the feeding grounds is added on, the relatively small advantage to late maturation is changed to a large advantage to early maturation (Borisov, 1979; Law and Grey, 1989). Remaining on the feeding grounds is now itself risky, and a fish that does not mature until, say, 8 years old is most likely to be caught before it spawns. Given these arguments, the decreasing age-at-maturation observed since the feeder fishery was set up (Borisov, 1979; Jørgensen, 1990) is particularly interesting (Fig. 1).

Northeast Arctic cod, like North Sea cod, show strong asymmetries in selection generated by different patterns of fishing. (The asymmetries are contingent on the growth model used, in particular on the assumption of a trade-off between reproduction and somatic growth.) It is easy to apply selection for early maturation, but hard to reverse this. If the fisheries were closed altogether, selection would evidently be weak and, if fishing were confined to the spawning grounds, selection for late maturation would still be much weaker than the current selection for early maturation. This could be an important issue in evolution of the yield from the stock. Current patterns of fishing are selecting a life history in which the cod allocate resources to reproduction rather than somatic growth. The sustainable yield associated with the life history selected under such fishing could be less than half the yield potentially available through evolution of the life history (Law and Grey, 1989). In other words, it seems easier to make this stock evolve towards low yield than towards high yield.

The message from these studies is that fishing generates substantial selection on traits determining yield. Indeed it would be hard to design a practical scheme of fishing in which there was no selection. The estimates given are only first attempts, and one might debate some of the assumptions involved: undoubtedly the estimates could be improved and refined with more knowledge of the stocks and patterns of fishing. Yet there can be little doubt that, overall, fisheries are highly selective.

Genetics of production-related traits

Selection differentials generated by fishing are not sufficient to cause evolution. Evolution requires, in addition, that there should be genetic differences between the fishes caught and those that escape. The important phenotypic traits are quantitative, affected by genes acting at many loci, and quantitative genetics is therefore the appropriate framework for analysis of such evolution (Falconer and Mackay, 1996; Kearsley and Pooni, 1996; Lynch and Walsh, 1998).

The most important single issue to settle is the proportion of phenotypic variance inherited to future

generations. In quantitative genetics, this proportion is the heritability (h^2) of a trait and, in the short term, the change R in the trait's mean value from one generation to the next (the selection response), due to a selection differential S , is given by the equation $R = h^2 S$. Clearly, the rate at which the trait evolves is proportional to its heritability; a trait with a low heritability changes slowly, irrespective of how large the selection differential is.

As a general rule, heritability is expected to be lower the more closely a trait is associated with fitness, because genetic variation is most rapidly eroded in such traits (Falconer and Mackay, 1996). Life-history traits, being essentially components of fitness, should therefore have relatively low heritability. In keeping with this, Mousseau and Roff (1987) found a mean heritability of 0.26 for life-history traits, as opposed to 0.46 for morphological traits, in a review of over 1000 estimates for wild outbred species. Although relatively small, a heritability of 0.2 to 0.3 is still enough to cause a substantial selection response in a small number of generations. For instance, McAllister *et al.* (1992) noted that the decline in body weight in stocks of pink salmon could be accounted for by values in the range 0.18 to 0.25.

Fish are in no way exceptional to the general rule. There is a substantial literature on the genetics of growth and maturation, mostly from salmonids such as rainbow trout (*Oncorhynchus mykiss*) and Atlantic salmon (*Salmo salar*), motivated by selective breeding for aquaculture (Gall, 1983; Gjedrem, 1983; Refstie, 1987). The distribution of heritabilities for body size is very much as would be expected: weight has a mean 0.24 (s.d. 0.15; from 28 studies), and length has a mean 0.30 (s.d. 0.21; from 17 studies). Data on heritability of age-at-maturity are more scarce but lie in the same region, with a mean of 0.31 (s.d. 0.19; from 8 studies). Even though these heritabilities are not large, major gains in production-related traits have been achieved in salmonids by selective breeding: evidently these heritabilities are sufficient to permit a rapid and substantial selection response.

However, direct extrapolation from values obtained in breeding experiments to wild stocks would be unwise. A heritability is the ratio of two variances, the additive genetic variance (measuring the variation on which selection can act) divided by the total phenotypic variance (Falconer and Mackay, 1996). The phenotypic variance includes both a genetic component and a component determined by the environment, and both the additive genetic variance and the environmental variance are context-dependent. In the wild, away from carefully controlled experimental conditions, substantially more variation between individuals due to their different environments might be expected. With this problem in mind, Weigensberg and Roff (1996) compared heritability estimates obtained under laboratory conditions to those obtained in the wild, and could find

no statistically significant difference between them. Although phenotypic variance under laboratory conditions was smaller than that in the field, typically the reduction is not substantial (mean ratio of laboratory to field estimate of phenotypic variance was 82% in 13 comparisons, excluding *Drosophila*).

