

FISHERIES-INDUCED SELECTION PRESSURES IN THE CONTEXT OF SUSTAINABLE FISHERIES

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ABSTRACT

Man has a major impact on marine environments through exploitation of fish resources. Fisheries can induce different selective pressures, either directly, i.e., through elevated mortality (which is often highly selective) or through ecosystem-level responses, as exploitation affects food availability and predation risk in both target and nontarget species. Responses to selection can be observed at two levels. First, at the community level, some species may suffer more from effects of harvesting than others; some may even increase in abundance. Responses by species to exploitation are associated with their life histories. In particular, species with late maturation at large size and with low population growth rate tend to undergo more pronounced declines than early-maturing species with rapid growth. Second, the phenotypic composition within species may also change. If phenotypic variability has a genetic basis, then fisheries-induced selection can result in evolutionary change in life-history traits influencing sustainable yields, behavioral traits (e.g., gear-avoidance behavior), and morphological traits. We discuss the possible implications of fisheries-induced adaptive changes for sustainable fisheries management.

Fishing is probably the major source of mortality in most commercially exploited fish stocks. The great majority (69%) of important marine fish stocks are either fully exploited, overfished, depleted, or recovering (FAO, 1999). At the same time, many nontarget species are influenced. Fishing practices can also cause physical damage to the environment. The heavy impact exerted by modern fisheries on marine ecosystems has raised concerns about sustainability, not only from the traditional viewpoint of single-species fisheries but also from that of ecosystems (Jennings and Kaiser, 1998; Hall, 1999; Tegner and Dayton, 1999; Gislason et al., 2000; Kaiser and de Groot, 2000). A further risk to sustainability, not yet seriously considered in fisheries management, is genetic change in individual stocks in response to the selective effects of fishing (Hutchings, 2000b; Stokes and Law, 2000), which may adversely affect long-term yield and other stock properties (Sheridan, 1995; Trippel, 1995; Conover, 2000; Law, 2000).

Rapid phenotypic changes can certainly be caused by artificial selection under controlled conditions. Fishes are no exception, as evidenced by hundreds of years of goldfish breeding and, more recently, selection in aquaculture. Rapid phenotypic change has also been observed in manipulative field experiments (Reznick et al., 1990; Reznick, 1993), but only recently has it been realized that human activities can cause genetic change in fishes in the wild. So far as we know, the first paper on such concerns was published by Miller (1957) at a time when evidence of genetic changes was still inconclusive. The first paper on potential genetic changes in a marine fish stock was by Borisov (1978). The topic received several pages in a textbook of Pitcher and Hart (1990). Theoretical work on fisheries-induced genetic change began with Favro et al. (1979) and Law and Grey (1989), and the first thoroughly analyzed case study was published by Rijnsdorp (1992, 1993). Since knowledge on the subject was summarized by Stokes et al. (1993), evidence has accumulated that significant genetic changes can take place over time scales relevant

for fisheries management (Law, 2000), yet such changes do not enter into present management considerations.

Here, we try to pull together results and ideas on how fishing can cause selection in the wild. Selection is here defined as a process that causes relative abundances of different types of individuals to change in a predictable way because of predictable changes in birth and death rates associated with specific characteristics of the individuals. Selection can operate equally well on variability between and within species, but the outcome can be fundamentally different in these two cases. In communities, the relative abundances of species can change. Within species, species characteristics can change because of adaptive evolutionary change in their genetic composition. Genetic changes can adversely affect traits related to yield, and moreover, such changes may not be readily reversible (Law and Grey, 1989; Rowell, 1993; Heino, 1998).

ORIGIN OF SELECTION: EFFECTS OF FISHERIES ON POPULATIONS AND ENVIRONMENTS

Fisheries-induced selection pressures originate because fishing inevitably changes the environmental conditions fish experience. The effects of fishing are diverse, but the most obvious and direct is elevated mortality risk in a harvested stock, at least during some life stage. Even if conditions for the remaining fish remained unchanged (which of course they do not), change in the mortality regime would cause selection on life-history traits. Survival is 'hard currency', so selection pressures are often strong. Even completely unselective increase in overall mortality is expected to fuel selection on life-history traits (Roff, 1992; Stearns, 1992; Heino and Kaitala, 1999; Conover, 2000). Of course, fishing mortality is typically highly selective, for example in size, sex, maturity, behavioral patterns and activity, and spatial location. Selectivity on one basis may arise from selectivity on another. For example, sex and behavior are often linked, and harvesting with passive gear may result in higher mortality in the more active sex.

Individual growth rate often increases in harvested fish stocks as the stock abundance decreases. A decrease in stock abundance can result in greater per capita availability of resources and therefore improved growth, but it need not; the newly available resources may be consumed by another species, which increases in response to reduced competition. Negatively density-dependent individual growth has nevertheless been documented in marine fishes such as capelin (Gjøsaeter, 1998), herring (Shin and Rochet, 1998), flatfishes (Rijnsdorp and van Beek, 1991) and gadoids (Jørgensen, 1992; Helser and Almeida, 1997; Godø, 2000), as well as in many freshwater fishes, including salmonids (Healey, 1980; Post et al., 1999) and percids (Spangler et al., 1977; Persson et al., 2000). Density-dependent growth is also the mechanism behind the so-called compensatory response of an exploited stock: increased yield per recruit that partly compensates for lower recruitment.

