



# Genetic diversity of marine fisheries resources

## Possible impacts of fishing

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## PREPARATION OF THIS DOCUMENT

Conserving biodiversity in the ocean has been more neglected than that on land, yet the ocean is rich in genetic, species and ecosystem diversity. Fishery resources are an important subset of the world's biodiversity. They are affected by human activities including fishing, aquaculture and other development sectors. The present paper is a general review on genetic diversity of marine fishery resources with particular emphasis on the impact of fishing. Understanding the impact is an important prerequisite in our effort to develop the strategy for prevention of possible loss in biodiversity.

The paper was written by Dr. Peter J. Smith of New Zealand, who has been working in fisheries with a strong interest in biodiversity. The author is grateful to Dr Devin Bartley, FAO Fisheries Department for the helpful comments on a draft of this paper and also to Dr Purwito Martosubroto for his assistance. The views expressed in this paper are solely those of the author and do not necessarily represent the views of FAO.

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**ABSTRACT**

This report reviews the evidence for the genetic impact of fishing on marine fisheries resources. The most widely used method for measuring genetic diversity in natural populations has been protein electrophoresis; marine teleosts have levels of genetic diversity ranging from 0.0 to 18% and marine invertebrates from 0.4 to 32%. Genetic studies have shown that populations of marine species are less differentiated than freshwater species, experience temporal genetic changes, can be changed locally by pollution, and contain cryptic species.

Genetic changes in populations occur through selection or drift. In natural populations fishing is a major source of mortality and is non random with respect to age and size of individuals. A common observation in heavily exploited teleost fisheries has been a decline in the age and/or size at sexual maturity. Size selective fishing would favour early maturity. However growth rate in some fishes is density dependent and increases when the stock is reduced; faster growth rates lead to a reduction in the age or size at onset of sexual maturity. Thus it is not possible to determine if the observed changes are genetic or compensatory in response to reduced stock density.

Genetic drift is unlikely to be a major factor influencing levels of genetic diversity in many marine fisheries, except for some populations, e.g. giant clams, which have been reduced to near extinction levels. Some rare and endangered freshwater fishes show low levels of genetic diversity. There is no evidence for loss of genetic diversity in collapsed stocks of pelagic species. While the stocks have collapsed from a commercial perspective most have maintained large population sizes at their lowest state.

The use of hatcheries to produce seed for aquaculture and enhancement could lead to loss of genetic diversity in natural populations through escape of farm stock or inappropriate choice of broodstock.

Experimental studies are required to determine the heritability and the response to selection of life history characters of exploited species, and to determine if relaxation of fishing pressure allows the recovery of "fast growing" and "late maturing" genes or gene complexes in populations. Also it would be desirable to monitor levels of genetic diversity in recently exploited or highly exploited species. A combination of experimental and field studies would permit a more rigorous testing of genetic changes in exploited populations.

If genetic changes are demonstrated in exploited species then changes to management would be needed to conserve natural levels of diversity.

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## INTRODUCTION

Loss of biodiversity is of increasing concern around the world. Most attention has been on terrestrial environments and in particular tropical rainforests where both habitat destruction and species diversity are high. In the aquatic environment conservation has focused on freshwater environments some of which have suffered dramatic and irreversible damage (Micklin 1988, White 1988). In North America 27 species of freshwater fishes in three genera have become extinct during the past century (Miller *et al.* 1989). For the marine environment the species extinction list is restricted to mammals and birds and the list of threatened or endangered species is dominated by mammals and birds with a few anadromous fishes (Meffe 1987, Upton 1992). Marine fishes that are slow growing and have low fecundity are vulnerable to overfishing: several species of shark may soon be endangered if current exploitation levels are not reduced (Manire and Gruber 1990), while the common skate has been brought to the brink of extinction by commercial fishing (Brander 1981).

Biodiversity has been broadly defined as 'the degree of nature's variety' (McNeeley 1988) and as 'the variety of life and its processes' (Hughes and Noss 1992) and encompasses all species of plants, animals and micro-organisms and their ecosystems (Kapoor-Vijay 1992). Biodiversity is recognised at four levels:

- a. genetic diversity: the sum total of information in the genes of individual organisms of a species,
- b. species diversity: the number and frequency of organisms in a given area,
- c. ecosystem diversity: the variety of ecological processes, communities and habitats within a region, and
- d. landscape diversity: the spatial heterogeneity of the various land uses and ecosystems within a larger region from 100 to 10 000 000 km sq. (Noss 1983, Norse *et al.* 1986, OTA 1987).

Species and ecosystem diversity are high in the marine environment, there are more phyla and classes represented in the marine than terrestrial environment with organisms ranging from unicellular plants and animals through to whales. There are approximately 20 000 species of teleost accounting for nearly half of the vertebrate species. Some 9 000 teleost species are exploited and for 22 species the global catch is in excess of 100 000 tonnes per annum. Around 58% of fishes are marine and although the oceans cover 2/3 of the planet most marine fish are found in coastal waters which represent less than 10% of the planet's surface.

It has been suggested that the coastal zone is being altered as fast as tropical forests, and simply knowing which ecosystems have more or less species is misleading (Ray 1988). The relative lack of knowledge concerning the loss of marine diversity is in part due to the remoteness and difficulty of monitoring marine habitats. Loss of forest diversity occurs through simplification, fragmentation, and selective destruction (Norse 1990) especially when management is focused on a few species (Cairns and Lackey 1992). Similar processes are operating in coastal seas through land reclamation, pollution and over harvesting. Productivity in land-based farming is highest where systems have been simplified and similar trends are emerging in coastal environments with the development of aquaculture and enhancement (Ray 1988).

Genetic conservation of aquatic resources has centred on freshwater and anadromous resources where the problems of habitat alteration, introductions, and overfishing are greatest and most urgent (Ryman 1981, 1991, Meffe 1987, Skaala *et al.* 1990, Hindar *et al.* 1991, Minckley and Deacon 1991, Nyman 1991, Moyle and Leidy 1992, Cloud and Thorgaard 1993). Increasing attention is being directed towards the loss of genetic diversity in the marine environment and reviews of this subject have been presented by FAO 1981, 1993, Polunin 1983, Nelson and Soule 1987, Ray 1988, Carlton 1989, PDT 1990, Upton 1992, Munro 1993, Policansky 1993.

The focus of this paper is on genetic diversity in the marine environment and the possible impact of fishing. Genetic changes due to exploitation have been reported in a wide variety of fisheries from the Arctic Ocean to tropical African lakes. Reports of genetic responses to exploitation were first made in the 1970s, before

direct methods for measuring genetic diversity, such as allozyme electrophoresis, were developed. Much of the evidence for genetic changes in fish stocks is based on life history characters, such as growth rate, size at age, and size or age at first maturity. These characters are influenced by both genetics and the environment. The complex and poorly understood relationships between the genetic components of life history characters and the non genetic responses of these traits to changes in population density and environmental parameters make it difficult to separate the genetic and non genetic impact of fishing on natural populations. Therefore it is necessary to outline the major factors producing changes in fish stocks before discussing genetic diversity and the evidence for the genetic impact of fishing.

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## CHANGES IN FISH STOCKS

Populations of marine fishes fluctuate in abundance due to both climatic events and to the effects of fishing. Some stocks have been shown to fluctuate in abundance over centuries (Cushing 1982, Soutar and Isaacs 1969), while others show variation in recruitment, of an order of magnitude, over a few years (Cushing 1975, 1982, Kawasaki *et al.* 1991). Climatic events can produce both short-term and long-term changes in fish stocks. Cushing (1975) has suggested that the link between climate and production is due to the match or mismatch in production of fish larvae and their food, especially in temperate waters where fish tend to spawn at fixed periods while the food production cycle varies.

Temporal replacement of one species by another has occurred within fisheries. In the western English Channel during the late 1920s and 1930s the herring population declined and was replaced by the pilchard (Cushing 1975). There is no evidence that these changes were due to fishing, rather they are associated with a rise in sea temperature which led to a replacement of cooler water species by warmer water species of teleosts and invertebrates (Southward 1963). Off California stocks of sardine declined during the 1950s and were replaced by anchovies (Ahlstrom 1966). This decline is linked with change in temperature but was enhanced by fishing (Beverton 1990, Cushing 1982). Fish scales preserved in anaerobic sediments off California have provided a chronological record of the abundance of pelagic fishes which show fluctuations in abundance of sardines and anchovies over hundreds of years (Soutar and Isaacs 1969).

There is increasing evidence for synchronous changes in fish stocks at the global level. Changes have occurred in widely separated stocks in spite of different management practices between regions (Maan 1993). For example catches of sardines in the Peruvian and Californian upwelling fisheries have varied synchronously with sardine catches off South-east Asia over the past 80 years (Maan 1993). El Niño events in the Pacific produce low catches of sardine off Peru and high catches of jack mackerel off Tasmania (Maan 1993). These observations provide strong evidence that large scale climatic events have a major influence on the abundance of fish stocks so that monitoring of climatic events may provide a predictive tool for quota setting (Maan 1993).

Many fisheries have shown a successional pattern of exploitation: the collapse of single species followed by exploitation of other species in time or area. The Norwegian pelagic fleet moved from herring to capelin to mackerel during the 1960s (Garrod 1973). In the North Sea fisheries landings were relatively constant at 1–1.5 million tonnes per annum for 50 years, but increased rapidly in the 1960s with the development of industrial fisheries, firstly on juvenile herring and mackerel and later on Norway pout, sand-eel and sprat (Hempel 1978). As sole stocks were depleted fishers moved to other areas (Garrod 1973). This pattern of replacement has not been due to an increase in abundance of secondary species, but to a change in fishing targets following over exploitation of the primary species (Daan 1980). In Pacific salmon fisheries some minor stocks have disappeared with heavy exploitation (Loftus 1976). In the Irish Sea the common skate *Raja batis* was once common but is now very rare. The species is slow growing, with a high age at first maturity and low fecundity, in comparison with demersal teleosts which are the target species in the Irish Sea trawl fisheries (Brander 1981).

Pelagic fish appear to be less resilient to long-term climatic changes than demersal species due to their lower fecundity (Cushing 1975) and shorter life histories (Maan 1993). In addition their schooling behaviour makes them more vulnerable to industrial fishing methods (Rothschild 1986) and several species have collapsed (shown a rapid and dramatic decline in abundance) in the past 50 years. Fishing has been the main cause of collapse in stocks of the Atlantic herring, the Pacific herring, the Pacific sardine, Japanese sardine, South Atlantic pilchard, Peruvian anchovy, Barents Sea capelin, and Pacific mackerel (Beverton 1990). In nine out of ten cases collapsed stocks have recovered when fishing has been stopped or cutback, with a tendency for those stocks with the most severe decline to show the slowest recovery. Only the Icelandic spring spawning

herring stock, which collapsed in the late 1960s and early 1970s, has shown no sign of recovery to date (Beverton 1990).

The “gadoid outburst” (Cushing 1984) and associated rise of industrial fisheries in the North Sea may be attributed in part to the decline in herring stocks (Beverton 1990) which released food for gadoid recruits, but the rise in gadoid stocks originated from natural changes in the ecosystem. The spring production of the zooplankton *Calanus*, the principal diet of cod larvae, was delayed about one month in response to cooler sea temperatures in the 1960s and 1970s, providing a better match between food density and cod larvae, which are produced at a fixed spawning season (Cushing 1984).

Major changes in biomass and species composition has occurred in the Northwest Atlantic demersal fisheries over the past 30 years (Fogarty 1992). The Georges Bank fishery changed from one dominated by gadoids in 1963 to one dominated by dogfish in 1986, a change brought about by high fishing mortalities on cod and haddock and an increase in abundance of dogfish (Sissenwine and Cohen 1993).

In a typical response to fishing a stock will show a decrease in average age as the older and larger fish are removed, leaving a higher proportion of faster growing young fish; this “fishing up” effect was first described by Baranov (1918). Growth in fish is in part density dependent and so when the biomass is reduced through fishing the growth rate may increase and, under moderate exploitation, even lead to an increase in average size at age. For example in the southern Baltic stock of flounder *Platichthys flesus* the average age of fish and the catch rates declined as the fishery expanded between 1905–25, but the average length and weight of fish increased (Kandler 1932). However, by 1931 the average length had started to decrease as the increase in growth rate was unable to compensate for the rate of removal of fish from the population (Kandler 1932). This fishing up effect was viewed positively as it improved the economic value of the stock (Kandler 1932). In the plaice *Hippoglossoides platessoides* fishery on the Grand Banks the average size at age increased between the 1950s to 1970s even though catch rates fell over the same period in response to an increase in exploitation (Pitt 1975). There were no significant trends in temperature over the period that may have affected growth rates, but a reduction of plaice density and of competitors through heavy fishing made more food available for plaice (Pitt 1975).