Heritability estimates of body weight of Atlantic salmon from sea ranching are particularly interesting in this context. Jónasson *et al.* (1997) tagged salmon parr of known parents, released them, and measured the weights of those that returned after one winter (grilse) and two winters at sea; these fish therefore experienced the full range of environmental conditions in the sea. The heritability of weight of grilse was 0.36, similar to that of grilse in farms; the return rate of salmon after two winters at sea was too low for reliable estimates to be obtained. Thus the only experiment to date in which heritability has been estimated incorporating environmental variation at sea gives results of the same order as those from farmed fish.

Discussion

There can be no question that fishing causes evolution of phenotypic traits of fish; the existence of additive genetic variation has been demonstrated beyond reasonable doubt, and directional selection pressures on this variation caused by fishing are substantial. What is much less clear is how fast evolution is taking place. It is uncertain whether such evolution contributes significantly to the phenotypic change happening in many fish stocks, or whether it is operating on an altogether longer time scale.

Does this ignorance about the rate of evolution matter? I think it does, for several reasons. (1) Large changes are taking place in phenotypic traits of major fish stocks (Table 1) and the cause of these changes is often in doubt. (2) The traits changing are key ones of fisheries: a 34% decline in body weight in pink salmon, for instance, represents a major loss in yield to the fishery if the number of fish harvested remains unchanged (McAllister *et al.*, 1992). (3) While the environmental factors affecting growth and maturation may fluctuate or eventually change little more, some kinds of directional selection caused by fishing continue, cohort after cohort. (4) Genetic change caused by fishing will not be readily reversed by altering, for instance, the patterns of fishing: it appears to be much easier to select for early maturation than for late maturation (Law and Grey, 1989).

If we are to become better informed about evolution driven by fishing, there are at least four research priorities:

- (1) What are the selection differentials associated with different management options? It is feasible to

estimate the strength of selection with information collected for management purposes, as shown above, and selection differentials could be a standard input into assessment of heavily exploited stocks.

- (2) What are the heritabilities of traits under selection? This is a hard problem because heritability needs to be estimated under the conditions in which fishes live in the wild. To date, this has only been done once, and first indications suggest heritabilities of the same order as in experimental conditions. Somewhat easier, but still informative, would be a compilation of phenotypic variances of traits in the wild relative to those that apply in aquaculture; this would give a rough indication of the factor by which aquaculture estimates of heritability need to be reduced for describing evolution in the wild, if additive genetic variance remains the same.
- (3) What is the rate of evolution in large-scale fishing experiments? An experiment proposed by McAllister *et al.* (1992) on pink salmon would be instructive. This was envisaged as a large-scale, size-selective fishing experiment with a non-selective control, carried out under natural conditions, and making use of the many stocks of this species on the western seaboard of Canada. The rate at which the selected stocks diverge from the control would settle the issue of the rate of evolution, and the selection response together with the selection differential could be used to estimate the heritability.
- (4) To what extent can time series of traits be accounted for in terms of environmental variables? What residual remains in the series once the changes associated with the biotic environment (condition factor, abundance of conspecifics, prey, predators, etc.) and the physical environment (currents, salinity, temperature, etc.) have been taken out? If there still remains a signal that is monotonic with time in a stock continually subject to exploitation, is this consistent with directional selection operating on the trait?

This still leaves open some important issues, such as genetic correlations in the life history of fish, which will need eventually to be understood. But if there were some answers just to the questions raised above, we would be a good deal further forward.

In summary, this paper calls for an evolutionary perspective to fisheries management. Are the selection pressures caused by fishing compatible with maintaining the long-term value of the stock? What precautionary methods of management could be put in place to reduce deleterious effects of selection? Can we go beyond the problems to the potential benefits of evolution caused by fishing? What management would set evolution on a path towards a life history that maximizes yield after

evolution (Law and Grey, 1989)? Can adaptive management strategies be put in place updating the pattern of harvesting as the stock evolves (Heino, 1998)? These are basic questions that need to be resolved for management of exploited fish stocks in the long term.

Acknowledgements

I thank C. T. Marshall for helpful discussions, and T. K. Stokes and A. B. Thompson for guidance and permission to use their unpublished research results.