The change in the growth conditions might induce selective pressures on size-related traits such as maturation, but growth conditions vary also naturally, and consequently, size-related traits in fish are often very plastic (Stearns and Crandall, 1984; Rochet, 1998). Changes in growth rate during the juvenile period may also interact with natural mortality rate. Natural mortality typically decreases with increasing size in small fish, as they outgrow some of their predators. If growth rate increases, individuals are exposed to high mortality risk for a shorter period, and total juvenile mortality can decrease.

Several excellent recent reviews emphasize that the effects of fisheries on these so-called ecosystem effects extend far beyond the target fish stocks (Jennings and Kaiser, 1998; Hall, 1999; Kaiser and de Groot, 2000; see also Gislason et al., 2000, and other papers in the same volume). For exploited stocks, changes in the biotic environment can result in new selection pressures through changed predation regime or resource availability, but the magnitude of such selection pressures and their possible manifestations are completely unknown for nontarget species.

LEVELS OF RESPONSE: POPULATIONS AND COMMUNITIES

Fishing removes individuals of both target and nontarget species, and it is selective with respect to size, shape, behavior, habitat, location, etc., of the fishes. Species as well as individuals differ in these characteristics, so responses to selection might be observed at both levels. At the level of communities, relative abundances of species can change. At the level of species, distribution of relevant phenotypic traits can change. Because variability between species is far larger than that within species, however, the effects of selective mortality are expected to be more readily seen at the community level than at the level of species. Community-level data are also likely to be available more often than data at species level—trends in relative abundances of species can often be estimated from catch statistics, whereas data documenting phenotypic variability within species requires that measurements be carried out at the level of individuals.

RESPONSES TO SELECTION AT THE COMMUNITY LEVEL.—Fishing alters size structure, diversity, trophic structure, and species composition of fish communities (Jennings and Kaiser, 1998; Pauly et al., 1998; Hall, 1999). Some fish species show stronger declines under exploitation than others. For example, different species of skates show strikingly different abundance trends in intensively fished regions (Walker and Hislop, 1998; DFO, 2000; Sosebee and Terceiro, 2000): some, such as thorny skate (*Raja radiata*) and little skate (*R. erinacea*), are often able to maintain their abundances and might even have increased locally, whereas others have declined to the extent that near extinctions of common (*R. batis*) and barndoor skate (*R. laevis*) have been reported (Brander, 1981; Casey and Myers, 1998).

Different abundance trends might result simply from differences in fishing mortality: target species are expected to decline most. Another trend is toward 'fishing down food webs': species at high trophic levels are the initial targets, but as their abundances decline, species at lower trophic level gradually become targets (Pauly et al., 1998). Clearly, however, species' life-history characteristics also play an important role. Large, late-maturing species are frequently said to be more prone to fisheries-induced declines than small, early-maturing species. Individuals of early-maturing species have a better chance of reproducing before becoming vulnerable to fishing, and small, early-maturing species tend also have high potential rates of increase, which enable them to withstand high fishing mortality (Brander, 1981; Walker and Hislop, 1998). In contrast, fishes whose life histories confer a low maximum rate of increase (such as common skate and barndoor skate) may be brought close to extinction even by low incidental fishing mortality.

Recent studies in a wide range of species have given more weight to the argument that a species' life history is an important determinant of its vulnerability to exploitation, even when phylogenetic (and probably trophic) effects are controlled for. The best-studied examples come from the northeast Atlantic and the North Sea (Jennings et al., 1998,

1999). Between 1925 and 1996, the North Sea bottom-dwelling fish community showed increases in abundances of species that have small maximum body size, grow fast, and mature early at small size (Jennings et al., 1999). In comparisons between pairs of related species, the one that had slower growth and matured later at larger size decreased more in abundance than its relative with higher potential rate of population increase. Similar results came from analysis of abundance trends in the northeast Atlantic: species that decreased in abundance relative to their nearest relatives had larger maximum body size, matured later, and had lower potential rate of population increase (Jennings et al., 1998).

In principle, if fishing pressure is relaxed, recovery of the community should be possible as long as no species have been fished to extinction and fishing has not resulted in irreversible damage to the physical environment. The time needed for a stock to return to its original abundance is expected to depend on the degree to which it has been depleted, as well as on the intrinsic rate of increase of that species: severely depleted stocks with low rates of increase will require long times to recover. At the community level, minimum recovery time is determined by the species with the longest recovery time.

In practice the recovery of stocks and communities that have been severely depleted is often extremely slow (Hutchings, 2000a), even slower than could be expected on the basis of their low abundance. A good example is the bottom-dwelling fish community of the Newfoundland region (DFO, 2000): despite several years of very low fishing effort, recovery of most of the stocks has been negligible. Potential causes are related to life histories of these stocks, irregularity of recruitment for natural reasons, and trophic interactions. Another example is the Norwegian spring-spawning herring: it took 30 yrs to rebuild the stock after the collapse in the 1960s (Torensen and Østvedt, 2000). Partial closure of the trawl fishery in the southeastern North Sea resulted in changes in size structure of the demersal fish community but not its species composition (Piet and Rijnsdorp, 1998).