The development of a theory of fishing is accredited to Baranov in the Russian Federation and to Thompson in the USA. This area of population dynamics was expanded and developed by many others to become the core of fisheries science. The management models are based on the concept of surplus production and the maximum sustainable yield. Populations are assumed to be in equilibrium and reach an optimum size in accordance with the carrying capacity of the environment. When the population is reduced through fishing, then recruitment and growth increase to return the population to equilibrium. The compensatory increase in growth and recruitment in response to exploitation is common and widely reported in the fisheries literature. These compensatory changes have masked genetic changes in life history characters due to exploitation and made genetic effects difficult to detect.







## GENETIC DIVERSITY IN MARINE SPECIES

### Measuring genetic diversity

Gel electrophoresis coupled with histochemical staining of specific proteins was developed in the 1960s and became the most widely used method for measuring genetic variation in natural populations. The technique is relatively inexpensive and provides a measure of many variable and non variable genes in individuals and populations. The gel phenotypes are easy to interpret and there are computer programmes available for data analyses. Most surveys of genetic diversity in marine species have used proteins, and diversity is measured as the average heterozygosity over many protein loci (heterozygosity is the proportion of individuals that are heterozygous at a single gene locus).

Protein genes represent only about 10% of the genome, so that variation measured by protein electrophoresis may not be representative of the whole genome. The relationship between protein heterozygosity and fitness is uncertain although there is evidence for a positive relationship between heterozygosity and life history characters such as growth rate, disease resistance, and developmental stability (Mitton and Grant 1984, Allendorf and Leary 1986, Danzmann *et al.* 1989).

The rapid advances in molecular biology have provided a range of techniques for direct examination of variation in DNA. To date most populations studies have used restriction fragment length polymorphisms of the mitochondrial genome. The mitochondrial (mt) DNA is small and relatively easy to purify, and the fragments generated with restriction enzyme digests are easy to interpret. Variations in fragment numbers are generated by additions and deletions of restriction sites, and in fragment lengths by insertions or deletions of blocks of bases. Similar techniques can be applied to nuclear (n) DNA, but the considerably larger size of nDNA means that small pieces of the genome have to be analyzed with specific probes. Several regions of the nuclear genome contain multiple repeats of short minisatellite sequences which are resolved as DNA fingerprints. The hypervariable nature of these variable number tandem repeats has led to widespread use of DNA fingerprinting in forensic studies, but the technique has had limited application in marine population studies (Baker *et al.* 1992).

The development of the polymerase chain reaction, PCR, method has provided the means to amplify small fragments of the genome. With appropriate size primers the method can be used to screen for genetic variation in individuals and populations, alternatively amplified fragments can be sequenced. Application of these new genetic methods may produce new insights into the genetic structure of natural populations, as did protein electrophoresis in the 1970s and 1980s, although to date the methods have not been used widely with marine species.

Karyological methods can be used to measure genetic variation, either as chromosome number or banding polymorphisms. The techniques are laborious in comparison with electrophoretic techniques and require the use of live fish for chromosome preparations, thereby reducing their potential application with many marine species.

Morphological characters, the tools of traditional taxonomy, have been used to describe variation among individuals and populations. The characters used are meristic (countable) such as number of fin rays or vertebrae and morphometric (measurable) expressed as ratios of standard length or fork length. Morphological characters have limitations for describing intraspecific genetic diversity as they are polygenic and expression can be modified by the environment. Their use in population-stock identification studies has been superseded for the most part by the development of direct genetic methods.

The life history strategies and characteristics of a species have been determined by evolutionary and



ecological processes. These strategies and characters will determine both how a population responds to exploitation and be modified by exploitation (Garrod and Knights 1979, Garrod and Horwood 1984). The life history traits determining fitness in fish populations are growth rate, age and size at first maturity, life span and fecundity. These traits all exhibit phenotypic plasticity and respond adaptively to changes in the environment, in addition the traits are heritable and population means can be changed through a differential mortality. The relative importance of phenotypic plasticity and genetic change is unknown for most species (Wootton 1990) and because of the difficulties of resolving the genetic and environmental components, life history characters have not been as well studied as protein markers in marine species. It is likely that life history characters are influenced by a large number of segregating loci (Bentsen 1994). Heritability estimates are available for some life history characters for species used in aquaculture (see references in Wilkins and Gosling 1983, Gall and Busack 1986, Crandell and Gall 1993a 1993b), and coupled with the results from selection programmes (e.g. Gjedrem 1983) demonstrate the genetic base of these characters. However, transplant experiments with cutthroat trout *Salmo clarkii* and charr *Salvelinus malma* have shown that fish can adjust age at maturity non genetically to changes in growth rate (Jonsson *et al.* 1984).

## Levels of genetic diversity

Invertebrates generally have higher levels of genetic diversity than vertebrates as measured by protein electrophoresis (Nevo 1978). Within the vertebrates amphibia have the highest and teleosts the lowest levels of genetic diversity (Ward *et al.* 1991). The ecological significance of these findings have been debated for marine species (Nevo 1978, 1983, Nelson and Hedgecock 1980, Smith and Fujio 1982, Mitton and Lewis 1989, Waples 1991). Marine invertebrates show wide variation in levels of genetic diversity. In 26 species of mollusc heterozygosities range from 2 to 32% (Johannesson *et al.* 1989). Crustacea have lower levels of genetic diversity ranging from 0.4 to 10.9% in 44 species of decapod (Nelson and Hedgecock 1980), from 0.8 to 6.4% in six species of tropical decapod and two species of tropical Stomatopod from the Gulf of Carpentaria (Redfield *et al.* 1980), and from 0.6 to 3.33% in 13 species of Australasian prawns (Mulley and Latter 1980).

In marine teleosts heterozygosities range from 0.0 in the anglerfishes *Lophius litulor* (Fujio and Kato 1979) and *L. piscatorius* (Leslie and Grant 1991), *Liparis tanakai* (Fujio and Kato 1979) and three species of Cottidae (Johnson and Utter 1976) to more than 17% in the pelagic *Cololabris saira* (Fujio and Kato 1979) and coastal *Fundulus heteroclitus* (Mitton and Koehn 1975). The mean heterozygosity for 106 marine species was 5.5% with high levels in Clupeiformes, Atheriniformes, and Pleuronectiformes and low levels in Gadiformes and Scorpaeniformes (Smith and Fujio 1982). Elasmobranchs have low heterozygosities (MacDonald 1988, Smith 1986). There have been relatively few studies of mtDNA diversity in marine species and most species tested have low intraspecific sequence diversities (Ovenden 1990), although the Japanese scallop *Pactinopectin yessoensis* has high diversity (Boulding *et al.* 1993).

## Genetic differentiation in marine populations

Many electrophoretic studies of allozymes have been undertaken for the purpose of stock identification or delineation while more recent studies have included the use of direct DNA markers. As might be expected in the marine environment there is less genetic differentiation among populations of teleosts than there is with anadromous and freshwater species. There are fewer isolating barriers to gene flow, which occurs through either larval drift or adult movement, in the continuous realm of the oceans. The proportion of genetic diversity due to population subdivision rises from 1.6% in marine species to 3.7% in anadromous and to 29.4% in freshwater species (Gyllensten 1985). Likewise the level of genetic differentiation measured with mitochondrial DNA is lower in marine than freshwater fishes (Awise *et al.* 1987). Nevertheless discrete genetic stocks of marine fishes are recognised with proteins (see review in Smith *et al.* 1990). Genetic differentiation is negatively correlated with dispersal ability in some species of inshore fishes (Waples 1987), starfishes (Williams and Benzie 1993) and crustacea (Mulley and Latter 1981a 1981b). The use of more sensitive DNA techniques is revealing finer population structure, for example a major genetic break was detected in populations of the horseshoe crab *Limulus polyphemus* off Florida tested with mitochondrial DNA (Saunders *et al.* 1986) but not with allozymes (Selander *et al.* 1970), similar results were found over the same areas for

the American oyster *Crassostrea virginica* (Buroker 1983, Reeb and Avise 1990). In the deep water teleost orange roughy *Hoplostethus atlanticus* allozyme studies of Australian and New Zealand populations have revealed little genetic sub division (Smith 1986, Elliot and Ward 1992) whereas mitochondrial DNA studies have revealed genetic sub division (Smolenski *et al.* 1993, Smith and McVeagh unpub.). A large mtDNA sequence divergence was found between Arctic and coastal cod *Gadus morhua* (1.8–5.6%) but a low divergence between coastal localities (< 1%) in the NE Atlantic Ocean (Dahle 1991).

Some species of marine invertebrates with sedentary adult stages, but pelagic larval stages, have shown significant genetic differentiation over short (< 5 km) geographical distances, while others show large scale genetic uniformity of allele frequencies over hundreds to thousands of kilometres (Benzie and Williams 1992, Burton 1983, Hedgecock 1986, Kordos and Burton 1993, Williams and Benzie 1993). Localised differentiation, termed genetic patchiness (Johnson and Black 1982), appears to originate from pre-recruitment processes in the sea urchin *Echinometra mathaei* (Watts *et al.* 1990), limpet *Siphonaria jeanae* (Johnson and Black 1982, 1984), gastropod *Drupella cornus* (Johnson *et al.* 1993) and queen conch *Strombus gigas* (Campton *et al.* 1992; Mitton *et al.* 1989). However, micro-geographical genetic changes in other invertebrates are thought to be due to post-settlement selection (e.g. abalone *Haliotis rubra*, Brown 1991), although some observations on spatial genetic change in the genus *Mytilus* are due to species mixing (Koehn 1991). The most convincing example of post-settlement selection is from the studies of Koehn and co workers on the *leucine aminopeptidase* (*LAP*) polymorphism in the blue mussel *Mytilus edulis*. Steep clines in *LAP* allele frequencies in *M. edulis* along salinity gradients in Long Island Sound (Koehn *et al.* 1980) and at Cape Cod (Koehn *et al.* 1976) and in *Mytilus trossulus* on the west coast of North America (McDonald and Siebenaller 1989) are due to post recruitment selection on ocean derived seed (Hilbish 1985, Hilbish and Koehn 1985). In spite of gene flow between populations genetic differentiation occurs in response to strong selection.

## Temporal genetic changes

Temporal changes in allele frequencies have been reported in several species of marine teleost through repeat sampling of the same locality over time or the sampling of discrete year classes. Given that most genetic studies of marine populations have utilised protein electrophoresis, estimates of temporal genetic changes are restricted to periods within the past 25 years. One of the longest studied markers is the haemoglobin polymorphism in the Atlantic cod *Gadus morhua* for which allele frequencies in Norwegian populations have remained stable over a 25-year period (Gjosaeter *et al.* 1992; Jorstad and Naevdal 1989). Populations of the red drum *Sciaenops ocellatus* in the Gulf of Mexico show stability in allozyme and mtDNA genotypes among year classes (Gold *et al.* 1993).

In contrast genetic changes have been noted over short time periods between year classes of seabream *Chrysophrys auratus*, (Smith 1979), tarakihi *Cheilodactylus macropterus* (Gauldie and Johnston 1980), killifish *Fundulus heteroclitus* (Mitton and Koehn 1975), and the crested blenny *Anoplarchus purpureus* (Johnson 1977). Major shifts in allele frequencies at one enzyme locus were reported in a reef fish, the damselfish *Stegastes partitus*, from Florida over two generations (Lacson and Morizot 1991). A population of damselfish with atypical allele frequencies was found to have typical allele frequencies when resampled three years later. It was suggested that typical allele frequencies were re-established by high levels of gene flow into a perturbed population (Lacson and Morizot 1991). Genetic changes observed in populations of chinook salmon *Oncorhynchus tshawytscha* from the Pacific coast of Oregon appear to result from genetic differences between batches of hatchery released fish (Bartley *et al.* 1992b, Waples and Teel 1990).

In the Atlantic eel *Anguilla rostrata*, which has a single spawning ground, there are significant genetic differences between adults and elvers, and among localities along the east coast of the United States (Williams *et al.* 1973). These genetic differences must develop during the elver stages when they drift from the common spawning ground in the Sargasso Sea (Williams *et al.* 1973).

Homozygous excess has been reported in allozyme studies of marine organisms, especially in marine molluscs where the excess is most notable in larval and juvenile stages (Singh and Green 1984, Zouros and Foltz 1984). Such excess occurs in large populations and is unlikely to be due to genetic drift or technical

scoring errors, and the cause of this widespread phenomenon remains obscure (Zouros and Romero-Dorey 1988).

## Cryptic species

Several allozyme studies have revealed cryptic species in coastal fisheries and have shown that resources considered to be single taxa consist of two or more species. Examples of cryptic species have been found in squid (Brierley *et al.* 1993, Carvalho *et al.* 1992, Smith *et al.* 1981), octopus (Levy *et al.* 1988), bivalves (Grant *et al.* 1984, Richardson *et al.* 1982, Sarver *et al.* 1992), swellfishes (Masuda *et al.* 1987), silversides (Prodohl and Levy 1989), lizard fishes (Shaklee *et al.* 1982, Waples 1981, Yamaoka *et al.* 1989), bone fishes (Shaklee and Tamaru 1981, Shaklee *et al.* 1982), and small pelagics (Daly and Richardson 1980, Smith and Robertson 1981).

