THE EFFECTS OF FISHING ON SPECIES AND GENETIC DIVERSITY

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> “There are genes that have not changed since the very first single-celled creatures populated the primeval ooze. There are genes that were developed when our ancestors were worm-like. There are genes that must have first appeared when our ancestors were fish. There are genes that exist in their present form only because of recent epidemics of disease. And there are genes that can be used to write the history of human migrations in the last few thousand years.” M. Ridley (1999) reflecting on the human genome.

ABSTRACT

The preservation of genetic resources has become an important element of conservation. This overview is meant to provide an understanding of the importance of conserving genetic variation both at the level of species and of populations within species. The loss of species in the marine environment is not as extensive as in freshwater or terrestrial systems. However, we have an imperfect knowledge of both the numbers of marine species and of extinction events. New species are still being discovered, even in well-studied areas, while proving that something is no longer there has produced conservative estimates of losses. Extinction of marine mammals and gastropod molluscs has been documented. Of these, overfishing has caused the extinction of the Steller’s sea cow and was instrumental in the loss of the Caribbean monk seal.

Within species, genetic diversity is partitioned among and within populations. Overfishing is seen as the major threat to the loss of marine populations while habitat degradation is threatening anadromous, estuarine and freshwater species, and population extinction has been documented. The number of spawning components is a guide to assisting managers in preserving this aspect of within species diversity, as they are often identifiable in space and time. Certain species, such as herring have a large number of populations, while others such as mackerel have fewer.

Fishing can also alter genetic diversity within populations, even when numbers are high. When fishing is highly selective, it has the potential to permanently change the characteristics within a population, usually in directions of less economic value. Removing large fish generally appears to favour slow-growing, early maturing fish.

At all three levels of organization previous paradigms have not stood the test of time. Marine species can go extinct; marine fish have much more genetic structure than previously supposed; selective fishing can cause heritable differences in yield and life-history traits.

INTRODUCTION

The cells of all living organisms contain a genetic code that directs biochemical processes and development. This code is composed of only four letters, A, G, C and T (or U) which transcribe, in groups of three, into one of twenty different types of amino acids, the so-called "building blocks" of proteins. The nature of a protein can influence various characteristics of an individual, from temperature tolerance to coloration or body size. This translation of the code is the same in all organisms from dandelions to whales and although established billions of years ago, was only revealed to us in the 1950s. From this basis the great diversity of living organisms has grown.

The genetic code has another distinguishing property and that is replication. The code is responsible for living organisms producing similar copies of themselves. The code is the reason that children look like their parents or grandparents, and why cod produce other cod. However, most advanced organisms do not produce exact copies of themselves (clones). Instead the codes provided by the mother and by the father are recombined to produce a unique individual in their offspring. The manner in which this occurs follows the rules of heredity, giving genetic data a unique theoretical base and genealogy, which is very different from all other types of data we collect.

Any group within which genetic material can be exchanged between individuals, across generations (a species), represents a unique evolutionary lineage that cannot be replaced once lost. Within it is the story of the generations that have occurred from the pre-Cambrian seas through to historical times. While some would argue that species that have no closely related living relatives are more deserving of conservation than those with a number of close relatives (cf. Vecchione *et al.,* 2000), the fact remains that the combination of genes in any species is unique.

The maintenance of genetic diversity in marine species has become an important element of conservation. This overview is meant to provide an understanding of the importance of conserving genetic variation both at the level of species and also of populations within species. Specifically, the effects that fishing practices have on genetic diversity at the species, population and genetic levels of organization are briefly reviewed and, wherever possible, examples are provided.

"ONE FISH, TWO FISH, RED FISH, BLUE FISH" – THE LOSS OF SPECIES IN THE MARINE ENVIRONMENT

The irrevocability of extinction is a prime motivator for conservationists. Most would agree that the loss of a species is something to avoid, and that humans have a stewardship responsibility in this area. However, species extinction also poses a major threat to biological diversity that reverberates through the levels of species assemblages and ecosystems. Further, when species of commercial interest go extinct, or are reduced to low levels, harvest pressure is often transferred to others with similar traits, magnifying the impact of loss on the system. Increasingly, scientists and economists are aware of the implication of species loss and it's effect on biological processes and ecosystem function as well as on human society (Ehrlich and Ehrlich, 1994).

Extinction has always been a part of the earth's history and fossil records tell us that the average longevity of a species is on the order of one to 10 million years, at least for marine invertebrates (May *et al.,* 1995). Currently, there is an accelerated loss of species due to human activities. It has been suggested that recent extinction rates are 100 to 1000 times higher than the pre-human levels, with these rates potentially increasing by a factor of 10 in the near future (Pimm *et al.,* 1995).

Is species extinction a problem in the sea? One of the difficulties of addressing the issue of species loss in the marine environment is that we do not have an accurate list of the organisms that live there, or indeed, anywhere on earth. To date, about 300 000 marine species have been described globally, although precise estimates are hindered by deficiencies in our ability to recognize and name them. This has resulted in misidentification and changes to the numbers as mistakes are corrected (Vecchione *et al.,* 2000). Scientists differ in their estimates of the total number of marine species, including as yet undiscovered organisms; some think that there are only about 800 000 (GESAMP, 1997) while others suspect that there might be several million or more (Malakoff, 1997). This discrepancy is seen to differing degrees in different groups, depending upon how well known they are. For example, Grassle and Maciolek (1992) have suggested that the global species list just for the deep-sea invertebrates living in marine sediments might be as high as 10 million (only about 100 000 have been described). This has been logically contested by Poore and Wilson (1993) with support from May (1993), who predicted that the numbers will be much lower (5 million and 500 000 respectively). The inconsistency is in part due to the methods of extrapolating discovery rates from newly explored habitats to broader oceanic areas. Overall, our sampling of deep-sea environments has been very sketchy and when new habitats are first explored it is expected that new species will be discovered. A recent research programme on Tasmanian seamounts identified about 300 species of fish and invertebrates, with approximately one-third new to science (Koslow *et al.,* 2000). With vast areas, such as the West Indian Ocean, requiring scientific study, it may be some time before we have more precise estimates of the number of species on this planet.