In general, recovery of a community may be impeded by complex trophic interactions. Community dynamics may have multiple stable states, such that the community cannot return to its original state without a major perturbation. A stock can only grow if it has sufficient resources to feed on and if survival during all life stage is sufficiently high. Good survival during early life stages may, for example, require an initial cohort large enough to saturate predators and decrease per capita mortality. Once a stock has been pushed to low levels, strong cohorts may be produced only under optimal environmental conditions.

RESPONSES TO SELECTION AT THE SPECIES LEVEL.—Any increase in mortality, be it selective or nonselective, will cause selection on life-history traits. Fishing typically results in differential increase in mortality among individuals within a population. Most fishing gears are selective; the ones that are considered to be rather nonselective (such as some seines) can still cause substantial selective mortality because of nonrandom distribution of fish in space.

Individuals within a population are different from each other for many reasons. Much of the variability is simply ontogenetic: fish grow larger as they get older. Environmental variability causes variability even among individuals of the same age. For example, growth rates are influenced by both biotic (e.g., food availability) and physical factors (e.g., temperature). Fish can also respond adaptively to environmental variability: because of phenotypic plasticity, the same genotype can give rise to different phenotypes under different environmental conditions. For example, age and size at maturation are strongly

influenced by growth regime (Stearns and Crandall, 1984). Finally, genetic differences among the fish can cause phenotypic variability. To the extent that genotypic variability is linked to phenotypic variability in traits under selection, fisheries-induced selection can result in evolutionary change, that is, change in the genetic composition of the population.

Changes in phenotypic composition of populations subject to exploitation are best documented for life-history traits related to maturation and growth (Ricker, 1981; Trippel, 1995; Rochet, 1998; Godø and Haug, 1999; Law, 2000), although we have no reason to believe that other traits could not respond as well (see the next section). Large portions of the documented changes probably represent phenotypic plasticity and can probably be explained by the so-called compensatory mechanisms (Reznick, 1993; Trippel, 1995), that is, increased individual growth rate at decreased stock abundance. The extent to which genetic components influence the documented life-history changes is still largely an open issue.

Intensive selection can remove large amounts of existing genetic diversity. Some genotypes may be lost because of directional selection; others may disappear simply because of chance events associated with lower abundance. The latter effect is unlikely in most marine stocks that have large population sizes but may be a concern in freshwater fishes such as salmonids. It would mean that, even if selection pressure were reversed after a period of intensive directional selection, recovery of the population toward its original phenotypic state might be extremely slow. Selection pressure toward the original phenotypic state, in the absence of fishing, might also be much weaker than the selection caused by intensive fishing (Law and Grey, 1989; Rowell, 1993). Inability of a population to return to its original abundance (Hutchings, 2000a) might further hamper its genetic recovery.

TRAITS UNDER SELECTION

Selection works on differences between individuals. Below, we categorize variable traits as belonging to one of three broad categories: life-history traits, behavioral traits, and morphological traits.

LIFE-HISTORY TRAITS

Life-history traits are those that determine the age schedules of mortality and reproduction in populations. They strongly influence stock productivity, so changes in them are of immediate interest to management of fish stocks.

Growth Rate.—Fish grow throughout their lives. The idea that fishing can select for slower individual growth dates back to Miller (1957). Experiences from aquaculture, where selection for increased growth rate has successfully taken place, indicate that such selection could lead to genetic changes in the wild as well, but genetic decrease in growth rate can easily be masked if fishing results in greater food availability for the surviving fish (Ricker, 1981).

At least two mechanisms could select for slow growth. The first is related to behavior: fast-growing individuals need to forage more actively, so they are more likely to be caught by fishermen (Favro et al., 1979). The change in growth rate would therefore be a consequence of an evolving behavioral trait. Quantitative data would be necessary to assess

this hypothesis: does the decreased mortality risk of more passive foraging offset the losses in energy gain?

The second mechanism is based on size selectivity of fishing mortality (Miller, 1957; Spangler et al., 1977; Favro et al., 1979; Ricker, 1981). Many fishing gears (e.g., trawls and gill nets) are size selective, such that small individuals have low probability of being caught. Harvest strategies often take advantage of the size selectivity of gear (Hilborn and Walters, 1992). Even if the gear is not very selective, a minimum size limit can make fishing mortality highly size selective. In both cases, fish that grow more slowly enter the vulnerable size classes later. The benefit of decreased fishing mortality must be weighed against the potential costs of slower growth. Most important, fecundity usually increases roughly linearly with weight in fish (Pitcher and Hart, 1990; Roff, 1983). The risk of dying from nonhuman predation may also increase because of negatively size-dependent natural mortality (Pitcher and Hart, 1990; Wootton, 1998). Obviously, the question of whether these costs will offset the benefits has no general answer.

A trend toward smaller body size in an intensively fished brown trout population led Favro et al. (1979) to try to determine whether the documented decrease could be caused by genetic change. On their assumptions of decreased fecundity as the cost of slow growth and simple but not unrealistic genetics, the documented decrease could well have been due to size-selective fishing mortality. Kirkpatrick (1993) has studied the effect of size-selective mortality on growth in a quantitative genetics model, showing that substantial changes can occur rapidly, but his model did not account for size-dependent fecundity.