Conversely, the lack of genetic differences between colour morphs of the small serranid fishes of the genus *Hypoplectrus* suggest that they compose a single species (Graves and Rosenblatt 1980). Likewise the lack of genetic differences between specimens of the pelagic armourheads *Pseudopentaceros wheeleri* and *P. pectoralis* from the North Pacific Ocean lead to the conclusion that the armourhead consists of a single metamorphic species with different morphologies between life-history stages (Humphreys *et al.* 1989). Lack of genetic differences at 33 loci between two species of rock lobster *Jasus edwardsii* from New Zealand and *J. novaehollandiae* from Tasmania indicates that these are conspecific populations (Smith *et al.* 1980).

## Pollution induced genetic changes

The effects of pollution on coastal resources are often dramatic with mass mortalities in local stocks, reduction in species diversity, and changes in species composition. Local areas may be closed to harvesting. Sources of pollution include heavy metals, pesticides, oils and detergents, and thermal and radioactive discharges. There are limited reports of genetic changes due to marine pollution, in part because of the difficulty of measuring genetic changes in fish populations in which recruitment can be from outside the polluted area. Most examples of pollution induced genetic changes are for species with limited dispersal abilities; molluscs may be recruited from outside the area of pollution but the juvenile and adult stages are sessile.

The extensive studies of Nevo and coworkers on genetics of pollution in the Mediterranean have shown that genetic changes occur in natural populations of marine organisms exposed to local pollution events (Nevo *et al.* 1984, 1987). As a result genetic markers have been proposed as a monitoring tool for marine pollution (Ben-Shlomo and Nevo 1988; Nevo *et al.* 1984). Laboratory studies on molluscs and crustacea have demonstrated differential survival of allozyme genotypes exposed to heavy metals (Hvilsom 1983; Lavie and Nevo 1982, 1986; Nevo *et al.* 1981). Similar changes in gene frequencies have been detected in marine organisms exposed to crude-oil (Battaglia *et al.* 1980; Nevo and Lavie 1989; Nevo *et al.* 1978) although Fevolden and Garner (1986) found no evidence for genotypic selection in *Mytilus edulis* exposed to low concentrations of oil in Norwegian fjords. In laboratory tests on pairs of species exposed to marine pollutants those species with the higher level of genetic diversity showed greater survival (Nevo *et al.* 1986).

There are fewer reports of genetic changes in teleosts due to pollution. Temporal shifts in allozyme frequencies were greater at polluted than none polluted sites in Baltic populations of the fourhorn sculpin *Myoxocephalus quadricornis* (Gyllensten and Ryman 1988). However, it is not clear if these genetic changes are due to a direct selective mortality or due to invasion of polluted sites by new stock (Gyllensten and Ryman 1988).

## Life history characters

Most marine fishes and invertebrates are iteroparous, reproduce over several years, whereas the Pacific salmon, genus *Oncorhynchus*, are semelparous, reproducing once in their lifetime. Many species are highly fecund and the life history includes a dispersive phase (Fogarty *et al.* 1991). However, there are considerable

interspecific variations in lifespan and fecundity, and many of the widely distributed species exhibit long spawning seasons with the time of spawning varying latitudinally. In the pink salmon *Onorhynchus keta* the time of return for spawning has a genetic component (Gharret and Smoker 1993). In the European scallop *Pecten maximus* transplant experiments have demonstrated a genetic component to spawning period and there are intra-stock differences for this character (Cochard and Devauchelle 1993, Mackie and Ansell 1993). Size at sexual maturity varies between intraspecific stocks in skate *Raja radiata* (Templeman 1987) and American plaice *Hippoglossoides platessoides* (Roff 1982). Herring *Clupea harengus* and European plaice *Pleuronectes platessa* show geographic variations in fecundity (Mann and Mills 1979) and cod *Gadus morhua* intraspecific differences in age at maturity (Garrod and Horwood 1984).

There is a significant correlation between the age at first reproduction, mortality and growth rate in teleosts and it has been suggested that these correlations are the result of an evolutionary trade-off between growth, reproduction and survival (Roff 1984). Fishing theory predicts that an increase in fishing mortality will produce an increase in growth and recruitment. Whether the onset of sexual maturity is determined by age or size it will be changed by increased fishing mortality: faster growing fish will reach the minimum size more quickly and mature at an earlier age, alternatively if the onset of maturity is determined by age, then fish will mature at a larger size. The complex and poorly understood relationships between the genetic components of growth rate and the size and age of first maturity, and the non-genetic responses of these traits to changes in population density and other environmental parameters, especially water temperature, make it difficult to separate the genetic and non genetic impact of fishing on natural populations.





## FORCES SHAPING THE GENETIC STRUCTURE OF POPULATIONS

The major forces shaping the genetic structure of populations are genetic drift, selection and migration. Mutation and recombination generate new genetic variation but are not major forces in determining levels of intraspecific differentiation. Most population genetic texts provide explanations and discussions on drift, selection and migration; more detailed accounts on artificial selection in fish can be found in Gall and Chen (1993), Gjedrem (1990) and Kirpichnikov (1981), while the effects of drift and population size on genetic diversity are discussed in Soule (1986, 1987), Soule and Wilcox (1980) and in issues of Conservation Biology and Bioscience and are outlined briefly below.

Selection is the non-random survival of genotypes, brought about through differences between individuals in reproductive output and in survival of offspring. Under natural selection the most fit individuals leave more offspring than the less fit individuals. The degree of fitness is measured by  $s$  the selection coefficient, whereby the most fit genotype is given a value of 1 and less fit genotypes  $1-s$ . A selection differential of just a few percent can have a significant impact on a population over several generations.

Three basic types of selection have been recognised in populations: directional selection favouring one genotype or character, disruptive selection favouring two or more different types, and stabilising selection against extreme individuals. Fitness under these three types of selection can be considered in a simplified single gene model as:

	Genotypes		
	AA	Aa	aa
directional selection	1	1	1-s
disruptive selection	1	1-s	1
stabilising selection	1-s	1	1-s

Under directional selection allele frequencies would change, but alleles would not be lost unless drift impacted on a small population, because allele  $a$  is “protected” in the heterozygous condition. Under disruptive selection the population could diverge into two sub-populations fixed for  $A$  and  $a$ , the diversity remaining high. Under stabilising selection the heterozygote is advantaged and the proportion of heterozygotes in the population reaches an equilibrium value. In natural populations fitness of a genotype is unlikely to be constant over time and will change with environmental conditions including population density. Frequency-dependent selection is thought to be important in maintaining genetic variation when rare alleles have some selective advantage. The life history characters are likely to be polygenic, controlled by a large number of genes, in which case the response to selection will alter the average allele frequency of the genes coding for the trait (Bentsen 1994).

Genetic drift occurs through the random sampling of gametes at each generation. This produces chance fluctuations in allele frequencies from one generation to the next and in small populations the random changes may result in loss of alleles. Drift is probably the major force determining gene frequencies in very small populations, but is less important in large populations. Inbreeding, the mating between related individuals, also occurs in small populations. Inbreeding is most likely to occur in small isolated populations such as may occur in hatcheries or in endangered species, where there is a greater probability that two related individuals will mate. Mechanisms for avoiding inbreeding need to be considered in aquaculture and in enhancement programmes (Gall 1987).

The rate of loss of selectively neutral variation due to drift is dependent upon population size and the number of generations, and is described as  $H_t = H_0(1-1/2N_e)^t$  (Wright 1969), where  $H$  is heterozygosity,  $N_e$  the effective population size and  $t$  the time in generations.  $N_e$  is usually much smaller than the actual population



size as only the breeding adults contribute to the population (Bartley *et al.* 1992a).  $N_e$  is difficult to measure and there are few estimates of  $N_e$  for marine species. However, this population statistic is important in managing genetic resources and population geneticists are beginning to develop means to estimate  $N_e$  from allelic and genotypic data (e.g. Waples 1990, Bartley *et al.* 1992a).

The effective population size is decreased by an unequal sex ratio, and by variation in reproductive success which can be large in marine species with high fecundity and overlapping generations (Nelson and Soule 1987). To ensure that 99% of genetic diversity is retained per generation would require a minimum  $N_e$  of 50 with equal numbers of males and females. While no single value of  $N_e$  is appropriate for all species, due to variation in life histories (Kapusinski and Lannan 1986), a minimum  $N_e$  of the order of 500 has been proposed for the long term preservation of genetic diversity (Franklin 1980, FAO 1981).

Genetic differences between populations evolve when there is little or no gene flow between them and are augmented by selection; migration counteracts the effects of drift and selection by reintroducing alleles to populations. Even a small amount of migration between populations is sufficient to eliminate differentiation due to drift, for example in two ideal populations with sizes of  $N$  and which exchange a proportion  $m$  through migrants each generation, then no significant divergence will occur between the populations if  $Nm > 1$  (Lewontin 1974, Slatkin 1985). The population size of many commercially important marine species is likely to be large ( $>1\ 000$ ) and small absolute numbers of migrants per generation will prevent divergence due to drift.

Drift will act on all loci in the same way whereas selection may act differently on different loci. The relative contributions of drift and selection to the observed allele frequency variation in marine populations is uncertain. There is evidence for strong selection at some enzyme loci for example in blue mussels *Mytilus edulis* (Koehn *et al.* 1983) and in mummichog *Fundulus heteroclitus* (Powers *et al.* 1983). However, drift would appear to account for the genetic differences between odd- and even- year pink salmon *Oncorhynchus gorbuscha* which inhabit the same environment (Aspinwall 1974).

Loss of genetic diversity occurs through drift, primarily in small populations, and through the selective removal of specific genotypes. In theory any activities or processes that selectively harvest individual types or severely reduce population size will change the genetic structure of natural populations. In addition diversity can be lost when small populations are swamped by introducing large numbers of individuals from a different gene pool. This situation would be rare in natural populations, but could occur in enhancement programmes and has been recorded with escapes of farmed salmon (Hindar *et al.* 1991).





## SELECTIVE EFFECTS OF FISHING

Fishing is a selective agent and has the potential to change populations. Many fishers target a particular species or group of species and target large adults as opposed to juveniles. It is well known that different fishing methods catch different size fish in the same area, e.g. the trawl and longline fisheries of the North Atlantic Ocean (ICNAF 1963) and the seine, gillnet and troll fisheries for Pacific salmon off British Columbia (Ricker *et al.* 1978). In spite of this potential for selection, evidence for genetic changes due to fishing, especially in marine populations, has been limited. In an early review Miller (1957) concluded that there was little evidence for any heritable changes due to exploitation or introductions in freshwater fishes. Since that period there have been several reports of genetic changes in fish populations associated with heavy fishing pressure. Most reports are based on a change in life history characters over time, and these characters may change non-genetically in response to environmental change.