However, some parts of the world's oceans have been intensively studied, and the discovery rate of new species in those areas is lower. For example, the marine waters of Britain and Ireland have been well studied since the 18th century. Of the 331 species of fish in the region listed by 1992, only 17 were described after 1900 (Costello *et al.,* 1996). However, among the smaller forms of life, new discoveries continue even in these relatively well-studied environments (Costello *et al.,* 1996). Those have included the exciting discovery of two new phyla (major groupings of species) of small marine organisms in recent decades. The discovery of phyla is truly extraordinary as the 1.5 million or so species described on the planet can all be classified into only about 43 phyla. In 1983, the Danish zoologist, R.M. Kristensen discovered the phylum Loricifera living in the tiny spaces between marine gravel in sediments off the French coast (Kristensen, 1983). Since then at least 10 more species have been described (with rumours of 100s under investigation!), including inhabitants of coastal areas of North America. And in 1995 in the Kattegat between Denmark and Sweden, another new phylum (Cycliophora) was discovered living on the mouth bristles of the Norwegian lobster and feeding on scraps of the lobster's food (Funch and Kristensen, 1995; Conway Morris, 1995).

This is not to say that only the smaller forms of life have remained a mystery. As recently as 1991, a new species of beaked whale (*Mesoplodon peruvianus*) was described from Peru (Reyes *et al.,* 1991) and it is likely that yet others remain to be found. The most famous example of a new discovery is the coelacanth (*Latimeria chalumnae*), often referred to as the "living fossil" (Figure 1). The coelacanth lineage was thought to have been extinct for *80 million years* when a live specimen was brought ashore by a fisherman off the eastern coast of South Africa in 1938. Miraculously this specimen made it into the hands of people who could recognize it and alert the scientific community. Efforts to discover where the fish came from eventually identified a small population living off the Comoros Islands between Mozambique on the African continent and Madagascar, where it had been caught with enough frequency for it to have been given a name in the native language. Just recently a second population was discovered from North Sulawesi (Erdmann *et al.,* 1998; Fricke *et al.,* 2000). This second find has since been described as a new species, *Latimeria menadoensis*, using genetic evidence. In 2000, a third population (perhaps another species?) was verified in the St. Lucia Marine Protected Area on the northeast coast of South Africa. The total number of coelacanths may be greater than 100 000 (Hissmann *et al.,* 1998). Clearly there remains much to learn about life in the oceans.

Just as we do not know precisely the number of species in the world's oceans, neither do we know how many have gone extinct due to human activities. Carlton (1993) has claimed that hundreds of marine invertebrates have not been seen since the 18th and 19th centuries (while recognizing that a number of factors other than extinction may account for some of these). There have also been cases where a species has been declared extinct, as with the hydrocoral *Millepora boschmai*, only to be found at a later date (Carlton, 1993). It is much harder to prove that something is no longer there than to prove that it is, especially when much of the marine environment is not readily accessible. This reality has sparked a debate on "burden of proof" that remains to be resolved. Comparatively, there are many more documented cases of extinction in freshwater and on land than there are in marine environments (cf. Culotta, 1994; Huntsman, 1994; Ryman, 1995; Malakoff, 1997; Powles *et al.,* 2000). This has been interpreted by some to reflect a resiliency of marine species to human impacts (cf. Huntsman, 1994; Powles *et al.,* 2000; Hutchings, 2001). However, particular groups of marine organisms do appear to be more vulnerable. Extinction of marine mammals (e.g. Steller's sea cow, Caribbean monk seal), gastropod molluscs (e.g. eelgrass limpet, Asian periwinkle), anadromous fish (New Zealand grayling), and an Australian red alga (*Vanvoorstia bennettiana*) have been documented, while several species of skates, sharks, sturgeons, pipefishes, seahorses and groupers, amongst others, are believed to be at risk (Carlton, 1993; IUCN, 1996; Musick *et al.,* 2000; Powles *et al.,* 2000; Morris *et al.,* 2000). Additionally, species such as the Great auk and the Sea mink, which depended upon the marine environment, have also been lost.

The role of fishing in extinction events

Of the documented marine species extinctions, fishing is directly accountable only for the loss of the Steller's sea cow, a large, slow moving marine mammal native to the Bering Sea. Within 27 years of discovery in 1741 it was driven to extinction by visiting sea-otter hunters, who used it for food. In the case of the Caribbean monk seal, an aggressive fishery for the skins and oil decimated numbers quickly once Europeans populated the West Indies in the 1600s (Debrot, 2000), though a few individuals survived the exploitation only to be persecuted by fishermen. The last sighting of this shy, formerly wide-ranging tropical species, was a small group of seals reported in 1952 (Wing, 1992, as cited in Debrot, 2000). Is it coincidental that marine mammals were the first to be exploited to extinction? Seals, sea cows and whales have particular characteristics that contribute to their vulnerability: (1) they take several years or more to mature, (2) when they do have offspring, they have only one or two annually, (3) they are large, and (4) they spend part of their lives in confined habitats (beaches, ice flows, coastal waters); the last characteristic making them easy to hunt, even when scarce.

Typically, for anadromous fish (fish that spend part of their time in freshwater and part in the open ocean) and fish living in estuaries and lagoons, habitat degradation is the most common factor leading to extinction from rivers and watersheds. Habitat changes can occur through the construction of bridges and dams, and through pollution. Because anadromous fish return to confined freshwaters to spawn, they also have been heavily fished. Overfishing in combination with habitat loss and other factors increases the vulnerability of anadromous fish to extinction (Powles *et al.,* 2000). The New Zealand grayling is the only extinct anadromous fish documented to date. It was endemic to New Zealand, where it was abundant when Europeans first colonized in the 1860s. Habitat destruction, overfishing and the introduction of trout led to its extinction within 50 years. Currently, the sturgeons (*Acipenser* spp.) are the most vulnerable group of anadromous fish in North America, with the shortnose and white sturgeon listed as endangered by the American Fisheries Society (Musick *et al.,* 2000). There are 27 species of sturgeon (some are entirely freshwater) and all are listed as either endangered or threatened by CITES. Sturgeons also have special characteristics which render them vulnerable to extinction: (1) very low productivity, (2) specialized habitat requirements, and (3) large size – at approximately 6 m in length, the beluga sturgeon is the largest freshwater fish.