An important caveat in interpreting the theoretical results above is that the authors assume that growth rate can evolve but that other traits cannot. Other life-history changes could evolve more easily and provide superior means of coping with fishing mortality. Another possibility is that change in growth is a mechanistic consequence of evolution in some other trait. An obvious candidate trait is age at maturation—earlier maturation results in smaller size at age after maturation (see below). Higher reproductive effort at age has exactly the same consequence. These possibilities should be ruled out before genetic change in growth rate is invoked.

Ricker's (1981) study on changes in size of five species of Pacific salmon (*Oncorhynchus* spp.) is the classical example in which the size of the fish in the catch has decreased. Because most of the species are harvested with size-selective gear, such decreases could potentially represent adaptive responses to fishing. Interpretation of the changes is more complex, however, because changes in size are often coupled with changes in age at maturation. Further, samples contain mixtures of fish at different ages, so some changes may reflect only change in age structure of the stock. The case of pink salmon (*O. gorbuscha*) is more straightforward to interpret, however (Ricker et al., 1978). Pink salmon almost always matures at age two, and it is harvested only toward the end of its life. The observed decrease in size of the fish therefore probably reflects a true decrease in individual growth rates. Because harvesting usually results in improved rather than worsened feeding conditions, the decrease is unlikely to be primarily of environmental origin. Although the decline in size has occurred in parallel with some decreases in surface temperatures near the coast, the temperature effect is not sufficient to explain the size decrease. The decrease in growth is therefore likely to have a genetic basis. The observed rate of decline in size is possible with moderate heritability of weight ($h^2 \sim 0.3$). Further, there is evidence that the decline in size started only in the early 1950s when the fisher-

men probably changed their fishing practices such that size selectivity increased (Ricker et al., 1978).

Note that Pacific salmon might be more prone to decrease in size than most other fish because they reproduce only once and then die; that is, they are semelparous. If a semelparous fish manages to mature before growing to the size range in which it is vulnerable to fishing, it gains a large survival advantage. This advantage might offset the cost of decreased fecundity. On the other hand, fish that reproduce several times and continue to grow after maturation (as most fish species do) can only slightly delay reaching the vulnerable size range by growing more slowly, whereas they suffer the fecundity disadvantage for the rest of their lives. Although the question can only be settled with the aid of quantitative models, the improved survival seems unlikely to offset the loss in fecundity. A genetic decrease in individual growth therefore seems an unlikely general response in harvested stocks, but growth rate might change in response to change in other traits. This possibility is discussed below.

Age and Size at Maturation.—Timing of maturation strongly influences the expected lifetime reproductive success of an individual. Growth typically slows after maturation, so early maturation results in a smaller size at age later in life. Because fecundity depends on individual size, individuals face a trade-off between current and future reproductive success. The balance depends critically on mortality regime, which is well known from life-history theory. Mortality regime has been greatly changed by exploitation in large number of fish stocks.

Beginning with Borisov (1978), the possibility that intensive harvesting can select for earlier maturation has raised increasing concerns. The argument is that, in heavily exploited stocks, fish that delay maturation for too long have very little chance of surviving to maturity and are thus expected to have almost zero fitness. Maturation being a heritable trait (Roff, 1997), exploited stocks would then be expected to evolve toward earlier maturation (Borisov, 1978; Rago and Goodyear, 1987; Law and Grey, 1989), even if the situation is not quite that extreme. This theoretical prediction agrees with the observation that age at maturation has declined in many exploited fish stocks, mostly gadoids and flatfish that have traditionally matured late (Trippel, 1995; Rochet, 1998; Law, 2000). In many cases, size at maturation has also changed.

The interpretation of the observed changes in maturation is not clear. Growth conditions are well documented to have improved in many exploited stocks. Because maturation usually depends on size, acceleration of growth results also in accelerated maturation. This is the so-called 'compensatory response' hypothesis (Policansky, 1993; Trippel, 1995), which is typically invoked to explain earlier maturation in exploited stocks; this hypothesis was already known at the time of Borisov (1978). The more controversial hypothesis states that the life history changes in exploited stocks represent adaptive evolutionary responses (Borisov, 1978; Law and Grey, 1989; Policansky, 1993; Trippel, 1995). These two hypotheses are not mutually exclusive: the changes can have both environmental and genetic components.

The problem is in disentangling environmental and genetic changes. An elegant solution has been proposed by Rijnsdorp (1992, 1993). The so-called reaction norm for age and size at maturation gives age- and size-specific maturation probabilities for immature fish with different growth rates. In other words, it describes how fish cope with variability in growth rates. The reaction norm can be estimated from the appropriate data and is largely independent of long-term changes in growth (Fig. 1). Therefore, by focusing on