### Evidence for genetic changes due to selective fishing

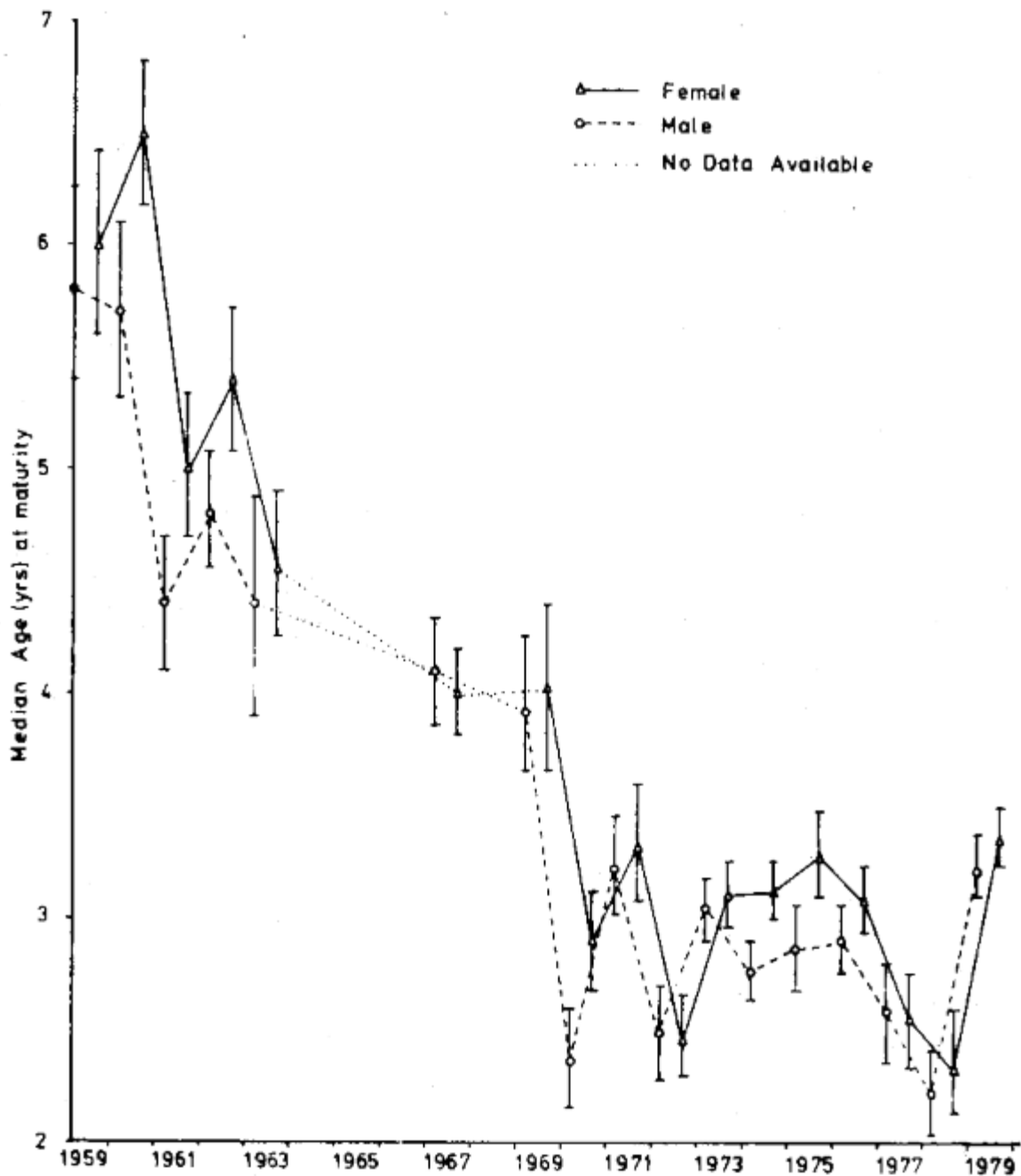
#### a. Selection for small size and early maturation in cod *Gadus morhua*

The Atlantic cod has been exploited throughout the coastal waters of the North Atlantic Ocean for centuries, but biological sampling of catches has been carried out only for the past 50 years. The discovery and excavation of a fishing schooner lost off the coast of Nova Scotia in the 1750s provided a unique opportunity to compare cod lengths, based on measurements of cleithra bones from the pectoral girdle, between the 18th and 20th centuries (Kenchington and Kenchington 1993). Modern hook caught cod off Nova Scotia are much smaller than cod caught during the 1750s, although cod of similar maximum size are occasionally caught (Kenchington and Kenchington 1993).

On the Scotian shelf in the Northwest Atlantic catches peaked at over 80 000 tonnes in 1968 and were accompanied by a marked decline in biomass and corresponding decline in mean size and age of cod (Beacham 1983a). In addition the median length and age at maturity declined: the median age at sexual maturity declined from >5 years in the 1960s to < 3 years in 1978 (Fig. 1) for both males and females (Beacham 1983a). Cod that matured at smaller or younger sizes would have a selective advantage under heavy fishing pressure as the larger and older maturing cod would be captured before the onset of sexual maturity (Beacham 1983a). Similar observations have been made for Atlantic cod at West Greenland, where the average age at first maturity declined from 9.9 years in 1917 to 6.4 years in 1936 in the northern fishery and from 9.3 years in 1922 to 7.6 years in 1936 in the southern fishery (Hansen 1949).

In the Arcto-Norwegian stocks of Atlantic cod the majority of the fish matured at 8–10 years in the 1930s but by the 1970s the majority of cod matured at 6 years (Borisov 1979). This decline has been attributed to a selective removal of late maturing cod from the population (Borisov 1979). No trend in length at age was noted over a 40-year period suggesting that growth was not density dependent, although a decline in length at age in the last half of the 1980s coincided with a decline in relative abundance of capelin, the major prey item for large cod (Jorgensen 1992). Law and Grey (1989) have suggested that fisheries on the younger 4-year old “feeding stocks” in the Barents Sea and on the Spitzbergen Shelf should be restricted and fishing concentrated on the larger spawning fish on the Norwegian coast. This fishing pattern would select for late maturing individuals and give an increase in yield.





**Figure 1.** The median age at sexual maturity for Atlantic cod caught in Fishery Division 4W on the Scotian Shelf, Canada between 1959–79. The triangles joined by a solid line are female data and the circles joined by a dashed line are male data, the dotted line indicates no data available and the vertical bars indicate 95 % confidence limits. (Data from Beacham 1983a).

### **b. Selection for early maturation in the haddock *Melanogrammus aeglefinus***

The haddock has been heavily exploited in the demersal fisheries of the northwest Atlantic. Catches of haddock from the St Pierre Bank off Newfoundland rose rapidly to a peak of 58 000 tonnes in 1955, based largely on an exceptional year class in 1949. This large catch was followed by a decline to around 6 000 tonnes in 1957 and further reductions to less than 1 000 tonnes in the 1970s (Templeman and Bishop 1979a). Biological data collected between 1948–51 and 1969–75 show a decline in the mean age at 50% maturity (Fig.2.) from 4.6 to 3.3 years in males and from 5.9 to 4.3 years in females (Templeman and Bishop 1979b). Beacham (1983b) has pointed out that this decline occurred over a period of both increasing and decreasing growth rates, so that the change in age at maturity is not simply related to changes in growth rate

due to the compensatory effect of reduced biomass, but is most likely genetic.

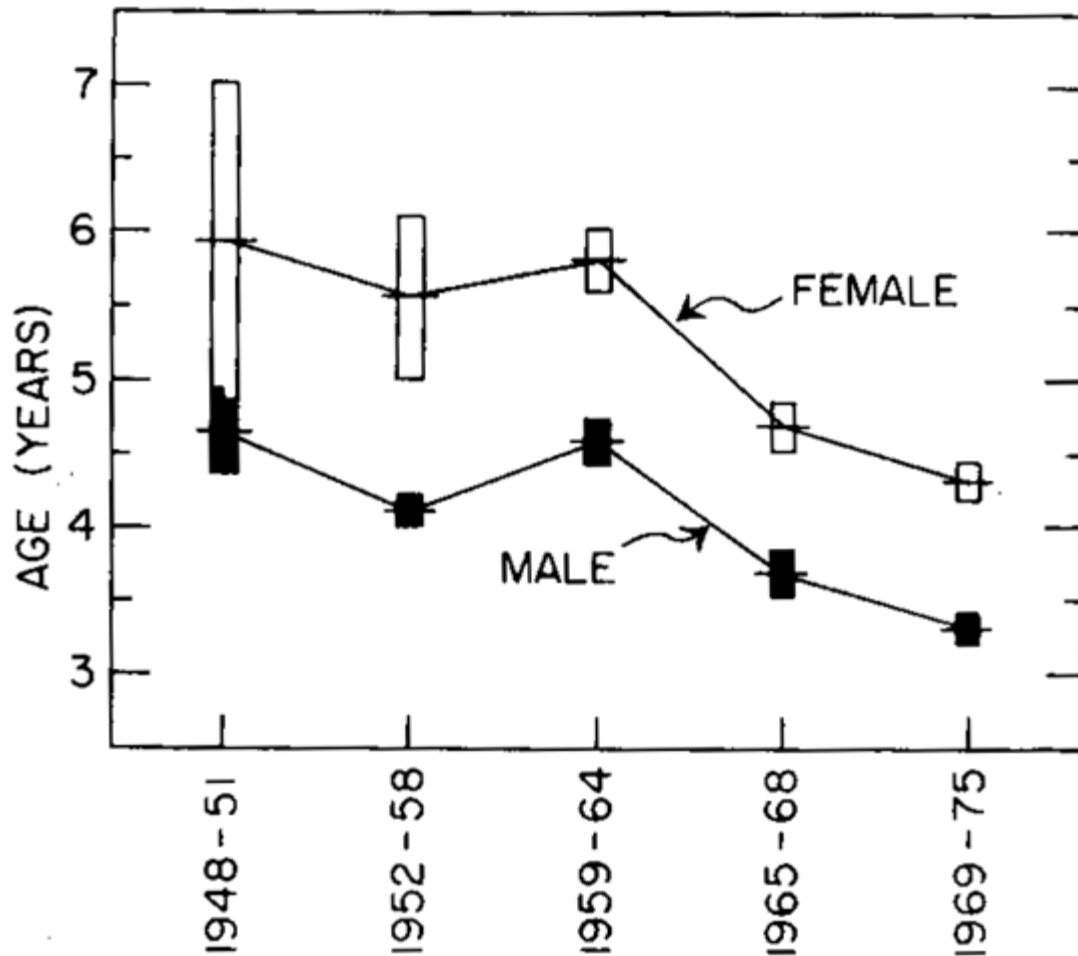


Figure 2. Trends in the mean age at 50% sexual maturity for male and female haddock on St Pierre Bank, Canada between 1948–75. The vertical bars represent the 95% confidence limits. (Data from Templeman and Bishop 1979b).

On the Scotian Shelf haddock catches peaked in 1965 at more than 50 000 tonnes and subsequently declined to less than 11 000 tonnes in 1967. Over the same time period the median length at sexual maturity was relatively constant but the median age at maturity declined between 1959–64 and 1975–79 from 3.9 to 2.7 years for males and from 4.4 to 3.0 for females (Beacham 1983c).

### c. Selection for early maturation in flatfishes

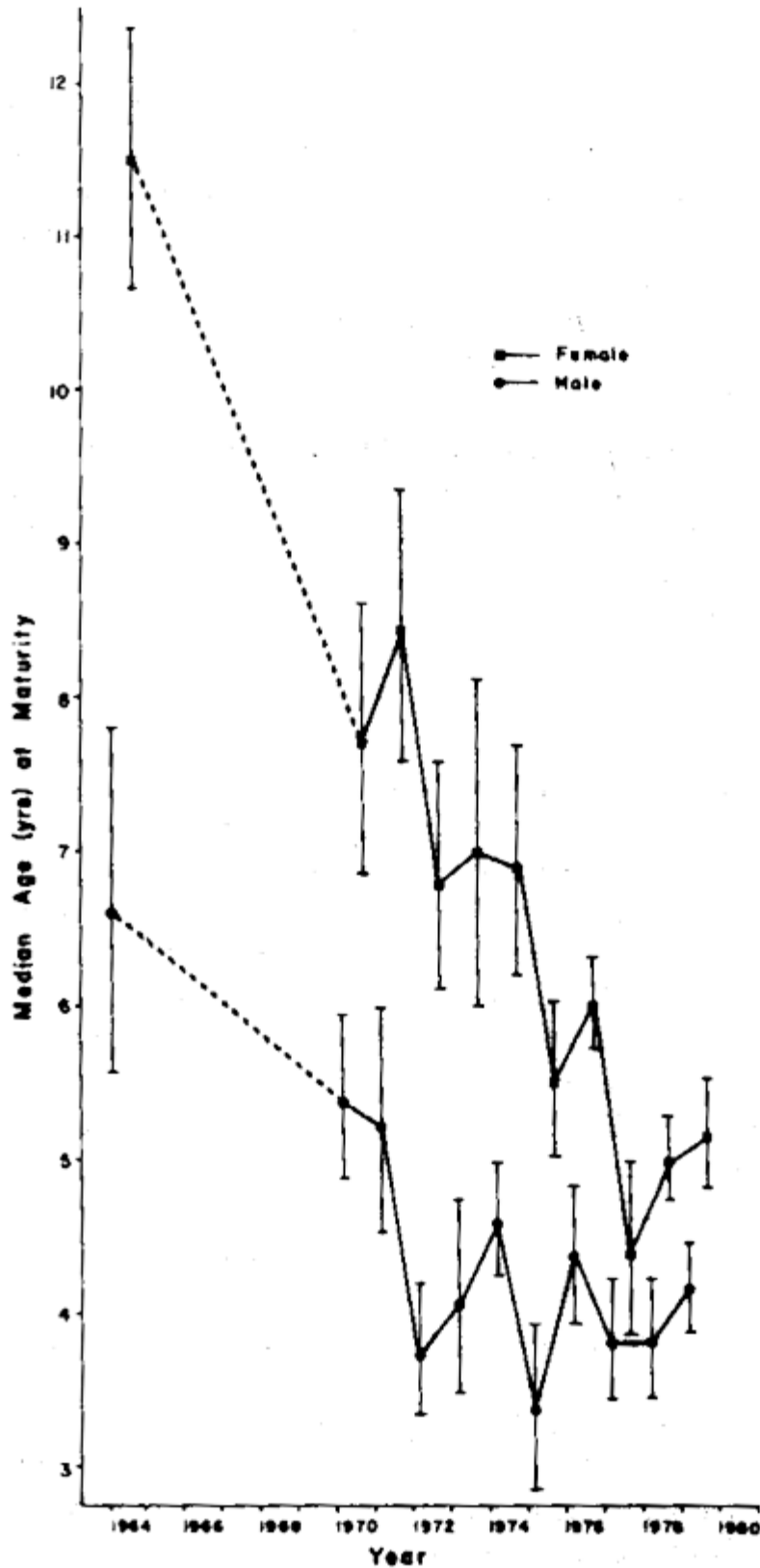
On the Grand Bank in the Northwest Atlantic the catch of plaice *Hippoglossoides platessoides* increased during the 1950s and peaked at around 90 000 tonnes per annum in the 1960s before declining to around 45 000 tonnes (Pitt 1975). Over the period 1959–72 the mean size at age increased gradually, while the age at sexual maturity declined (Pitt 1975). Average length was correlated with stock abundance, but not water temperature, leading Pitt (1975) to conclude that the changes in size at age were to a large extent due to a reduction in density. The cause of the decline in age at maturity is less clear as there are regional variations in the age at maturity; in some areas faster growing fish mature at a greater age than slow growing fish from other areas (Pitt 1975). Fishing is likely to remove a higher proportion of the faster growing fish, producing a decline in the age at maturity but which was not due to a density dependent increase in growth rate.