Amongst the purely marine fish, sharks, rays, jewfish, groupers, Pacific rockfish, swordfish and marlins share one or more of the following characteristics: (1) large body size, (2) naturally lower numbers, (3) relatively long life-spans, (4) late maturation and reproduction, and (5) occupation of coastal waters with humans. Many species of shark, including the great white shark, are listed by the IUCN as vulnerable to extinction, while 37 species of groupers are considered threatened (Morris *et al.,* 2000). Other marine species are both rare and have localized distributions, rendering them vulnerable to habitat deterioration and overfishing (incidental fishing in the case of non-commercial species). Swaby and Potts (1990) classified the distribution of 165 rare marine fish in Great Britain and found that more than one-third had restricted distributions, which were often clearly defined by habitat boundaries. In contrast, other species have very large population sizes and occupy large areas of ocean, lay large numbers of small eggs, and have eggs that may drift long distances before hatching. Cod, haddock, small tunas, anchovy and mackerel fit this description, as do many invertebrates. These species are less likely to become extinct as the greatest threat facing them, overharvesting, is likely to be abetted for economic reasons at relatively high abundance. To date, there are no documented extinctions of marine fish or invertebrates due to fishing (McKinney, 1997). However, Powles *et al.,* (2000) recently concluded, "there is no reason to assume that extinction is not a potential problem in the sea."

THE LOSS OF POPULATIONS AND THE IMPACT ON GENETIC DIVERSITY

Long before a species declines into extinction it will suffer a reduction in the level of genetic diversity within and among its populations. Often range contraction and fragmentation of former distributions occur (e.g. Musick *et al.,* 2000). Fragmentation causes the formation of small isolated populations, which are more vulnerable to genetic degradation. While documented extinctions of marine species are rare, the extinction of populations (extirpation) is more common (Musick, 1998; Musick *et al.,* 2000). The salmon of the Pacific (chinook, sockeye, coho, pink and chum) have numerous populations, and 106 have become extinct on the west coast of the United States (Nehlsen *et al.,* 1991), with another 142 extirpated in Canada (Slaney *et al.,* 1996). Levin and Schiewe (2001) estimate that, over the last thirty years, salmon have been extirpated from 40% of their former range in the Pacific Northwest. The Adriatic Sea stock of the beluga sturgeon is now extinct due to exploitation. Amongst mammals, the Atlantic Ocean population of the gray whale has been hunted to extinction, and the Gulf of St Lawrence walrus population is extirpated (cf. Powles *et al.,* 2000). As many as 82 species of marine fish in North America alone have populations that are believed to be under some level of extirpation risk (Musick *et al.,* 2000).

Principles of genetic variation

A gene is part of the genetic code responsible for producing a specific trait. The four letters of the genetic code are found in sixty-four combinations, although there are only twenty different types of amino acids. Different combinations of the code can produce the same amino acid, and when this happens the same protein is produced despite the differences to the code. Conversely, changes to the gene code may result in different proteins being produced, potentially creating differences in performance or physical traits. Such alternative variants of a specific gene are called alleles. The number of different alleles is a measure of genetic variation or diversity. The average effect of substituting one allele for another is referred to as "additive genetic variance." The genetic variation of a species is distributed both within populations, expressed as differences between individuals, and between populations, expressed as differences in the presence and frequency of alleles.

When different populations arise, with little or no connection between them, they become genetically different from one another. Loss of such populations thus results in loss of genetic diversity within the species. The existence of multiple spawning units is an indicator that populations may be reproductively isolated, particularly if the species shows spawning site fidelity or homing abilities. The organization of these populations in time and space, along with the ratio of within and among population variation are important to maintain in order to avoid negative genetic effects (Altukhov and Salmnekova, 1994).

Among populations, genetic diversity can also be lost when populations that are not normally in contact with one another, hybridize. This can occur when physical barriers are removed, when fish are introduced to an area or escape, or when migration patterns change due to environmental conditions. When populations are isolated for long periods, closely-linked genes may evolve to work well with one another. Subsequent hybridization of such populations may result in these gene complexes breaking down, resulting in a weakening of the population over subsequent generations (Hindar *et al.,* 1991). This phenomenon has been documented in Atlantic salmon (Ståhl, 1981; Emlen, 1991). There are also numerous cases of hybridization between closely related species occurring through introductions, resulting in a loss of diversity, particularly in freshwater (Harrison and Stiassny, 1999).

Why should we care about the genetic structure of a species? Natural selection ("survival of the fittest") will act within populations (for an example of this effect acting on grayling see Haugen and Vøllestad, 2000), while the genetic potential of the species to adapt to environmental change depends on the total genetic diversity represented among populations. Therefore, it is important to optimize both types of variation to maintain the full potential for evolutionary change within a species.

Identifying patterns of genetic diversity

One of the challenges of conserving genetic diversity is determining how genetic variation is distributed within a species. Total genetic variation within a species can be partitioned into variation within and among populations, and at various other geographic levels, such as between oceanographic regions. At one extreme, there are fish such as salmon with relatively high genetic diversity between populations resulting from their homing to specific rivers at spawning time (e.g. Gharrett and Smoker, 1993). At the other are species such as the great scallop (*Pecten maximus*), which have only 2% of their genetic variability between "beds" and 98% between individuals within "beds" (Heipel *et al.,* 1998). It has been shown that, on average, marine fish have about 6% of the genetic variation distributed among populations, while anadromous species have 11% and freshwater 22% (Ward *et al.,* 1994). These percentages are based on portions of the code that are believed to be "neutral," that is, not under selection, thus reflecting gene exchange between populations. Morphological variation and variation in genes under selection may be partitioned differently according to the environment.

Often the genetic structure of a species is not what would be intuitively expected. A growing number of studies are revealing genetic structuring among populations that were previously thought to have been homogeneous (e.g. Merkouris *et al.,* 1998; Shaklee and Bentzen, 1998; Ruzzante *et al.,* 1999; Aubert and Lightner, 2000). Even amongst species with large population sizes and wide distributions, the presence of genetically distinctive populations has been revealed (Mork *et al.,* 1985; Jørstad *et al.,* 1991; Ruzzante *et al.,* 1999; Shaw *et al.,* 1999) and mechanisms have been proposed to explain them (Hedgecock, 1994a, b; Larson and Julian, 1999). Recently, our view of coral reef fishes was altered when damselfish were shown to have a proportion of offspring settling locally, contrary to previous concepts (Jones *et al.,* 1999). Similarly, it was commonly believed that all European eel (*Anguilla anguilla*) migrate to the Sargasso Sea for reproduction and comprise a single large population. Wirth and Bernatchez (2001) have shown, using genetic tools, that there is significant population differentiation among eels and "the reproductive biology of the European eel must now be reconsidered."