References

- Beacham, T. D., and Murray, C. B. 1988. A genetic analysis of body size in pink salmon (*Oncorhynchus gorbuscha*). *Genome*, 30: 31–35.
- Blindheim, J., and Skjoldal, H. R. 1993. Effects of climatic changes on the biomass yield of the Barents Sea, Norwegian Sea, and West Greenland large marine ecosystems. In *Large Marine Ecosystems: Stress, Mitigation, and Sustainability*, pp. 185–198. Ed. by K. Sherman, L. M. Alexander, and B. D. Gold. American Association for the Advancement of Science, Washington. 376 pp.
- Bogstad, B., Hauge, K. H., and Ulltang, Ø. 1997. MULTSPEC – A multispecies model for fish and marine mammals in the Barents Sea. *Journal of Northwest Atlantic Fishery Science*, 22: 317–341.
- Borisov, V. M. 1979. The selective effect of fishing on the population structure of species with a long life cycle. *Journal of Ichthyology*, 18: 896–904.
- Bowering, W. R., and Brodie, W. B. 1991. Distribution of commercial flatfishes in the Newfoundland–Labrador region of the Canadian Northwest Atlantic and changes in certain biological parameters since exploitation. *Netherlands Journal of Sea Research*, 27: 407–422.
- Brander, K. M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES Journal of Marine Science*, 52: 1–10.
- Bromley, P. J. 1989. Evidence for density-dependent growth in North Sea gadoids. *Journal of Fish Biology*, 35(Suppl. A): 117–123.
- Charlesworth, B. 1994. *Evolution in Age-structured Populations*, 2nd ed. Cambridge University Press, Cambridge. 306 pp.
- Falconer, D. S., and Mackay, T. F. C. 1996. *Introduction to Quantitative Genetics*, 4th ed. Longman, Harlow.
- Gall, G. A. E. 1983. Genetics of fish: a summary of discussion. *Aquaculture*, 33: 383–394.
- Gjedrem, T. 1983. Genetic variation in quantitative traits and selective breeding in fish and shellfish. *Aquaculture*, 33: 51–72.
- Godø, O. R., and Moksness, E. 1987. Growth and maturation of Norwegian coastal cod and Northeast Arctic cod under different conditions. *Fisheries Research*, 5: 235–242.
- Haug, T., and Tjemsland, J. 1986. Changes in size- and age-distributions and age at sexual maturity in Atlantic halibut, *Hippoglossus hippoglossus*, caught in North Norwegian waters. *Fisheries Research*, 4: 145–155.
- Heino, M. 1998. Management of evolving fish stocks. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 1971–1982.
- Horwood, J. 1993. Growth and fecundity changes in flatfish. In *The Exploitation of Evolving Resources*, pp. 37–43. Ed. by T. K. Stokes, J. M. McGlade, and R. Law. Lecture Notes in Biomathematics, 99. Springer–Verlag, Berlin. 264 pp.
- Horwood, J. 1999. Population biology and ecology of the sole. *Journal of Resource Management*. [In press.]
- ICES 1992. Report of the Irish Sea and Bristol Channel Working Group. ICES CM/Assess 1: 208.
- Jennings, S., Reynolds, J. D., and Mills, S. C. 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society London Series B*, 265: 333–339.
- Jónasson, J., Gjerde, B., and Gjedrem, T. 1997. Genetic parameters for return rate and body weight of sea-ranched Atlantic salmon. *Aquaculture*, 154: 219–231.
- Jørgensen, T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *Journal du Conseil International pour l'Exploration de la Mer*, 46: 235–248.
- Jørgensen, T. 1992. Long-term changes in growth of North-east Arctic cod (*Gadus morhua*) and some environmental influences. *ICES Journal of Marine Science*, 49: 263–277.
- Kearsey, M. J., and Pooni, H. S. 1996. *The Genetical Analysis of Quantitative Traits*. Chapman and Hall, London. 381 pp.
- Law, R. 1979. Optimal life-histories under age-specific predation. *American Naturalist*, 114: 399–417.
- Law, R. 1991. On the quantitative genetics of correlated characters under directional selection in age-structured populations. *Philosophical Transactions of the Royal Society London, Series B*, 331: 213–223.
- Law, R., and Grey, D. R. 1989. Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology*, 3: 343–359.
- Law, R., and Rowell, C. A. 1993. Cohort-structured populations, selection responses, and exploitation of the North Sea cod. In *The Exploitation of Evolving Resources*, pp. 155–173. Ed. by T. K. Stokes, J. M. McGlade, and R. Law. *Lecture Notes in Biomathematics*, 99. Springer–Verlag, Berlin. 264 pp.
- Loeng, H. 1989. The influence of temperature on some fish population parameters in the Barents Sea. *Journal of Northwest Atlantic Fishery Science*, 9: 103–113.
- Lynch, M., and Walsh, B. 1998. *Genetics and Analysis of Quantitative Traits*. Sinauer, Sunderland, Massachusetts. 980 pp.
- McAllister, M. K., Peterman, R. M., and Gillis, D. M. 1992. Statistical evaluation of a large-scale fishing experiment designed to test for a genetic effect of size-selective fishing on British Columbia pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 1294–1304.
- Macer, C. T., and Easey, M. W. 1988. *The North Sea Cod and the English Fishery*. Lowestoft Laboratory Leaflet no. 61. Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, Lowestoft, England, UK. 22 pp.
- Marshall, C. T., Kjesbu, O. S., Yaragina, N. A., Solemdal, P., and Ulltang, Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 1766–1783.
- Michod, R. E. 1979. Evolution of life histories in response to age-specific mortality factors. *American Naturalist*, 113: 531–550.
- Millner, R. S., and Whiting, C. L. 1996. Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. *ICES Journal of Marine Science*, 53: 1185–1195.
- Mousseau, T. A., and Roff, D. A. 1987. Natural selection and the heritability of fitness components. *Heredity*, 59: 181–197.
- Myers, R. A., and Hoenig, J. M. 1997. Direct estimates of gear selectivity from multiple tagging experiments. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 1–9.