Beacham (1983b) has presented evidence for a decline in the median length and age at sexual maturity for plaice (Fig. 3) and yellowtail flounder *Limanda ferruginea* in several fisheries in the northwest Atlantic. This

decline in both size and age at maturity is not easily accounted for by an increase in growth rate due to the compensatory effect of reduced biomass (Beacham 1983b), but is likely to reflect a genetic change in the population.

In the yellowfin sole *Limanda espersa* fishery off the Russian Federation the size and age at which 50% of the females reached maturity declined from 29.9 cms and 8.5 years to 27.2 cms and 7.2 years over the period 1961–69 (Tikhonov 1977). An increase in fecundity in fish of the same size was recorded over the same period.

In contrast in the North Sea fishery an increase in growth rate in the sole *Solea solea* was related to food availability from trawling activities rather than a reduction in stock density (de Veen 1976). Size at maturity remained constant for a long period and then increased, while age at maturity did not change over the same period. Likewise Rijnsdorp *et al.* (1991) found no evidence for density dependent growth in adult sole and plaice *Pleuronectes platessa* over a 30-year period of high exploitation. In plaice the age at maturity, but not the size at maturity, varied over the period 1958–88 and was positively correlated with growth rate in juveniles. In sole there was no relationship between juvenile growth rate and age at maturation, and for both plaice and sole there was no consistent trend in growth rate or size and age at maturity (Rijnsdorp 1991).



**Figure 3.** The median age at sexual maturity for Atlantic plaice caught in Fishery Division 4W on the Scotian Shelf, Canada between 1964–80. The squares joined by a solid line are female data and the circles joined by a solid line are male data, the dotted lines indicate no data available and the vertical bars indicate 95 % confidence limits. (Data from Beacham 1983c).

#### d. Selection for smaller size at maturity in rock lobster

Observations on natural populations of rock lobsters suggest that the onset of sexual maturity is age and not size related. When the breeding stock of *Panulirus longipes cygnus* from the west coast of Australia is at low density the size at first breeding and upper size range of females is higher (Chittleborough 1979). Under crowded (unexploited) conditions the growth rate is retarded and the onset of sexual maturity occurs at smaller size (Chittleborough 1979). In *Jasus lalandii* in the Benguela ecosystem off South Africa the growth rates and the size at sexual maturity are greatest where food availability is high (Byers and Goosen 1987). A reduction in size at onset of egg production and an increase in asymptotic length was reported in the spiny lobster *Panulirus marginatus* from Hawaii following heavy fishing pressure on a virgin stock (Polovina 1989). This decline in size at onset of egg production in *P. marginatus* is in the opposite direction to that predicted from density relationships and may indicate a genetic change in the population.

#### e. Lowering the age of sex change in the shrimp *Pandalus borealis*

The pandalid shrimps are protandrous hermaphrodites (reproducing first as males) in which the age of first breeding and subsequent sex reversal is related to individual size (Charnov 1979). In the shrimp, *P. borealis*, fishery in the Skaggerak a reduction in size of females occurred over a period of heavy exploitation (Jensen 1965, 1967). The combined Danish and Swedish shrimp catch more than doubled between 1956 and 1960 while the percentage of large shrimps, predominately females, declined from 44% in 1944 to 14% in 1961. More surprising was the appearance of a small size class of females (Table 1), approximately the same size as the one-year old males. Small females (< 75mm) were not present in 1953, but by 1961–62 formed 21–30% of the catch (Jensen 1965). Charnov (1981) has suggested that increased fishing mortality on the large females has selected for individuals that mature as female at the age of first breeding.

#### f. Selection for late spawning in herring *Clupea harengus*

For species with an extended spawning period and associated seasonal patterns of behaviour and movement, fishing activities may inflict heavier mortality on one component of the resource. In seasonal and unrestricted fisheries there is a temptation for commercial operators to take as much of the catch as soon as the season opens. This may put greater pressure on early returning individuals and favour late returners. The first arrival and subsequent spawning of Atlantic herring *C. harengus* on the Norwegian coast has changed over a 60-year period (Devold 1963). Around the turn of the century herring first returned to the spawning grounds in September–October, but this return date has been delayed progressively so that by the 1950s herring did not appear on the spawning grounds until January (Devold 1963). Mathisen (1989) has suggested that this change is due to the effects of fishing which has selectively harvested the first returning sub groups of herring, so that with time these contribute less to the fishery and are replaced serially by later returning sub-groups.

**Table 1.** The decrease in mean size and the increase in relative frequency of small females in the shrimp fishery in the Skagerak between 1949–62. (Data from Jensen 1965)

Sex	Period			
	1949–53	1954–57	1958–60	1961–62
	average length (mm)			
Males and transition	74	69	68	67
Females	96	87	83	82
	percentage			
Males and transition	65	81	85	83
Females < 74mm	0	2	3	4
>75mm	35	17	12	14

This interpretation of Devold's observations must be balanced against non genetic changes which may have occurred over the period. Changes in the spawning time of other groups of Atlantic herring have been

explained by changes in environmental conditions. The herring is a phenotypically plastic species which has been subdivided into a large number of taxonomic groups based on morphometric characters and spawning periods and localities (Parrish and Saville 1965). The heritability of spawning time in herring is unknown, but there is evidence for a strong environmental component. In the Baltic, herring spawn between the spring and autumn (Aneer 1985) with the less fecund spawning in the spring and the more fecund in the autumn (Anokhina 1971). The disappearance of autumn spawners has been linked to improved feeding conditions, due to eutrophication, whereby adults have sufficient food reserves to spawn in the spring (Aneer 1985). In the northwest Atlantic Ocean, autumn- and spring- born herring, identified by otolith characteristics, have been found spawning in the opposite season (Messieh 1972).

In an extension of this selective spawning-fishery hypothesis Mathisen (1989) has suggested that the decline of the Peruvian anchoveta *Engraulis ringens* was accelerated by disruptive selective fishing on the “best reproductive units” leaving only the marginal groups to rebuild the stocks.

### **g. Selection for smaller size and reduced age in Pacific salmon**

In the Pacific salmon fisheries of British Columbia most fish are caught as mature adults when they return to rivers for spawning. In this respect the fisheries are less likely to demonstrate the ‘fishing up’ effect seen in trawl fisheries for marine teleosts. A detailed study of five species of Pacific salmon concluded that at least three species exhibited a decrease in mean size at age following years of size selective fishing (Ricker 1981). The gillnet and troll fisheries for coho *Oncorhynchus kisutch* and pink salmon *O. gorbuscha* tend to catch the larger fish and these species exhibited the greatest declines in mean sizes (Ricker 1981). The chinook salmon *O. tshawytscha* has decreased in both mean size (Fig.4) and age between 1951 and 1975 (Ricker 1980). Ricker (1981) suggested that this decrease in size and age was due to the troll fishery capturing both maturing and nonmaturing individuals which selects against late maturing individuals. However, the data are complex as the fishing methods and mesh sizes have changed over the sampling period and for *O. nerka* there was an increase in growth rate over the period which was related to oceanic cooling (Ricker 1981).

In the coho *O. kisutch* males mature after six months in the ocean as jacks or after 18 months as hooknose. These two alternative life history strategies are maintained by disruptive (natural) selection favouring small “sneaky” males and large “fighting” males (Gross 1985). The fishery has selectively harvested the larger fish (Fig.5) increasing the relative frequency of jacks (Gross 1991). However, Gross (1991) has shown that changes at other stages of the life cycle can influence the ratio of jacks to hooknose males. Stream clearance may reduce the available refuges for jacks, thereby favouring hooknose fish on the spawning grounds. Other environmental changes, such as eutrophication, may increase fry growth rate leading to an increase in the proportion of juveniles maturing as jacks (Gross 1991).

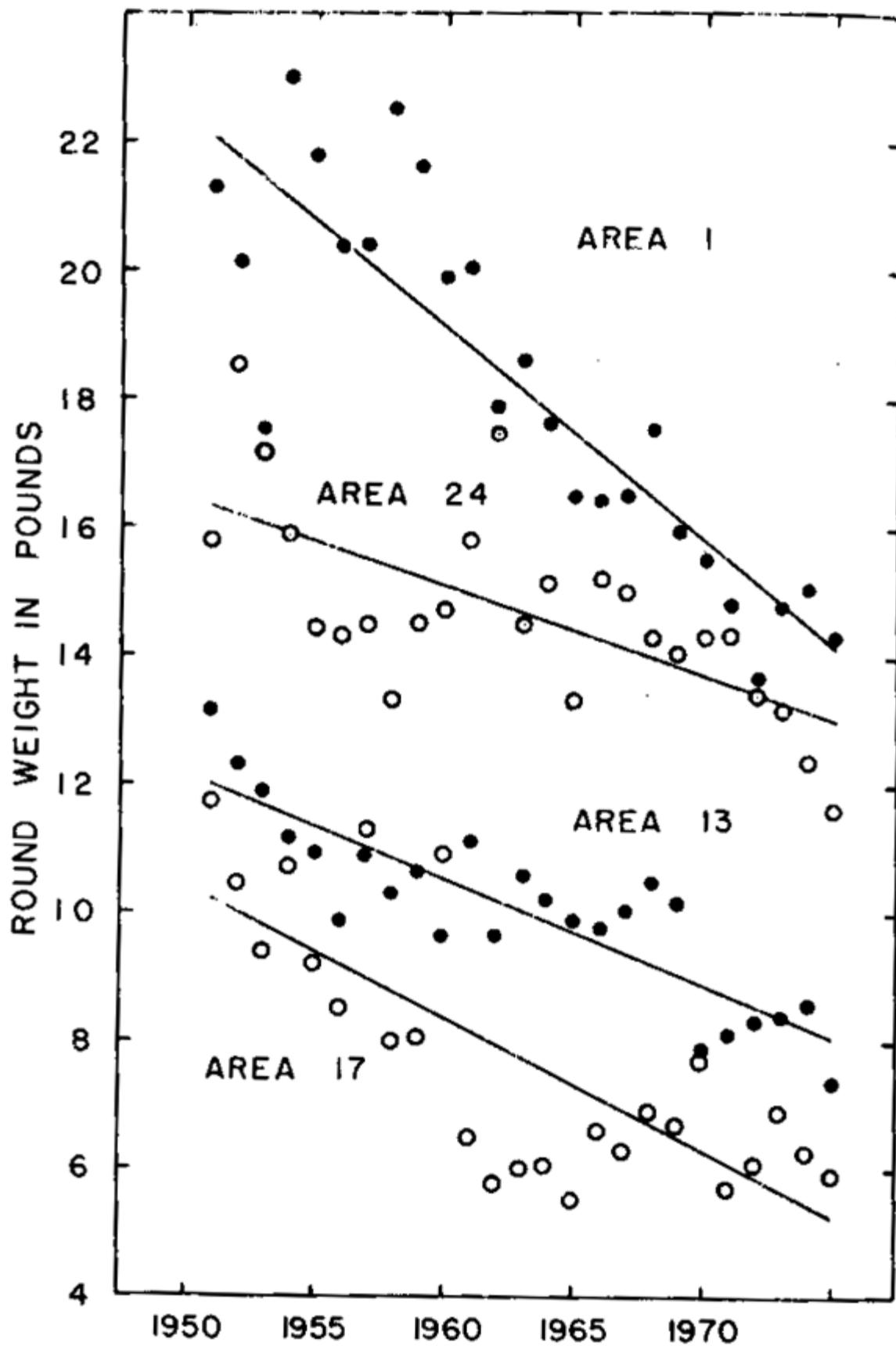
### **h. Selection for early maturity in Atlantic salmon *Salmo salar***

The Atlantic salmon *S. salar* exhibits wide variation in the mean age at first spawning between different river systems. It is believed that such variation is adaptive and maintained through natural selection (Schaffer and Elson 1975). Fishing pressure on returning adults has eliminated the larger and older fish from some runs leading to an early age of first returning fish (Schaffer and Elson 1975).