Examples of population structuring in marine fish

Atlantic herring is a fish that is characterized by a high level of biological complexity and population richness (Sinclair and Isles, 1988). In the Gulf of Maine and Scotian Shelf areas of the Western Atlantic, herring aggregate for a few weeks to spawn in a number of discrete locations, at different times of the year from April to November. Tagging studies have shown considerable migration and intermixing of spawning groups at other times of the year. However, spawners return to the same spawning location year after year, perhaps to their location of birth

(Stephenson, 1991). Genetic analysis of these populations has shown significant population structure (McPherson *et al.,* In press). Equivalent results were found in the Pacific herring, which has a similar stock complexity (O'Connell *et al.,* 1998).

Cod has a lower degree of stock structure than herring. Nevertheless, on the Eastern Scotian Shelf, at least four major groups have been identified, including spring and fall spawning components (Figure 2; DFO, 1998). In the northern cod stock complex, the collapse of the fisheries involved the loss of many spawning components (Figure 3). Genetic analyses have identified discrete populations within the complex (Bentzen *et al.,* 1996; Ruzzante *et al.,* 1998) and suggest that bathymetry and oceanographic processes may govern stock complexity.

For many groundfish in Atlantic Canada it is necessary to reconstruct a picture of the natural population structure. Haddock, in particular, have undergone an extensive range contraction over the last century (Kenchington, 1996) and now occupy only a portion of their former range, and cusk have undergone both range contraction and fragmentation since at least 1970 (Figure 4; DFO, 2000). In both, there may have been a parallel loss of genetic diversity.

Management

Clearly, information on the genetic composition and structure of a species has important consequences for fisheries management. It is very important that the management area coincides with the population (Stephenson and Kenchington, 2000). The management of the blacklip abalone in Australia is an example where genetic information has supported established management areas and provided insight into the biology of the species. Partitioning the genetic variance showed concordance with each of the Victorian State abalone management zones and also showed the Port Phillip Bay stocks to be genetically separated from the stocks along the open coast (Hanna and Huang, 1995). Further, the data revealed evidence of limited larval dispersal and inbreeding in some populations, alerting managers to their vulnerability to overexploitation. Genetic data can also be discordant with management boundaries. For example, Lankford *et al.* (1999) have shown that while the Atlantic croaker (*Micropogonias undulatus*) exhibits weak large-scale regional genetic differences between the Atlantic and Gulf of Mexico, there is no genetic differentiation among the Atlantic localities studied, including those north and south of Cape Hatteras, which was previously seen as a stock boundary.

Spawning components are often identifiable in space and time, thus allowing them to be managed separately. When genetic data are not available, maintaining viable population sizes of the full range of these spawning components is a precautionary management approach to preserving genetic diversity.

THE LOSS OF WITHIN-POPULATION GENETIC DIVERSITY

A population can *only* acquire new genes either through the immigration of individuals from surrounding populations or through the process of random mistakes (mutation) of the code (Figure 5). Apart from these two processes, the genetic diversity of a population is determined by its size and the selective forces acting on it. In general, mutations occur rarely, although there are cases where high levels of pollution or radiation have been shown to increase mutation rates. From an evolutionary perspective (tens of thousands of years), the process of mutation is the only way in which genetic variability is created, and without mutations there would be no biological diversity.

Natural selection can maintain or deplete genetic variation (Figure 5). Through selection, certain allelic combinations leave more offspring than others because they are better suited to the environment. When selection acts to destroy individuals with undesirable alleles, or causes one allele to become fixed in all individuals, it becomes a negative influence on genetic diversity. In situations where individuals inheriting different forms of the same gene from their parents (one from each) are favoured, selection causes genetic variation to be maintained. A second process acting to reduce genetic variance is called genetic drift. In all small populations, the frequencies of particular alleles change randomly from one generation to the next. By chance, some of the alleles of the parents may not be passed on to their offspring. The smaller the population, the more dramatic the fluctuation of allele frequencies, and the faster the loss of genetic variation (Franklin, 1980).

Small populations are also vulnerable to inbreeding, that is, production of offspring from matings between close relatives. If a population is small and isolated, inbreeding is inevitable. In many species, inbreeding is coupled with reduced viability and reproduction, as well as increased occurrences of diseases and defects. Physiological and behavioural phenomena, referred to as Allee effects (cf. Frank and Brickman, 2000) may also come into play in small populations, resulting in decreased reproduction.

Population geneticists have tools available to them to calculate the degree to which these processes are operating within a species. Fisheries scientists have focused primarily on the number of fish or their weight, but to understand the genetic structure, other factors must be considered. These include the sex ratio, whether different pairs produce different numbers of offspring, and whether the population has previously gone through a series of crashes or not. For example, for some species, genetic variation will be reduced if the sex ratio of breeders departs from 1:1. It is much better genetically to have a population of 50 males and 50 females than to have one of 10 males and 90 females, yet both have a total of 100 breeders. Similarly, the maximum genetic variation is produced in the population when all mating pairs produce equal sized families. In the case of the northern elephant seal, dominant bulls establish a harem and monopolize females, skewing the sex ratio through mating behaviour. This species was also extensively hunted in the 19th century and it is believed that the current population of over 120 000 arose from as few as 10 animals in the 1890s (Hoelzel, 1999). As expected, current levels of genetic variation are low.

How many fish do we have to leave behind? Recent theoretical work suggests that population sizes of the order of 1 000 to 5 000 spawners are required for long-term viability (Lynch and Lande, 1998). Previously suggested values of 500 or more breeders (Frankel and Soulé, 1981) appear to have been underestimated (but see Whitlock, 2000). These numbers seem small but remember that these are successful breeders, that is, fish that have offspring that survive to reproduce. We do not know how many fish in a spawning aggregation successfully mate or how many of their offspring survive to maturity. If at the same time we are fishing one sex over another (so that the sex ratio is not equal) or if the species is known to have a history of population crashes, we have to leave even more fish. Therefore, we have to hedge against these numbers, perhaps to an order of magnitude or more.