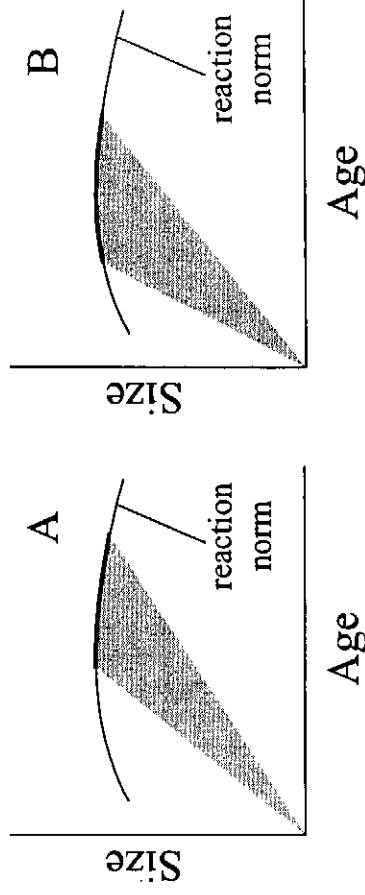


Figure 1. Using reaction norm for age and size at maturation to remove the effects of growth on maturation. The reaction norm gives the probability of maturing as a function of age and size. In this example it is assumed that this probability increases abruptly from zero (below the reaction norm) to one (above the reaction norm). Thus, an individual matures when its growth trajectory hits the reaction norm. The range of growth trajectories up to maturation observed under poor growth conditions is given by the gray triangle (A). Variability of growth allows observation of a certain part of the reaction norm, highlighted with a thick curve. During more favorable growth conditions, growth trajectories are shifted upward, and a partly different part of the reaction norm can be observed (B). The vertical position of the reaction norm is not influenced by the change in growth. Therefore, if only growth conditions have changed, the horizontally overlapping parts of the two reaction norms should not be significantly different. On the other hand, a significant vertical shift in the reaction norm indicates that an environmental change influencing maturation independently from growth has taken place and/or that a genetic change in maturation has occurred.

the covariation of age and size at maturation in the form of the reaction norm, we can filter the major environmental influence out of changes in age and size at maturation. Although horizontal shifts in the position of maturation reaction norms reflect mostly phenotypic plasticity, continual trends in the vertical position toward smaller size indicate genetic response to fisheries-induced selection. Of course, this kind of correlative approach can never provide unequivocal evidence of genetic changes.

Rijnsdorp (1993) applied the reaction-norm analysis to North Sea plaice (*Pleuronectes platessa*), which has been exploited intensively for more than a century. Both age and size at maturation have decreased in this stock since 1900. These changes coincide with increased growth in juvenile plaice. Thus, compensatory mechanisms obviously play a role in the observed changes, but the data also support the hypothesis that genetic changes have taken place: the reaction norm for age and size at maturation has changed significantly from 1904–1911 to 1960–1990 (Rijnsdorp, 1993).

The case of northeast Arctic cod (*Gadus morhua*) is also enlightening. Theoretically, the selection differential for earlier maturity should have been particularly strong in this stock (Law and Grey, 1989). Intensive harvesting has historically taken place in the spawning grounds. By delaying maturation, individual cod could postpone their exposure to increased mortality risk while gaining in terms of increased size and, after maturation, increased fecundity. This historical selection pressure for delayed maturation may be responsible for the late maturation traditionally observed in this stock (Law and Grey, 1989)—the median age at maturation was more than 10 yrs before the 1940s (Jørgensen, 1990). Since around 1930, however, when the modern trawler fishery at the feeding grounds started, the harvest pattern has changed such that harvesting is largely nonselective with respect to maturity. This change resulted in selection for earlier maturation. Indeed, the

decline in average age at maturation in this stock has been particularly strong (Jørgensen, 1990). Size at maturity has declined in parallel (Godø, 2000). Reaction-norm analysis indicates that these changes have a genetic component (M. Heino, U. Dieckmann, and O. R. Godø, unpubl.).

Analysis of changes in maturation at the community level reveals changes similar to those observed within single fish stocks. In exploited fish communities, species that mature late have decreased more in relative and absolute abundance than have early-maturing ones (Jennings et al., 1998, 1999).

Two theoretical studies indicate that decline in age at maturation could cause a major decline in sustainable yield (Law and Grey 1989; Heino 1998). Although both studies are somewhat limited because they do not take into account the effect of compensatory growth, their findings call for increased awareness of the possibility of evolutionary changes in the key life-history traits.

Reproductive Effort.—Most fish and shellfish exhibit indeterminate growth: they continue to grow after maturation, though at decreasing pace. The strategy at first seems perplexing, because energy allocated to body growth could in principle have been used to increase reproductive output, but it can be advantageous if the fecundity gain later in life associated with larger size is high enough to compensate for mortality risk and the immediate loss in fecundity (Heino and Kaitala, 1999).

If the fish are faced with increasingly high adult mortality, investment in future reproduction may not pay off. Consequently, selection will favor not only earlier reproduction but also higher reproductive effort at age, at the expense of body growth. This is a quite general prediction from life-history theory (Heino and Kaitala, 1999). Reproductive effort can be estimated most easily as the relative gonad weight (gonadosomatic index). Unfortunately the only stock for which suitable data are available for a test of the hypothesis seems to be the North Sea plaice. In accordance with the prediction, female plaice show slight increases in size-specific ovary weights over a period of ca. 30 yrs (Rijnsdorp, 1991), but the role of varying growth conditions in this change is unclear.