### **i. Disruptive selection in Pacific salmon**

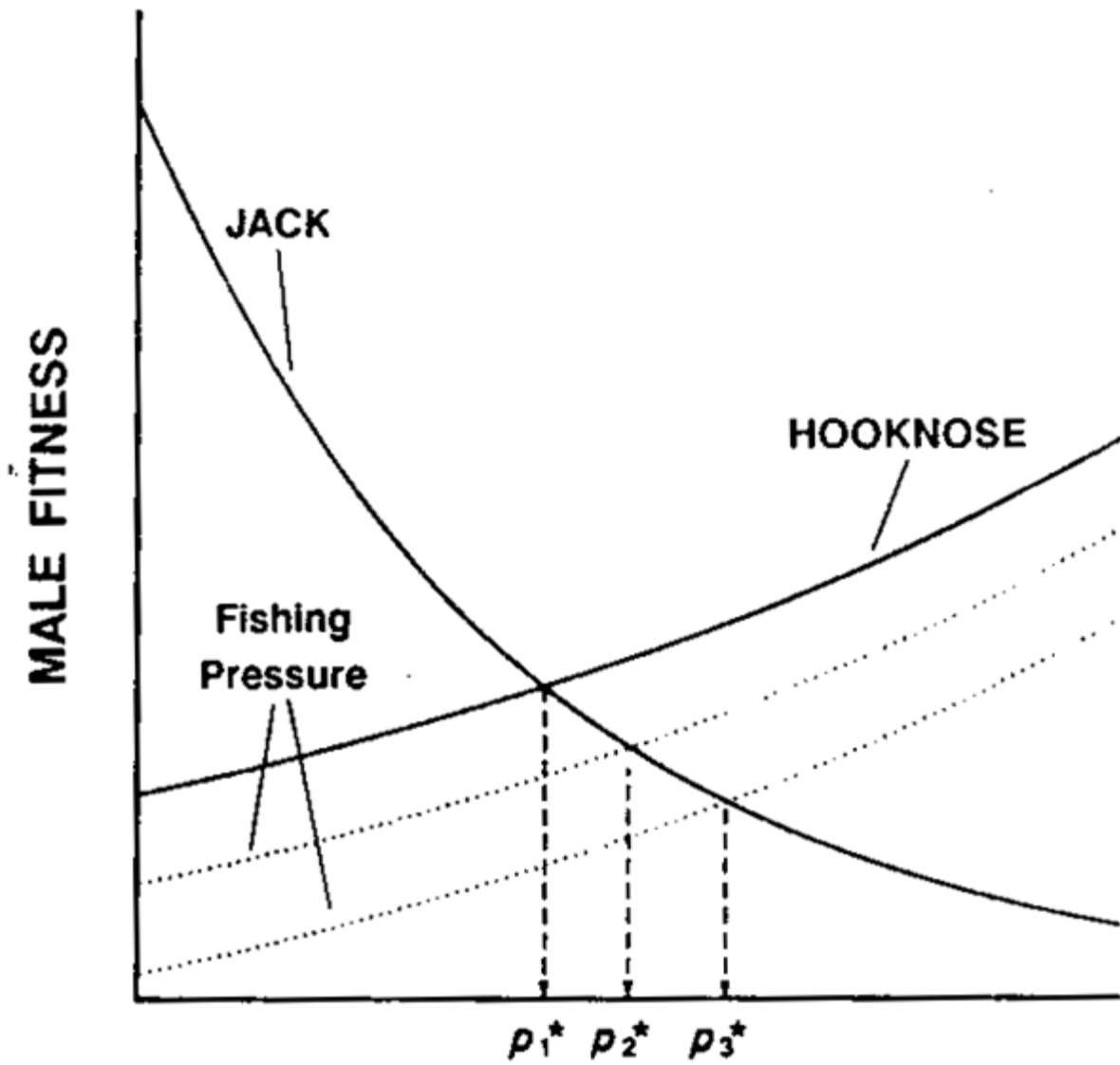
In species with a long spawning season unequal fishing pressure over the season may produce a selective mortality. In the Columbia River chinook salmon *Oncorhynchus tshawytscha* the spawning run lasted from April through to August with a peak in June-July when the fishery first developed last century (Thompson 1951). The fishery operated mostly over the summer when weather was suitable and the fish most abundant. Heavy fishing pressure on the peak run reduced catches so that by 1938 the overall numbers caught were reduced and the spawning run peaked early in May and in August (Fig. 6) with few fish caught in the original peak period of June-July (Thompson 1951). Mathisen (1989) has interpreted these observations as disruptive selection, selecting for both early and late spawners, which have not replaced the middle peak period

spawners.

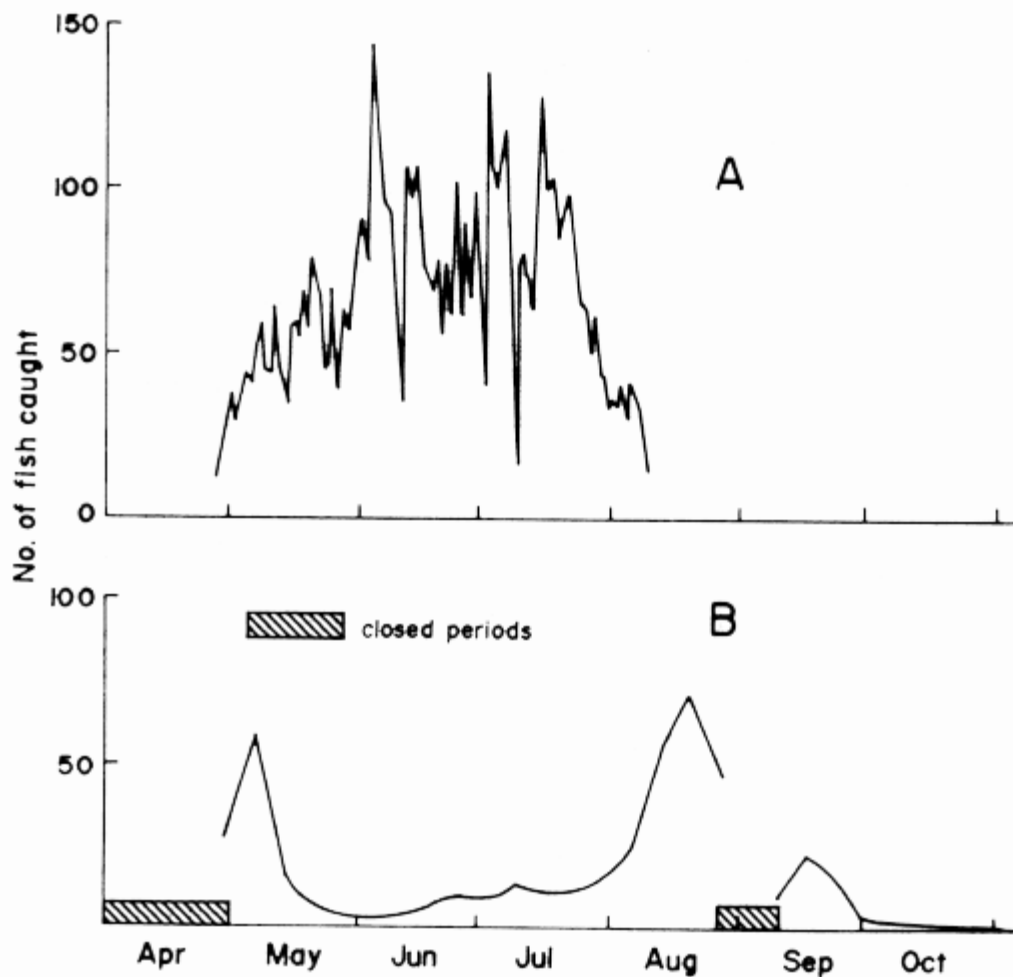


**Figure 4.** The median weights for troll-caught chinook salmon off British Columbia, Canada. (Data from Ricker 1981).





**Figure 5.** The effects of size-selective fishing on the relative fitness of hooknose and jack male4s of coho salmon. The selective removal of hooknose males increases the percentage of jacks in the fishery,  $p_1^*$  no fishing,  $p_2^*$  and  $p_3^*$  increasing levels of fishing. (Data from Gross 1991).



**Figure 6.** Seasonal changes in catches of chinook salmon in the Columbia River. A. Daily gillnet catches in 1876 and B. catches in 1938. (Data from Mathieson 1989).

Ricker (1982) has described a disruptive selection for size in the sockeye salmon *Oncorhynchus nerka*. The gillnet fishery has harvested fish from the mid size range favouring the survival of small 3-year ocean fish and large 4-year ocean fish. As a result the 3-year old fish have become smaller and the 4-year old fish larger, the difference between them increasing by about 500g (Ricker 1982).

### j. Selection for early maturation in lake fishes

Many lake fisheries use gillnets which selectively remove large heavy fish, producing a non random mortality with respect to size (Hamley 1975). In Canada whitefish are abundant and the lake whitefish *Coregonus clupeaformis* has supported fisheries in several lakes. A comparison of exploited and unexploited populations of lake whitefish showed the typical compensatory effects of fishing where growth rate increased with exploitation (Healey 1975). Growth rate in heavily exploited populations was similar to the most rapid growth rate in unexploited populations (Healey 1975). However, in heavily exploited populations fish matured at a younger age and smaller size than fish from unexploited populations.

In Lesser Slave Lake in Alberta the fish resources have been heavily exploited. The lake trout *Salvelinus namaycush* was fished out by the 1920s and other species have declined in abundance (Handford *et al.* 1977). Samples of *C. clupeaformis* were analyzed from commercial and research catches between 1941 and 1975. Following an initial increase in mean weight and length there was a decline in both length and weight at given age. By the 1970s fish of a given age were less than half the weight of fish of the same age in the

1940s, although mean length at age was about the same in the 1970s and 1940s (Handford *et al.* 1977). Similar observations have been made in other lakes (Handford *et al.* 1977). In addition the catches in Lesser Slave Lake showed an overall increase in mean age, a result to be expected under moderate levels of exploitation when selection favours slower growth rates and overcomes the counteractive effects of density dependent compensation (Handford *et al.* 1977). Lake fisheries for percids have shown similar patterns of an increase in growth rate and reduction in age of first spawning (Spangler *et al.* 1977).

The fish populations in Lake George, Uganda were studied between 1967 and 1972 where the cichlid *Tilapia nilotica* accounted for around 80% of the fish catch. Fishing has been the major source of adult mortality for this species which decreased in mean size from about 0.9 kg in 1950 to 0.4 kg in 1970. Over the same period the size at maturity decreased from 20–29cm to 18–24cm (Gwahaba 1973).

### k. Selection for morph type and reduced size in whitefish *Coregonus lavaretus*.

In Lake Femund in Norway the polymorphic whitefish consists of three morphs. A pelagic gillnet fishery started in the 1980s has selected against the pelagic morph which has decreased in proportion to the two other morphs and has shown a decrease in the proportion of large fish and a reduction in size at age (Sandlund and Naesje 1989).

### l. Loss of genetic diversity in orange roughy *Hoplostethus atlanticus*

In the 1980s a new fishery developed for orange roughy off the coasts of New Zealand and during the first ten years of exploitation the biomass was reduced by 60–70%. Genetic diversity, measured by gel electrophoresis, showed a significant decrease on three geographically isolated fishing grounds (Table 2) between 1982–83 and 1988 (Smith *et al.* 1991). The recent finding of new spawning grounds provides a further opportunity to test for genetic effects of exploitation on virgin stocks. Preliminary results from allozyme surveys indicate levels of genetic diversity similar to the pre-exploitation levels reported in 1982–83 (Smith unpub.). In a similar situation with the spiny lobster *Panulirus marginatus* no genetic changes were detected over a nine-year period following heavy exploitation of a virgin stock (Seeb *et al.* 1990).