Fishing and genetic diversity

The present rate of environmental change in marine ecosystems increases the importance of genetic variability in natural animal and plant populations to respond to these changes. At the same time, human activities may be reducing the genetic variability of these populations. New alleles are created over tens of thousands of years, while loss of alleles and allelic combinations can occur extremely rapidly, even within a single generation. Thorpe *et al.* (1995) reviewed the relative risks of various aspects of pollution, wild harvesting and aquaculture on genetic processes. Overharvesting and selective harvesting were described as having a high degree of impact. These can be affecting not only the target species but also by-catch and benthic organisms killed or disturbed by gear. For example, Hector's dolphin, a small marine mammal native to New Zealand, has been reduced to about 4 000 individuals and the species has undergone documented decline and range contraction. Recently, a time-series of genetic diversity was constructed, extending from 1870, when the first specimens were preserved, to the present. The authors found a significant decline in genetic diversity and predicted that one of the two remaining populations will be extinct, and that the other will have lost all of its diversity in the genes examined in less than 20 years (Pichler *et al.,* 1998; Pichler and Baker, 2000).

Entanglement in gillnets since 1970 is the primary cause of decline, resulting in the loss of genetic variation (Dawson, 1991; Martien *et al.,* 1999).

Selective fishing

Fishing is a highly selective process acting on the size of the organism captured as well as the location of the populations (Law, 2000). The fishery may also favour capture of one sex over another, altering the sex ratio or sex-specific size frequency, or both, of the breeding population. Fish that have extensive ranges and undergo migration may be under different selection pressures in different parts of their range due to different fishing methods or regulations. In the extreme case of anadromous fish, these locations can be very different habitats (marine and freshwater). Fishing therefore has the potential to effect the genetic diversity and genetic structure of a species. The following text draws heavily on the excellent reviews of this topic by Law (2000) and Smith (1999), and readers are directed to those papers for a more comprehensive treatment.

When a change in the physical characteristics of fish is observed it is difficult to determine whether that change is caused by fishing or by other factors. This is because the environment can modify the expression of physical attributes, and fish, perhaps because they are cold blooded, are strongly influenced by environmental conditions. The physical characters we see are the result of three influences: (1) genetics, (2) environment, and (3) the genetic-environment interaction. Determining the relative contribution of each can only be done experimentally. Many changes in the characteristics of fish populations that appear to have been brought about by fishing have been described. It is not as easy to determine whether these changes are permanent, due to the loss of alleles, or if they are the result of fishing selection changing the frequency of alleles.

Changes in the characteristics of fish over time are well documented for a number of exploited species. Examples of traits that are thought to be under fishing selection include the following:

- weight-at-age
- length-at-age
- age-at-maturity
- length-at-maturity
- spawning season
- number of eggs (salmon)
- size of eggs (salmon)

some of which are correlated (e.g. Rijnsdorp, 1993; Rowell, 1993; Millner and Whiting, 1996; Trippel *et al.,* 1997, Smith, 1999; Law, 2000).

A common feature among the groundfish of the Northwest Atlantic has been a decline in the mean size-at-age of fish over a period of 30 years (Smith, 1999). Figure 6 shows the dramatic change in size-at-age seen in haddock on the Eastern Scotian Shelf in three ages (3, 5 and 7 years) from 1970 to 2000. During the 1970s, 7-year-old haddock were on average 60 cm long. By the 1990s, the mean size had fallen to about 40 cm. These changes initially occurred when numbers of fish were high and appear to be independent of abundance (Figure 6). Similar trends are seen in other haddock stocks and in pollock (Frank *et al.,* 1997; DFO, 2000).

Fishing practices that remove the late-maturing fish may also cause changes to the population (Smith, 1994). Individuals that mature early are able to reproduce at least once before capture and so perpetuate genes for this trait. The majority of Northwest Atlantic cod, pollock and haddock stocks have shown a decline in both age and length at sexual maturity since the 1970s (Trippel *et al.,* 1997). The largest change was seen in the northern cod stock complex, which showed a 20% decrease in size-at-maturity during the early 1990s (Figure 7; Trippel *et al.,* 1997). Similar changes have been observed in the North Sea and in Pacific salmon, though in some cases (e.g. North Sea sole) the trend has been toward larger sizes (Law, 2000).

In general, by removing the larger fish from a population consistently over time (30 or more years for some fish), the remaining fish are slow-growing and early-maturing (Smith, 1999). These observations may be due to genetic changes induced by fishing, to environmental change, or to elements of both. Temperature is known to be highly correlated with weight-at-age of cod (Brander, 1995), and changes may be attributed to changes in the ecosystem, including the abundance of prey and the degree of competition for food.

For genetic diversity to be affected by selective fishing there must be a genetic difference between the fish caught and those left behind in the population (cf. Law, 2000). Selective breeding programmes for cultured fish (e.g. salmon; Jónasson *et al.,* 1999) and invertebrates (e.g. scallops; Perez and Alfonsi, 1999) have shown that significant amounts of genetic heritability (the proportion of variation in a trait that is inherited from one generation to the next) exist for a number of characteristics, including yield-related traits important to fisheries (Law, 2000). This is the basis upon which aquaculturists, breeding from the largest or fastest growing fish each generation, can increase their production. Generally, characteristics such as the number or size of eggs have been found to be heavily influenced by environmental conditions. However, Smoker and colleagues (2000) have recently shown a very high degree of heritability in both the number and size of pink salmon eggs produced, which was seen as important to the persistence of populations in fluctuating environments. This is one of the few examples where heritability estimates have been determined from field studies. Collectively, this body of research has demonstrated clearly that there is a significant amount of genetic control over those traits selected for by fishing (Law, 2000).