BEHAVIORAL TRAITS

Behavioral characteristics are heritable, like other biological features, and follow the same general laws (see, e.g., Kirpichnikov, 1981; Trexler, 1990; Roff, 1997). For fish, features like temperature preference, homing, avoidance of fishing gears, cannibalism, aggression, defense, etc. have been shown to have heritable components. In general, heritabilities in the range 0.1–0.4 can be expected. Most behavioral characteristics are determined by multiple loci, so correlations with other characteristics may also be common.

We will distinguish here between two types of fish behavior that are both important for selectivity and efficiency of fishing gear. Natural behavior includes distributional (horizontal and vertical) and migratory characteristics, whereas affected behavior is the recorded characteristics of an individual coming into the catching zone of fishing gears. Both types of behavior affect availability of fish to the fishing gear and hence its efficiency and selectivity (Wardle, 1993; Fernö and Olsen, 1994).

Natural Fish Behavior.—Fish are free-swimming individuals in three dimensions characterized by the geographical position and depth. The true position of an individual in space and time is influenced by external conditions such as mortality risk and availability of food, as well as by internal state of the individual and its genotype. Under undisturbed

conditions, fish are expected to choose their positions such that survival and feeding prospects are optimal (Fiksen et al., 1995; Slotte and Fiksen, 2000).

In many fisheries, demersal gears like bottom trawls, seines, nets, and baited lines are the dominant gears. They will be less efficient for pelagically distributed fish than for the bottom-dwelling component (see, e.g., Godø, 1994). Such an unbalanced exploitation may over time give rise to a stock with different distributional characteristics. Similarly, spatially heterogeneous exploitation pressure in the distribution area of a stock may over time lead to changes in distribution and migration if these properties are heritable. In particular, a systematic temporal and geographic heterogeneity in exploitation in the spawning areas may change the overall distribution and migration properties of the whole stock. For example, the importance of the traditional inshore Lofoten spawning grounds has gradually been diminishing in northeast Arctic cod (Sundby and Godø, 1994), perhaps as a result of hundreds of years of systematic and high exploitation in the traditional fishing areas of Lofoten (Øiestad, 1994). On the other hand, concentration of fishing effort around peak spawning could favor early and late spawners and therefore select for increased spread of spawning period.

Affected Fish Behavior.—Human disturbance can strongly affect behavioral characteristics and individual survival in terrestrial species (see, e.g., von Holst, 1998). Although some anecdotal evidence on behavioral changes in exploited stocks exists (Stone and Dixon, 2001), studies on such effects in the underwater world are certainly difficult. Technological progress during the recent decades has made such studies more feasible, however (Fernø and Olsen, 1994). Typical predator-avoidance reaction leads to an early escape from the catching volume of an approaching trawler. Observations with modern technology show strong reactions in some major commercial species like cod, haddock, and herring (Fig. 2). The individuals with the lowest threshold of reaction improve their escape probability (Ona and Godø, 1992).

For passive gears like gill nets, the individuals with the highest alertness will minimize their probability of being entangled, whereas the most assertive specimens are likely to be hooked on baited gears (Furevik, 1994; Løkkeborg, 1994). The effect of learning in relation to efficiency of fishing gears in the wild is unknown, but it is supposed to be substantial, on the basis of experience from laboratory and field experiments (e.g., Brown and Warburton, 1999). Miller (1957) suggested that angling selects for intelligent fish that are less vulnerable to lures.

Passive gears have been used for hundreds of years, whereas trawls and monofilaments were developed during the 20th century. Initially, small towed nets were deployed from sailing vessels or small motorized crafts. Similar gear and vessel combinations today would surely catch virtually nothing—unfortunately such experiments have not been reported. Nevertheless, a steady increase in efficiency has been necessary to keep fishing profitable, perhaps as a result of improved gear avoidance by the fish. Of course overfishing and reduced densities may play decisive roles, but in addition, exploitation is thought to have been selecting, to an unknown extent, for improved behavioral adaptations.

Improved avoidance behavior might have secondary effects on fish stocks. An individual that is too easily alerted and begins an unneeded avoidance reaction will lose some resources and time otherwise available for normal activities (Walters, 2000). Thus, fish might get ecologically less efficient, but the extent to which such behavior could affect energetics of an individual is unknown.