Table 2. Heterozygosity levels in orange roughy from three fishing grounds around New Zealand, sampled in 1982/83 and 1988, before and after heavy fishing. There is a significant decrease in heterozygosity on each fishing ground, probability < 0.02 - < 0.01. (Data from Smith *et al.* 1991)

Fishing ground	Year of sampling	Mean heterozygosity	Probability
Chatham Rise	1982	0.20	< 0.02
(Pacific Ocean)	1988	0.14	
East coast	1983	0.25	< 0.02
(Pacific Ocean)	1988	0.17	
Challenger Plateau	1983	0.22	< 0.01
(Tasman Sea)	1988	0.15	

### m. Increase in genetic diversity in sockeye salmon *Oncorhynchus nerka*

In sockeye salmon populations spawning in isolated lakes on the Kamchatka Peninsula the young spend one to three years in the lakes and then migrate to sea for a further one to four years, before returning as sexually mature adults. The males mature at two different size: as large males after two or more years at sea, and as small jacks or “kayiriki” after one year at sea (Altukhov 1990). In addition some lake residual males mature as “dwarfs” (Altukhov 1990). This sexual dimorphism is similar to that reported in coho salmon *O. kisutch* (Gross 1985). Large sockeye males have an advantage over small males on the spawning grounds, but small males are more successful in years of low water levels and in shallow spawning areas that the large males cannot penetrate (Altukhov 1990).

Over a 35-year period between 1935–76 the numbers of sockeye returning to Lake Dalneye, on the Kamchatka Peninsula, declined dramatically (Altukhov 1990), while the proportion of jacks increased in the returning males and the proportion of resident dwarf males in the population increased dramatically (Table 3). More recent allozyme studies of sockeye populations in three Kamchatkan lakes (Table 4) have shown that heterozygosity measured at two enzyme loci is greater in small males (jacks) than in large males (Altukhov 1993). Allele frequencies are similar between the two groups but small males are characterised by a significant excess of heterozygotes at the *phosphoglucosmutase* (*PGM*) locus and large males a significant excess of homozygotes in two lakes. Heterozygosity in females is intermediate between the large and small males (Altukhov 1990). Altukhov (1990) suggests that these changes in heterozygosity are due to the selective effects of fishing. While fishing may have favoured the survival of small males, as may have changes in the freshwater environment, there are no historical data available on allozymes for the two size classes of males. In three Kamchatkan lakes the level of heterozygosity at *PGM* increases with the proportion of small males in the lake (Altukhov 1990).

Kirpichnikov *et al.* (1990) have shown that during the fry stages slow growing individuals are less heterozygous than fast growing individuals. If these fast growing individuals mature early as dwarfs or as jacks, and in salmonids fast growth is associated with early maturity, then this would account for the observations of Altukhov (1990). The overall population heterozygosity has increased due to the indirect effects of the fishery favouring the survival of small males.

## Experimental studies on selection of aquatic organisms

### a. Selection for slower growth rate in *Oreochromis mossambicus*

*O. mossambicus* is widely used in tropical pond aquaculture. It is a mouth breeder and is easily reared in tanks. To measure the impact of selective fishing two populations were established and, after 39 months, harvested at two monthly intervals (Silliman 1975). Harvesting removed approximately 10% of the fish: one population was selectively fished by removing only fish that could not pass through a grid placed in the tank. The second control population was unselectively fished by removing a similar number of fish but from all size classes. After 63 months the fishing pressure was increased to 20% and continued for a further 12 months. To test for a genetic impact of fishing groups of 46 mature fish were removed from the selected and unselected populations after 77 months and ongrown for a further period. Growth was measured at 55–56, 118–119, and 150–151 days after the start of the second experiment. In both the selected and unselected populations males grew faster than females, but the males in the unselected population grew more rapidly than males in the selected population (Silliman 1975). Thus selective fishing resulted in a decline in growth rate in males in only three generations. It is likely that females were less affected by the size selection due to their slower growth rate than males.

**Table 3.** Numbers of sockeye salmon in Lake Dalneye, Kamchatkan peninsula, and the numbers of jacks and dwarf males over the period 1935–76. (Data from Krogius 1979, presented in Altukhov 1993)

Salmon	Period			
	1935–46	1947–56	1957–65	1966–76
Average no. spawners entering lake (10 000s)	63	10	6	1.6
Percentage of jacks in migrating males	0.2	0.6	4.3	37.5
Percentage of dwarfs in male population	26	49	74	89

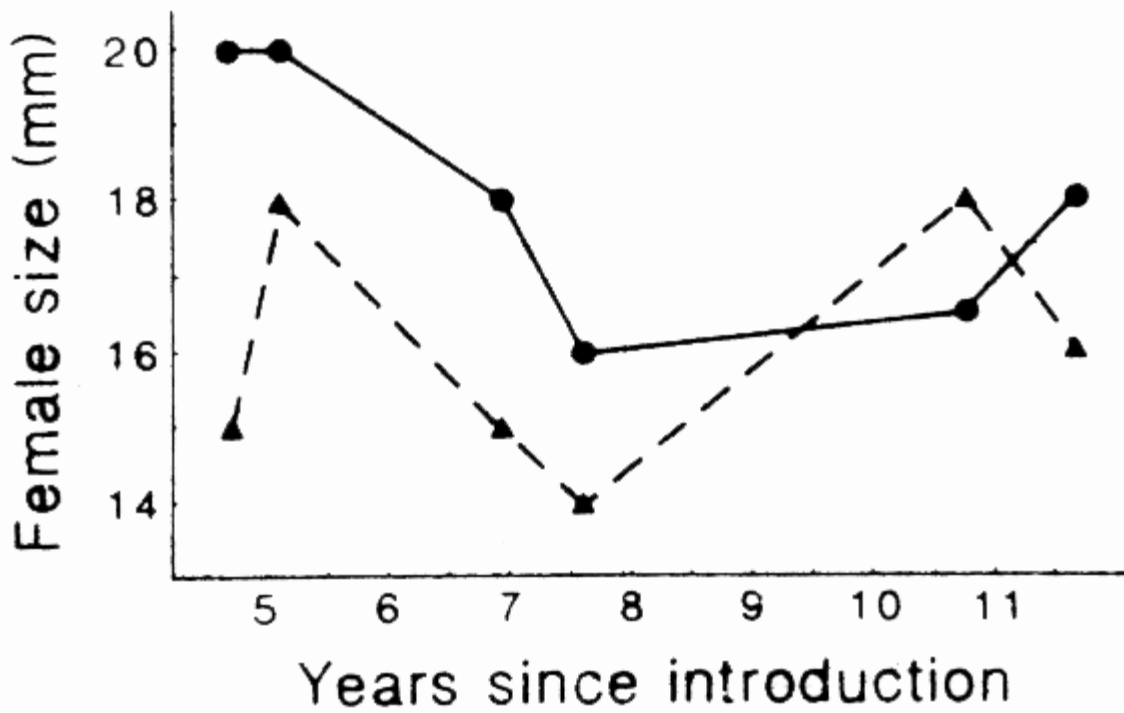
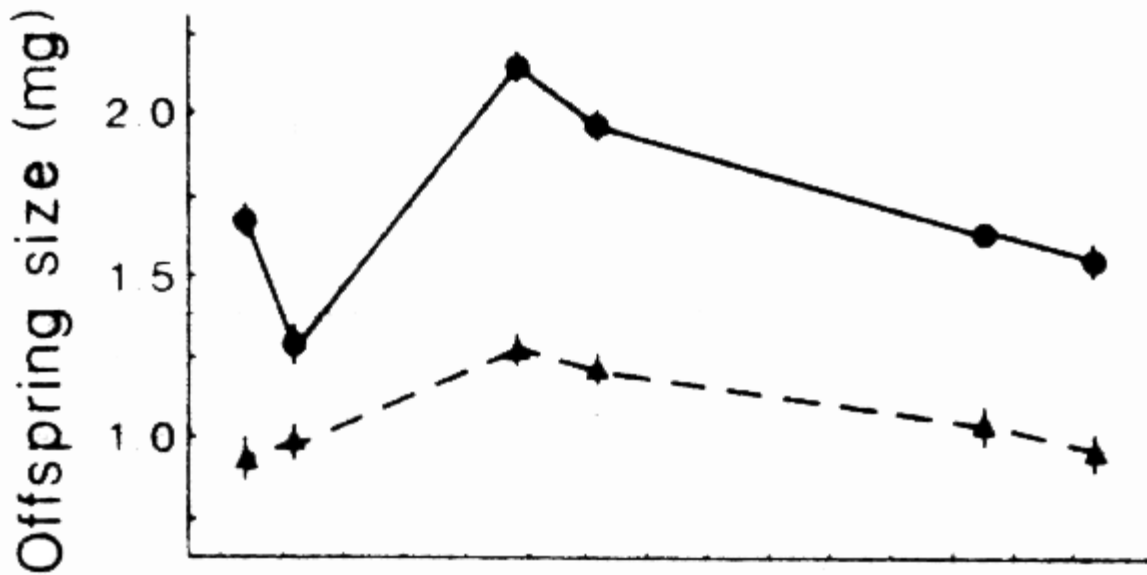
**Table 4.** Heterozygosity levels for *lactate dehydrogenase (LDH)* and *phosphoglucosmutase (PGM)* loci in sockeye salmon from three Kamchatkan lakes. (Data from Altukhov 1993)

Lake	Fish	Heterozygosity	
		<i>LDH</i>	<i>PGM</i>
L.Nachikinskoye	small males	.43	.55*
	large males	.39	.35*
L.Blizhneye	small males	.19	.56*
	large males	.03	.36
L.Dalneye	anadromous males	.21	.31
	dwarf males	.16	.62*

\* significant genetic imbalance

### **b. Selection for age and size at maturity in guppies *Poecilia reticulata***

Life history differences between populations of guppies are associated with predation: some predators (cichlids) prey on large sexually mature guppies and other predators (killifish) prey on small immature guppies. A population of guppies was transplanted from a river with a cichlid predator to a tributary site with no guppies but killifish predators. Over a period of 11 years the transplanted population produced larger offspring and larger females (Fig. 7) which first reproduced at a larger size than females in the control population (Reznick *et al.* 1990). Rearing groups of descendants from the two populations under similar laboratory conditions showed that the observed life history differences had a genetic basis (Reznick *et al.* 1990).



**Figure 7.** Size of offspring and average size of sexually mature females in transplanted and control samples of guppies over an eleven-year period on the Aripo River in Trinidad. Circles joined by a solid line are the introduced site and triangles joined by a dotted line are the control site. At the control site the main predator preyed predominantly on large guppies and at the transplant site the main predator preyed on small guppies. (Data from Reznick *et al.* 1990).

### c. Selection for size in *Daphnia magna*

A laboratory experiment was carried out with the water flea *D. magna* to measure the impact of two contrasting harvesting regimes, removing small individuals and removing large individuals (Edley and Law 1988). At the first harvest 50% of the stock was removed and there after 40% removed every eight days. Yields declined under both harvesting regimes, but were greatest in populations harvested for large individuals. Under the harvesting regime of removing small individuals the mean size at age increased as did the size at first reproduction, while under the harvesting regime removing large individuals, the reverse occurred with a decline in size at age and decline in size at first reproduction (Edley and Law 1988).

## Modelling studies on selective effects of fishing

Menshutkin *et al.* (1989) produced a simulation model of the sockeye salmon *Oncorhynchus nerka* fishery in Kamchatka. When growth was controlled by a single gene with two alleles the model population became unstable with loss of one allele, supporting observations that growth is under polygenic control. When growth was polygenic and multiallelic then the percentage of “fast growth” (which equate to early maturity) alleles increased in the selected population and the proportion of non migratory fish increased. These results would be expected from observations in the fishery where there has been an increase in the proportion of jacks and lake-resident fish (Altukhov 1990). Favro *et al.* (1979, 1982) used a simulation model to estimate the magnitude of genetic effects in a trout fishery subject to minimum size limits and in which growth was controlled by a small number of major genes. Results showed that mean size and total numbers decreased with moderate levels of fishing pressure and were in agreement with observations in a brown trout *Salmo trutta* fishery in Michigan. Extending the model to select for fish from a specific size range, whereby a minimum and a maximum size limit was set in the fishery, then the model showed that the double-size limit produced a similar decrease in larger fish as did conventional minimum size limits (Favro *et al.* 1980).

Law and Edley (1989) have used an age specific model to describe exploitation which acts as a selective force on genetic variation in life history characters. Selective fishing will lead to changes in life histories that in turn produce evolutionary changes in yield. In principle the fishery manager may opt for the harvest pattern that will select for an optimum life history which will produce the greatest yield, which the authors refer to as the “evolutionary stable optimal harvesting strategy” (Law and Edley 1989). Applying this model to the Arcto-Norwegian cod *Gadus morhua*, which has shown a decline in age at maturity, then an increase in yield could be obtained by selecting for late maturing fish. In practice this could be achieved by restricting fishing based on immature fish in the northern feeding grounds and focusing effort on the spawning fisheries (Law and Edley 1989).