Are these changes permanent or reversible? The persistence of fishing-induced genetic changes will depend upon the other selective forces operating on the species, the proportion of genetic diversity affected and the reproductive biology of the species. In some cases, altering fishing practices may not readily reverse genetic change (Law and Grey, 1989). Consequently, fishing may be able to cause substantial evolution in traits of the exploited species (Law and Rowell, 1993), although the time scale over which it operates is unknown. In his recent review, Law (2000) concluded:

> “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.”

CONCLUSIONS

For many marine species, fishing probably has the greatest impact of any human activity on the loss of within-species diversity, both within and among populations. The key to avoiding loss of genetic diversity is quite simple: maintain all spawning components (unless genetic information is available to support aggregation of units) at large enough population sizes to avoid unacceptable loss of genetic variability. However, even if population sizes are large, selection can result in the loss of alleles. Avoidance of fishery-induced selection is more challenging, but it may be useful to consider altering the size at first capture randomly by year to avoid strong selection for early maturing and slow growing fish. It is also important to note that while some stocks have made remarkable recoveries (including many whale species), they have done so from a narrow genetic base. This means that while everything may look good numerically, the population may have problems coping with environmental change or disease. Is it coincidental that the Caspian seal population fell to very low numbers in the late 1950s, recovered to a level of about 400 000, only to be hit with canine distemper and other viruses (cf. Stone, 2000)?

ACKNOWLEDGEMENTS

I thank Drs Mike Sinclair and Trevor Kenchington for reviewing the first draft of this manuscript and offering helpful references and direction, and Drs Patrick O’Reilly, Trevor Kenchington, Howard Powles and Ken Frank for commenting on the penultimate draft. I also thank Dr Ken

Frank for directing me to suitable figures to illustrate the points I wished to make and Arran McPherson for offering references and unpublished data. Many of the ideas in this paper were inspired by discussion within the ICES Working Group on the Application of Genetics to Fisheries and Mariculture.

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Figure 1. Maputo Museum photo of a Mozambique female coelacanth before dissection. The giant fish was 178 cm in length and weighed 98 kg. Only one Comoros Island coelacanth, caught in 1960, has rivalled it, at 180 cm and 95 kg. (Photo provided by Robin Stobbs and caption details provided by Jerome Hamlin, and downloaded from the worldwide web: www.dinofish.com).

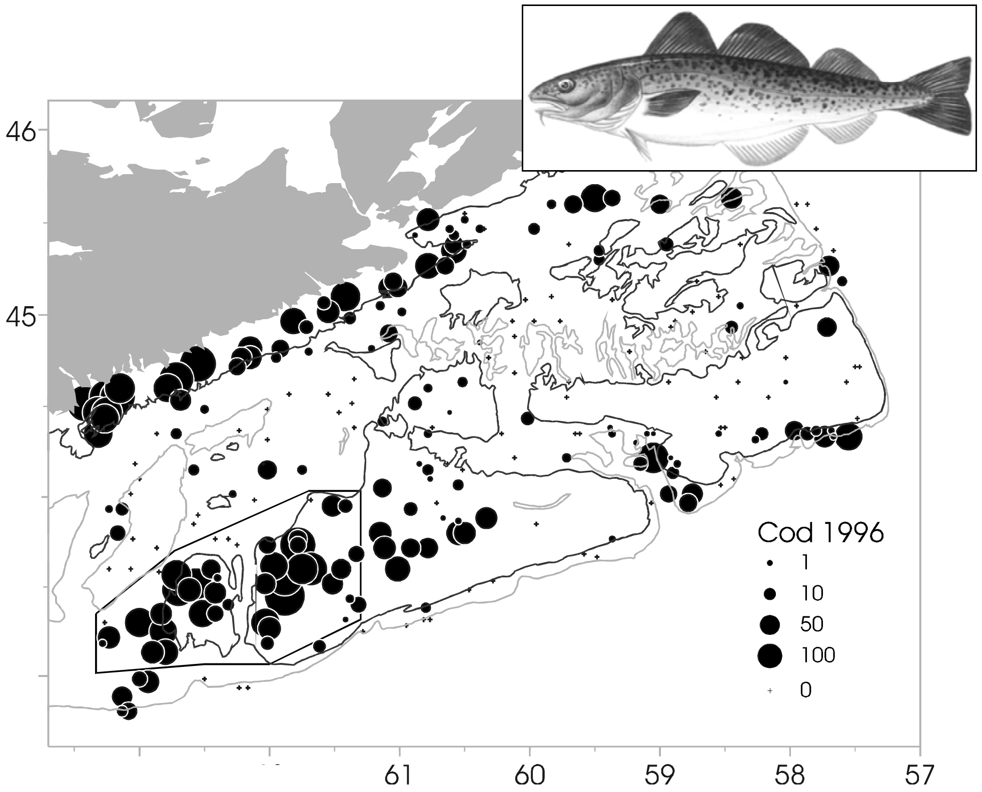


Figure 2. September/October 1996 longline survey catches of cod (kg) in NAFO Divisions 4VsW. The cod resource on the Eastern Scotian Shelf is a complex of spawning components including at least two major offshore groups and a chain of coastal spawning groups. In several of the spawning components (Sable/Western offshore and various inshore areas) there are also spring and fall spawning fish (DFO, 1998).