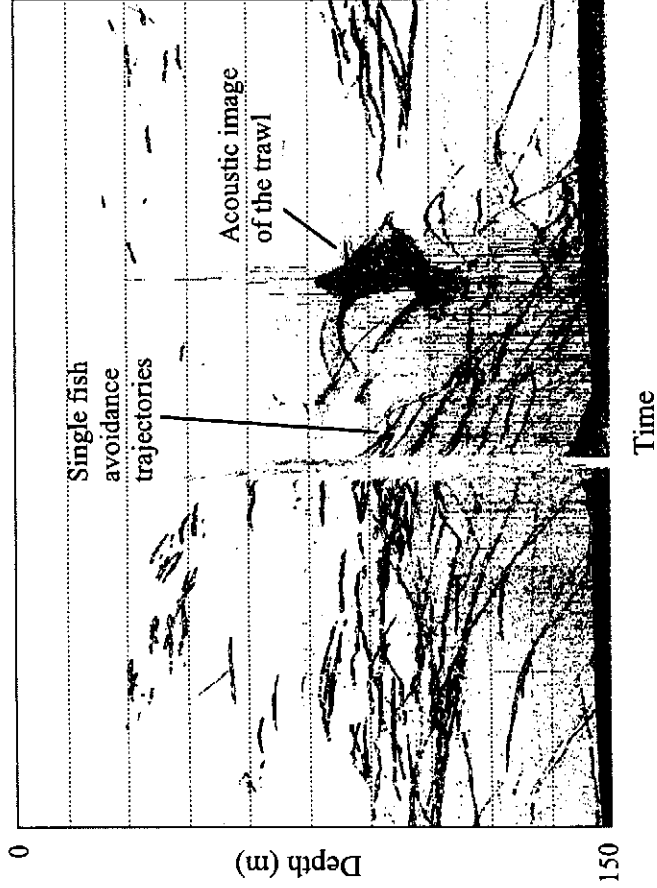


Figure 2. Echogram of cod avoidance reaction during pelagic trawling as observed from a free-floating buoy. The time span covered in the echogram is about 7 min.

MORPHOLOGICAL TRAITS

Fishing gear may select not only by size but also by morphological differences among fish of similar sizes. For gill nets in particular, efficiency of capture declines sharply when the ratio of the girth at the position where the fish was caught to the mesh perimeter deviates too much from unity (Reis and Pawson, 1999). If the maximum selectivity of a gill net is such that the fish cannot escape capture simply by growing rapidly through the vulnerable size range, selection should be possible for altered body dimensions. Either slimmer (i.e., more likely to pass through the net) or deeper (i.e., less likely to become entangled) body shape might help to decrease mortality risk.

Some evidence indicates that body morphology could influence vulnerability of fish to exploitation at the community level (Koslow et al., 1988), but no rigorous evidence on morphological changes in response to fishing seems to be available. This lack of evidence could result as well from the lack of attention as from the lack of such responses.

Responses to selection on morphological traits would be facilitated by the high heritability of morphological traits, as compared to life-history traits (Roff, 1997). Fish morphology is already known, from aquaculture experience, to respond readily to selection, but it could also be phenotypically plastic: in some fish, deeper-bodied forms develop in the presence of predators (Brönmark and Miner, 1992; Holopainen et al., 1997).

Changes in body morphology could also occur as secondary responses when other traits are evolving. If, for example, higher reproductive effort at age evolves, then the fish necessarily become more obese, but the functional significance of body shape may constrain such changes.

DISCUSSION

Here, we have reviewed some of the environmental changes induced by fisheries, selection pressures that are generated by these changes, and some of the most likely responses such changes could cause. The potential responses include evolutionary changes that may have adverse effects on sustainable yield. Even though the precautionary approach is becoming the dominant principle for development of modern fisheries management, the evolutionary aspects of long-term selective exploitation are still not seriously considered. Indeed, interest in the topic has been almost entirely academic (Stokes and Law, 2000). Although, admittedly, much of the evidence of evolutionary effects is vague and inconclusive, we believe that it is urgent to set this issue on the agenda and to include its considerations in the development of target biological reference points for future management regimes. Below we highlight the main reasons why consideration of fisheries-induced adaptive changes is important for fisheries management.

First, on the bright side, adaptations to fishing pressure enable fish to sustain higher fishing pressure. Earlier maturation increases the chances that a fish will reproduce before it gets caught. For example, the northeast Arctic cod stock could probably not withstand current fishing mortality, $F \sim 0.8$, if maturation still took place at 10–11 yrs, instead of the current median age of 6–7 yrs (Godø, 2000). Changes in behavior that increase probability of avoiding capture by fishing gear effectively decrease the fishing mortality imposed by a unit of fishing effort. Thus, other things being equal, adaptations can reduce the risk of collapse. Nevertheless, on short time scales this beneficial consequence of adaptivity is likely to be so small that it is overshadowed by other factors and thus has no implications for management. In the longer term, significant changes in age structure or catchability are probably taken into account in normal assessment practices. Note, however, that changes in catchability are dominated by the effects of adopting improved fishing technologies (an adaptive response on the part of the fishermen!).

From the human perspective, most of the fisheries-induced changes are undesirable. The worst possibility is that sustainable yield might decrease as a result of earlier maturation, as predicted by some simple models (Law and Grey, 1989; Heino, 1998). The main mechanism in these models responsible for the yield that decreases with age at maturity is that immature fish experience somewhat smaller fishing mortality than mature fish. Late maturation allows large biomass of immature fish to build up, and this biomass is responsible for the high productivity. This mechanism may not be generally applicable. Further, the models by Law and Grey (1989) and Heino (1998) ignore the compensatory effects, so the results must be treated with caution.

A more general mechanism for decreased yield as a result of fisheries-induced adaptive changes might be that biomass available for fisheries can decrease if selection results in slower growth and smaller size at age. This mechanism requires that small fish be excluded from the fishery, whether because of size-limit regulations, difficulty of capture, or lack of economic value. Slower growth may evolve either as lower growth rate per se or because of changes in maturation and reproductive effort. Second, if the size structure of an exploited population is truncated, resources that can be consumed only by the largest individuals are no longer available, so some potential productivity might be lost.