- Nelson, K., and Soulé, M. 1987. Genetical conservation of exploited fishes. In *Population Genetics and Fishery Management*, pp. 345–368. Ed. by N. Ryman, and F. Utter. Washington Sea Grant Program. University of Washington, Seattle. 420 pp.
- Øiestad, V. 1994. Historic changes in cod stocks and cod fisheries: Northeast Arctic cod. *ICES Marine Science Symposia*, 198: 17–30.
- Oosthuizen, E., and Daan, N. 1974. Egg fecundity and maturity of North Sea cod, *Gadus morhua*. *Netherlands Journal of Sea Research*, 8: 378–397.
- Peterman, R. M. 1987. Review of the components of recruitment of Pacific salmon. In *American Fisheries Society Symposium*, 1, pp. 417–429. Ed. by T. J. Pitcher, and P. J. B. Hart. Fisheries Ecology. Croom Helm, London. 414 pp.
- Refstie, T. 1987. Selective breeding and intraspecific hybridization of cold water finfish. In *Proceedings of the World Symposium on Selection, Hybridization, and Genetic Engineering in Aquaculture*, Vol. 1, pp. 293–302. Berlin.
- Reznick, D. N. 1993. Norms of reaction in fishes. In *The Exploitation of Evolving Resources*, pp. 72–90. Ed. by T. K. Stokes, J. M. McGlade, and R. Law. Lecture Notes in Biomathematics, 99. Springer-Verlag, Berlin. 264 pp.
- Ricker, W. E. 1981. Changes in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 38: 1636–1656.
- Rijnsdorp, A. D. 1989. Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.). *Journal du Conseil International pour l'Exploration de la Mer*, 46: 35–51.
- Rijnsdorp, A. D. 1992. Long-term Effects of Fishing in North Sea Plaice. PhD thesis, University of Amsterdam. 220 pp.
- Rijnsdorp, A. D. 1993. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia*, 96: 391–401.
- Roff, D. A. 1992. *The Evolution of Life Histories: Theory and Analysis*. Chapman and Hall, New York. 535 pp.
- Rowell, C. A. 1992. Selection Differentials Imposed by Fishing Activity on the North Sea Cod (*Gadus morhua* L.). D. Phil. Thesis. University of York, York, England. 157 pp.
- Rowell, C. A. 1993. The effects of fishing on the timing of maturity in North Sea cod (*Gadus morhua* L.). In *The Exploitation of Evolving Resources*, pp. 44–61. Ed. by T. K. Stokes, J. M. McGlade, and R. Law. Lecture Notes in Biomathematics, 99. Springer-Verlag, Berlin. 264 pp.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford. 249 pp.
- Stokes, T. K., McGlade, J. M., and Law, R. (eds) 1993. *The Exploitation of Evolving Resources. Lecture Notes in Biomathematics*, 99. Springer-Verlag, Berlin. 264 pp.
- Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. *BioScience*, 45: 759–771.
- Trippel, E. A., Morgan, M. J., Fréchet, A., Rollet, C., Sinclair, A., Annand, C., Beanlands, D., and Brown, L. 1997. Changes in age and length at sexual maturity of northwest Atlantic cod, haddock and pollock stocks, 1972–1995. *Canadian Technical Report of Fisheries and Aquatic Sciences* 2157. 120 pp.
- Veen, J. F. de 1976. On changes in some biological parameters in the North Sea sole (*Solea solea* L.). *Journal du Conseil International pour l'Exploration de la Mer*, 37: 60–90.
- Weigensberg, I., and Roff, D. A. 1996. Natural heritabilities: can they be reliably estimated in the laboratory? *Evolution*, 50: 2149–2157.