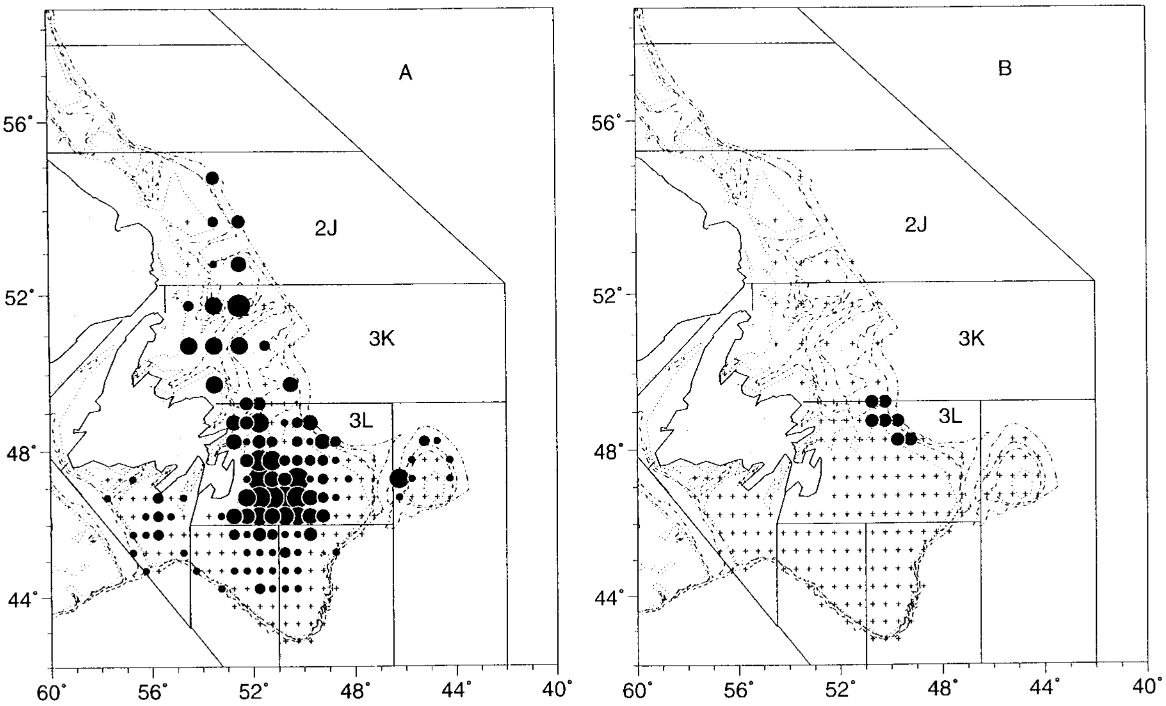
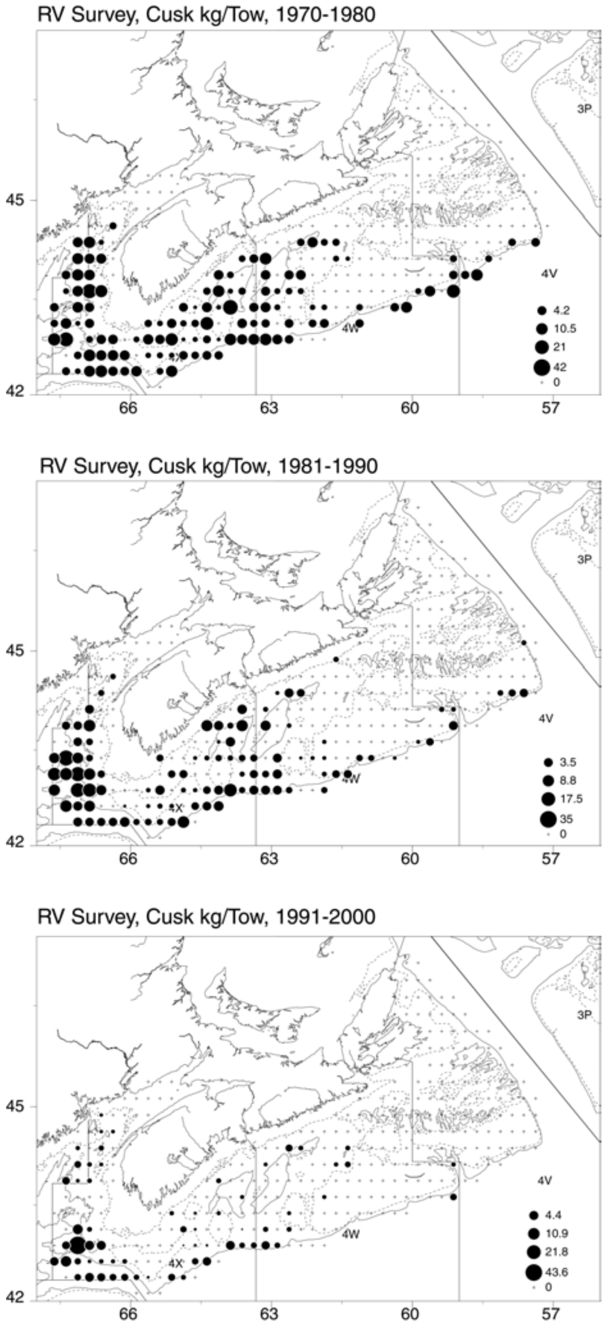


Figure 3. Erosion of spawning components and severe range contraction in northern cod stock complex of NAFO Divisions 2J3KL. A) Location of spawning stocks during the period 1948-1992, B) Location of spawning cod during the period 1990-1993. (Figure copied with permission from Frank and Brickman, in press, and originally adapted from Hutchings *et al.*, 1993 (A) and deYoung and Rose 1993 (B)).



RV Survey, Cusk kg/Tow, 1970-1980

RV Survey, Cusk kg/Tow, 1981-1990

RV Survey, Cusk kg/Tow, 1991-2000

Figure 4. Decadal-scale range contraction and fragmentation from 1970 to 2000 in cusk (*Brosme brosme*) on the Scotian Shelf, off the coast of Nova Scotia, Canada. Data are from the summer research vessel surveys conducted by the Department of Fisheries and Oceans, Canada, Maritimes Region (DFO, 2000).

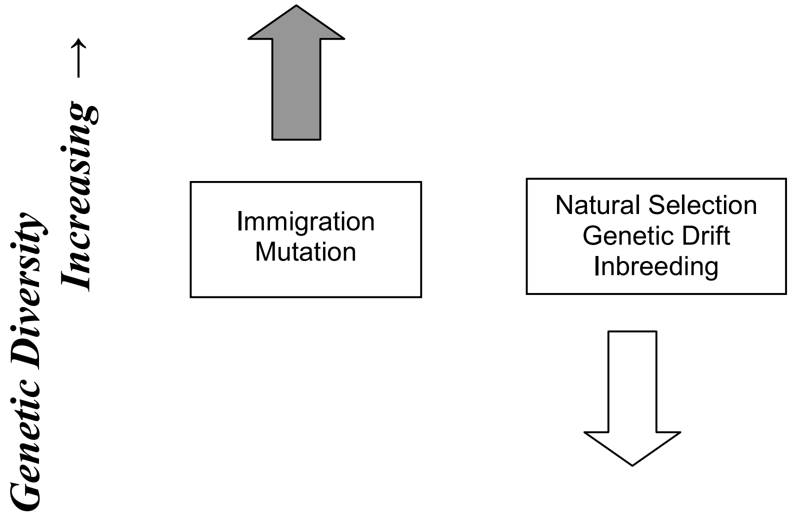


Figure 5. Genetic processes that affect genetic diversity. Processes under the dark arrow act to increase genetic diversity while processes above the white arrow either maintain or decrease genetic diversity. Population size is a key factor that determines which of these forces has the greater influence. Small population sizes facilitate the loss of genetic variation.