Smaller size at age might also be undesirable in its own right. In gadoids, small females produce smaller, less viable eggs and larvae than large females (Trippel, 1995). Larger fish usually have higher market value, and in recreational fisheries, large fish are often

much more highly valued than small ones. Shift in the size structure of a stock can also lead to higher levels of discarding.

In stocks that undertake extensive spawning migrations, decreased size might have further negative effects. Anadromous fish that migrate to spawn in fresh waters might not be able to reach the uppermost reaches of river systems. Even in purely marine fish, spawning migration imposes an energetic stress that would be relatively larger for smaller individuals. If feeding conditions before the migration are poor, the energetic stress might become too high for the fish maturing at small size, and they might either fail to reach the spawning grounds or skip the spawning altogether. Likelihood of recruitment failure under poor conditions could therefore increase. This scenario is not unlikely, e.g., for the northeast Arctic cod, whose feeding grounds are at the northern edge of the species' range and subject to considerable environmental fluctuations.

Behavioral adaptations that increase a fish's probability of avoiding capture may make it a less efficient forager (Walters, 2000). Very cautious fish will have less time available for foraging, and part of the resources available for them can then be consumed by other species of no commercial value. Fish may also choose to forage on suboptimal habitats or areas subject to less disturbance by fishing gear. Thus, some productivity of the aquatic ecosystem can be lost, at least from the human perspective.

Fish that best survive a period of high fishing pressure may not be the ones that would best guarantee the long-term viability of the stock. In particular, they may not be ecologically efficient when the fishing pressure is relaxed. The possibility that genetic changes in life-history traits and behavior contribute to the slow recovery of many overexploited stocks (Hutchings, 2000a) should not be dismissed.

In conclusion, the consequences of fisheries-induced selection are potentially serious and far-reaching, and they call for more attention. A further source of worry is irreversibility of fisheries-induced changes. The effects of fishing on abundance of target populations are often thought to be mostly easily reversed, albeit with some delay (Jennings and Kaiser, 1998). Many fish stocks recover very slowly, however, even when fishing pressure is significantly reduced (Hutchings, 2000a). For genetic recovery, the situation is probably even worse. First, selection pressures are not necessarily symmetric. Fishing can create a very strong selection gradient for early maturation, whereas in the absence of fishing, late maturity is only weakly selected for (Law and Grey, 1989; Rowell, 1993). Second, selection can crop genetic diversity from the population. If genotypes promoting late maturation are lost from the population, lack of genetic variability may hinder evolution toward delayed maturation, even when delayed maturation is strongly selected for.

The paucity of attention to fisheries-induced adaptive changes probably stems from two major reasons. First, evidence on fisheries-induced adaptive changes has been, and still is, scanty and correlative. Second, evolutionary changes are often thought to occur only at time scales irrelevant to fisheries management. Both concerns are valid and call urgently for more work. The lack of evidence is predominantly an empirical issue, and the situation can only be improved by an increase in effort to analyze existing data. We postulate that analysis of reaction norms will prove to be a very fruitful approach. Life-history models can help to identify the most likely changes and the stocks that are most vulnerable. In the future, monitoring programs should be devised for such stocks, as well as for the most valuable stocks. For the moment, the analyses must be based on phenotypic measurements—the genetics of maturation are not yet well enough known—but neutral markers can still provide valuable insights into the genetics of exploited fish stocks.

Analysis of the observed changes will give a better idea of the potential speed of adaptive changes in some examples. Generally, the speed depends both on the strength of selection pressures and on the heritabilities of relevant traits. The strength of selection can be assessed given sufficient knowledge of the ecology of a stock and fishing mortalities; beginning to assess the strength of these selection pressures in various fish stocks with different life histories and exploitation regimes will be an important task. Assessing heritabilities in the wild will be an important challenge—little is currently known about heritability of life-history or behavioral traits in the wild. Meanwhile, modeling approaches should be used to assess whether or not a given ecological setting gives rise to significant changes within time scales of interest, on the assumption of reasonable heritabilities.

A third issue that deserves urgent attention is the critical assessment of the consequences of adaptive changes on sustainable yield. Although age and size at maturation are obviously traits that affect sustainable yields, their actual effects are uncertain. Current models predicting a decrease in yield in response to earlier maturity are too simplistic, and it is important to know whether and to what extent that prediction holds in more realistic models. Here an ecosystem-oriented approach that takes compensatory responses adequately into account will be needed.

The possibilities for managing fisheries-induced adaptive changes are poorly known and should be immediately addressed. Decreasing fishing pressure helps to decrease the selection pressures but may not easily reverse them. A theoretical possibility is to harvest only mature individuals and thereby select for delayed maturation (Law and Grey, 1989; Heino, 1998), but that strategy may not be feasible in reality. Marine protected areas show some promise (Trexler and Travis, 2000). The possibility of using size-based management tools remains unexplored.

Fisheries-induced adaptive changes in exploited populations are occurring. They may have undesirable consequences for the characteristics of populations relevant to man, including sustainable yield. Worst of all, such changes may not be easily reversible. Consideration of fisheries-induced selection pressures therefore adds a new challenge for the precautionary approach in management of fish resources.

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