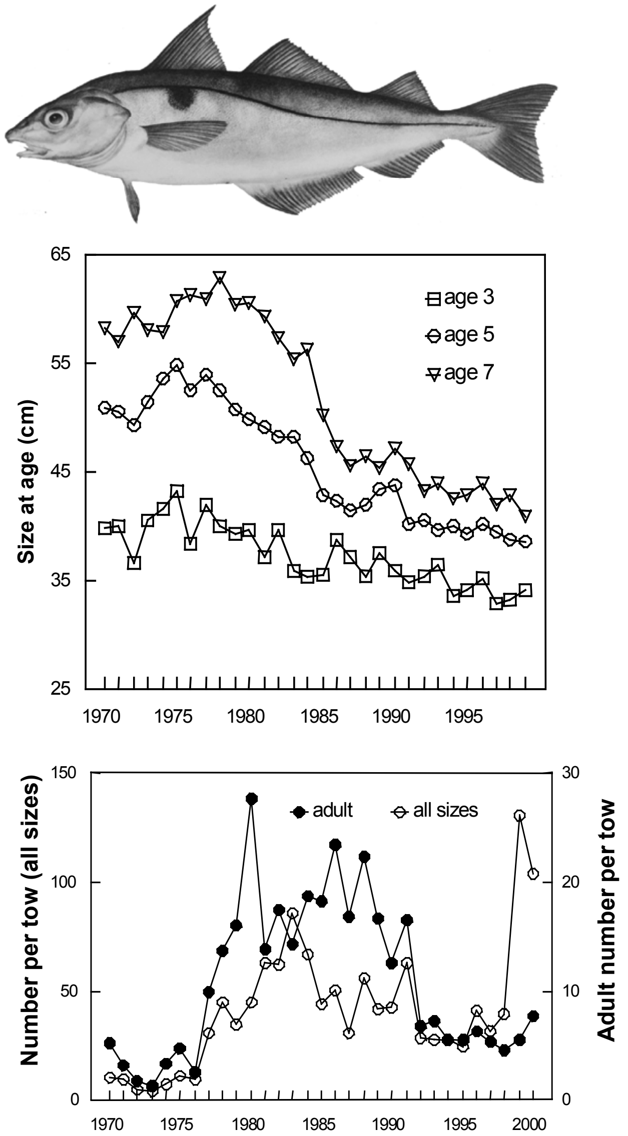
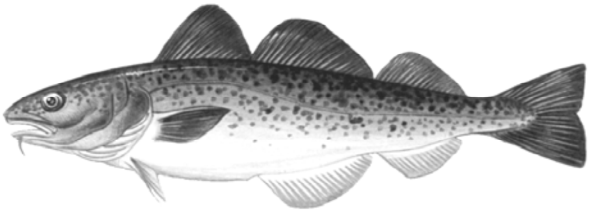


Figure 6. Changes in the mean length-at-age (3, 5 and 7 years) of haddock on the Eastern Scotian Shelf, and the mean number of fish per tow collected in the summer research vessel surveys from 1970-2000. (Figures and illustration provided by Dr K. Frank, DFO, Canada).



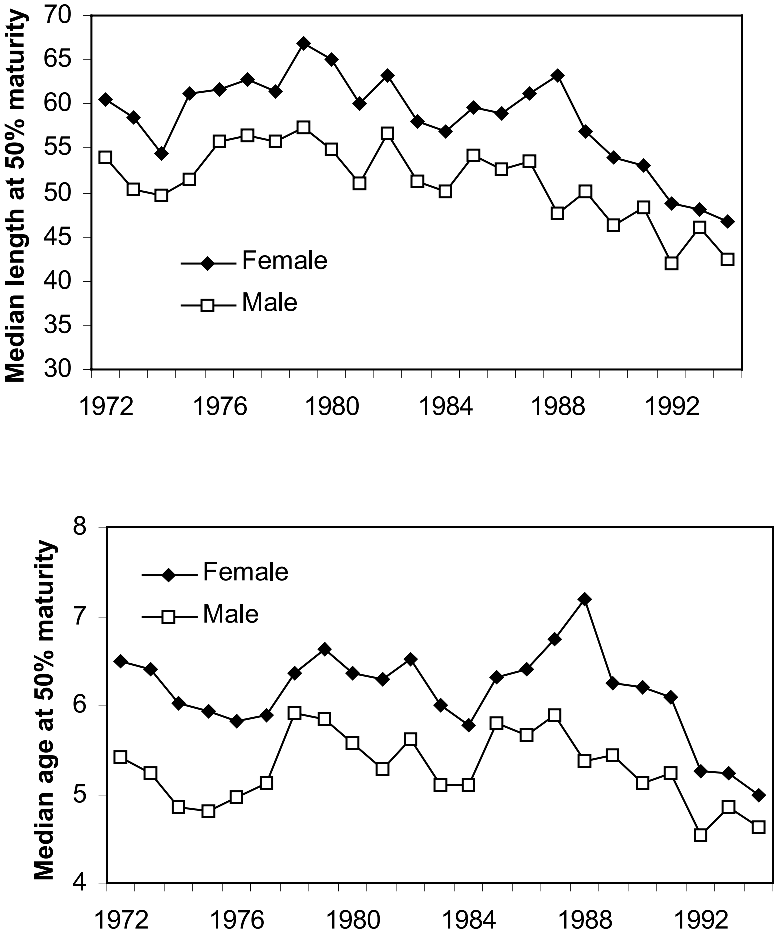


Figure 7. Changes in the median age and length-at- 50% maturity (in cm) of male and female northern cod collected from NAFO Subdivision 3Ps (1972-1994). Data are extracted from Trippel *et al.* (1997).