A large-scale experimental management approach to test the heritability of growth rate and the effects of size selective fishing on a natural population of pink salmon *Oncorhynchus gorbuscha* has been proposed by McAllister and Peterman (1992) with the overall aim of increasing catch biomass. This species, as with other west coast salmonids, has shown a reduction in mean size over the past twenty years (see section g above and Ricker *et al.* 1978) and there is uncertainty if the changes are due to selective removal of larger fish, to selective depletion of stocks with large body size, or to changes in oceanographic conditions (McAllister and Peterman 1992). Controlled selective harvesting of small fish would permit a test of the heritability of growth rate and, provided that growth rate is inherited, lead to an increase in mean size in the fishery. Monte Carlo simulations showed that block designs with few replicates and short duration times generated high statistical power for determining the importance of size selective fishing. In an extension of the experimental design McAllister and Peterman (1992) used a decision analysis to demonstrate that the experimental approach to management of the pink salmon stocks was likely to produce a higher harvest value than the current management practice.







## GENETIC CHANGES DUE TO DRIFT

Loss of genetic diversity due to genetic drift will occur in small populations. There are few examples of marine fish populations being reduced to the stage where genetic drift might be operating, but some populations of bivalves, such as giant clams and *Trochus*, have been severely depleted in the Indo Pacific Ocean as a result of overexploitation, and may be unable to survive without restocking. Protein electrophoresis of three species of giant clam has shown high levels of genetic diversity but the sampling was patchy and did not include samples from areas where the species are rare (Benzie 1993). In contrast rare and endangered freshwater teleosts in North America show reduced genetic diversity and several desert populations are characterised by zero variability (Echelle 1991). Low levels of heterozygosity in upper river populations of chinook salmon *Oncorhynchus tshawytscha* from the Columbia River basin, Oregon and California are thought to be the result of natural and human-related bottlenecks (Winans 1989, Bartley *et al.* 1992b). The northern elephant seal *Mirounga angustirostris* was heavily exploited last century and reduced to less than 100 individuals. The species shows reduced genetic variation measured by allozyme polymorphisms (Bonnell and Sealder 1974) and mtDNA sequences (Hoelzel *et al.* 1993) in comparison with populations of southern elephant seals *M.leonia* which, although exploited, numbers did not fall below 1 000 individuals (Gales *et al.* 1989, Hoelzel *et al.* 1993).

Experimental evidence demonstrates that inbreeding reduces productivity and size of fish. Populations of the eastern mosquitofish *Gambusia holbrooki* were established in artificial ponds based on one virgin female and one virgin male fish. In three pools the fish were full sibs and in four pools the fish were unrelated. Populations established with full sibs have a predicted 25% less genetic variation than unrelated individuals. After three generations the populations founded on unrelated individuals produced 35 times more juveniles than populations founded on related individuals and size of males at sexual maturity was greater in unrelated than related populations (Ledberg 1990).

The expansion of the aquaculture industry and the move to hatchery production of seed for both farming and enhancement programmes has led to a large number of hatcheries being established for marine and freshwater organisms. The high fecundity of these species allows the production of numerous seed from a few parents and the risk of loss of genetic diversity. Genetic studies of hatchery populations suggest that loss of genetic diversity is common and has been reported in hatchery salmonids in North America (Allendorf and Phelps 1980, Cross and King 1983, Leary *et al.* 1985, Verspoor 1988) and Europe (Ryman and Stahl 1980, Stahl 1983, Vuorinen 1984, Koljonen 1989), in sea bream in Japan (Taniguichi *et al.* 1983, Sugama *et al.* 1988) and in oysters (Gosling 1981, Gaffney *et al.* 1992, Hedgecock and Sly 1990), clams (Dillon and Manzi 1987, Benzie 1993), abalone (Smith and Conroy 1992) and shrimp (Sbordoni *et al.* 1986). In addition the life history characters of cultured Atlantic salmon *Salmo salar* often differ from those of wild stocks (Heggberget *et al.* 1993).

While loss of genetic diversity is of concern to aquaculturists the release, intentional or otherwise, of hatchery stocks has ecological and genetic implications for wild fisheries (Marnell 1986, Thomas and Mathieson 1993). The maintenance of some populations of Pacific salmon is dependent upon hatchery seed (Winans 1989) and more than 4 billion smolt are released annually in the North Pacific Ocean (Hindar *et al.* 1991). The genetic impact of large scale releases are uncertain but may have a negative impact on wild populations if the genetic differences between the hatchery stock and the wild population are great (Skaal *et al.* 1990, Hindar *et al.* 1991). This is especially relevant to salmonid populations that often are composed of genetically differentiated sub populations. A large number of genetic effects of cultured salmonids on native populations have been documented by Hindar *et al.* (1991). There is some evidence that introduced stocks of chum salmon *Oncorhynchus keta* do less well than native stocks and do not contribute to subsequent spawning runs (Altukhov and Salmenkova 1990), but in the Atlantic salmon *Salmo salar* electrophoretic evidence shows that escaped farm salmon interbreed with wild stocks (Crozier 1993). In Norwegian rivers significant

numbers of escaped farmed salmon have been identified in the spawning rivers (Skaala *et al.* 1990) and in extreme situations up to 80% of river spawners may be of farm origin (Hindar *et al.* 1991). In this situation with small natural populations there is a risk that released fish will swamp the native gene pool.

The concerns raised over the genetic impact of hatchery produced salmonids on wild stocks serve as a warning of the pitfalls for marine enhancement programmes. Genetic approaches to avoiding inbreeding and loss of diversity due to drift in hatcheries are well known (FAO 1981, Soule 1986, 1987, Gall 1987, Munro 1993) but the holding and spawning of large numbers of broodstock can present technical difficulties for marine species (e.g. Gervis 1993). The use of local broodstock, or broodstock genetically similar to local populations, is preferred to reduce the risk of introducing foreign alleles in the enhanced population. In addition proper hatchery management including maximising  $N_e$  (effective population size) and minimising inbreeding will be necessary.

The concept of genetic marking of hatchery released fish has appeal to fisheries managers wishing to measure the short-term impact of the released fish on the natural population, but the practice could have a long term genetic impact on the population. Most proposals for genetic marking identify rare alleles as the genetic tag to be selectively bred into the hatchery seed, usually through crossing a few parents carrying the rare allele. Even the use of 50 wild parents carrying the rare allele does not guarantee that some are not related, and without some knowledge of the genetic make-up of the carriers of the rare allele, there is a risk of producing seed that exhibits some loss of diversity.

## Genetics of collapsed populations

Several of the world's largest pelagic fisheries have collapsed in the past 50 years, although most have recovered slowly following a cessation of fishing (Beverton 1990). Limited genetic data are available for some stocks which have collapsed but need to be interpreted with caution. Low levels of genetic diversity in some mammalian populations have been explained by population bottlenecks, either natural (O'Brien *et al.* 1983) or due to overexploitation (Bonnell and Selander 1974, Hoelzel *et al.* 1993, Pemberton and Smith 1985). However, some other mammals which are not known to have passed through a recent bottleneck also exhibit low levels of genetic diversity (e.g. Simonsen 1982). Genetic data for the collapsed stocks were collected after the collapse and estimates of genetic change are based on a comparison with other populations or closely related species; it has not been possible to test directly for loss of specific rare alleles or reduction in average heterozygosity within populations. Loss of allelic diversity will occur before decreases in heterozygosity are detected (Waples *et al.* 1990) and short-term population bottlenecks will have little effect on heterozygosity, but may reduce the number of alleles present (Allendorf 1986). In addition the stocks may have collapsed from a commercial perspective, and fishing ceased due to economic reasons or management controls, but from a genetic perspective the species may have maintained large numbers of individuals. Examples of collapsed stocks are found in small pelagic species which at their peak have maintained very large population sizes with a mature biomass in excess of 1 million tonnes (Beverton 1990). The Icelandic herring which may have collapsed to 1/3 000 of its peak biomass would consist of around one million fish at its lowest recorded size, while other collapsed stocks have maintained larger population sizes (Beverton 1990).

The California sardine (*Sardinops sagax caerulea*) fishery collapsed in the late 1950s, and remained below 1/250 of its peak biomass for 20 years before showing signs of recovery (Beverton 1990). This species of sardine shows low genetic diversity relative to other clupeoids with a mean heterozygosity of 1.0% (Hedgecock *et al.* 1989). In fifteen other species of clupeoid the average heterozygosity is 7.1%, and ranges from 4.0 to 10.1% (Hedgecock *et al.* 1989). However, Hedgecock *et al.* (1989) suggested that this low genetic diversity is unlikely to be due to the collapse of the fishery as other populations of Pacific sardine in Baja California and the Gulf of California, which were unaffected by the collapse, also show low heterozygosities. However, the low level of genetic variation in *S. sagax caerulea* and the relatively small sample sizes have not permitted a test of the distribution of rare alleles which may be a more sensitive measure of genetic change in large populations. Other species of sardine which do not appear to have suffered a recent collapse also exhibit low heterozygosities (Kinsey *et al.* 1994, Menzes 1994).

The fishery for the Japanese sardine *Sardinops melanosticta* collapsed in the 1940s, falling from a peak catch of 2 700 000 tonnes in 1937 to less than 10 000 tonnes in 1965. The species disappeared in the northern part of its range, but subsequently recovered with catches peaking at over 1 000 000 tonnes per annum by the late 1970s (Kondo 1980). This species has an average heterozygosity of 6.4%, similar to two other clupeoids tested in the same laboratory (Fujio and Kato 1979). Even at the low point following the collapse of the fishery catches remained at thousands of tonnes per annum. Likewise with the South African pilchard *Sardinops ocellata* fishery, which collapsed in the 1970s from peak catches of over one million tonnes per annum to 11, 000 tonnes per annum in 1980, the average heterozygosity (5.2%) is similar to other clupeoids (Grant 1985).

The Georges Bank herring *Clupea harengus* fishery collapsed in the 1970s and the stock may have decreased to 1/1 000 of its peak biomass (Beverton 1990). Spawning herring were recorded on Georges Bank for the first time in 1986 and samples were collected for genetic analyses. The Georges Bank herring were found to be different to neighbouring populations in the Gulf of Maine at one enzyme locus and, coupled with a different year class structure to neighbouring populations, suggests that the stock recovered through resurgence and not recolonization (Stephenson and Kornfield 1990). The heterozygosity levels at two enzyme loci and the level of mitochondrial DNA diversity were similar to other spawning groups in the Northwest Atlantic Ocean, indicating no loss of genetic diversity following the collapse of the fishery (Stephenson and Kornfield 1990), although this comparison is made against other heavily exploited stocks of herring.

The bluefin tuna *Thunnus maccoyii* is heavily exploited in the Southern Oceans; the fishery has not collapsed but the parental biomass is only 10–20% of the 1965 level (Report 1993). Tissue samples collected in the New Zealand fishery during 1982–83 were tested for 14 variable enzyme loci and repeat tests made in 1992. There was no significant genetic change, measured as average heterozygosity and average number of alleles, over this ten- year period of declining biomass (Smith unpub). In contrast stocks of the orange roughy which have been reduced by 60–70% of the virgin biomass have shown a significant loss of genetic heterozygosity, but this has been attributed to selection and not drift, as the roughy stocks maintain large spawning populations and support reduced but significant (several thousand tonnes per annum) fisheries (Smith *et al.* 1991).





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## SUMMARY AND RECOMMENDATIONS

### Genetic changes due to selection

Experimental studies on aquatic organisms have demonstrated that selection can change the mean life history characters of populations within a few generations. In natural populations fishing is a major source of mortality and is non random with respect to age and size of individuals. Frequently the observed changes in life history characters in exploited populations are in the direction predicted from selection experiments and theory. In teleosts one of the most common observations has been a decline in the age and/or size at sexual maturity (and the examples cited are not exhaustive). Because the onset of sexual maturity is under both genetic and environmental control the genetic impact of fishing has been difficult to evaluate. Genetic concepts were not considered in the early fisheries literature reporting changes in life history characters, and the equilibrium models of fisheries management, which are ecologically based and dominated by compensatory effects, have overlooked a genetic component to fishing. It was not until Rickers (1980, 1981, 1982) and Beachams (1983a, 1983b, 1983c) detailed and thoughtful accounts were published in the early 1980s that genetic selection was considered to be a potential problem of overexploitation. All of the examples of selection have been in stocks which have been over exploited. Tighter management controls on stocks may help to reduce the likely genetic impact of fishing in the future.

If there is uncertainty about selection for reduced age/size at maturity in some species then stronger evidence for selection comes from size selection in coho salmon (Gross 1985, 1991) and from the long-term size changes in the semelparous Pacific salmon (Ricker 1980, 1981). Reduction in genetic diversity in orange roughy has occurred in virgin stocks that have been fished beyond the maximum sustainable yield.

In none of the fisheries exhibiting a genetic response to exploitation has there been a total curtailment of fishing to test if the original life history traits can be returned to their former state. Only in the anchovy *Engraulis capensis* has there been an increase in the length at 50% maturity following an increase in biomass due to recruitment, presumably as a compensatory regulation (Shelton and Armstrong 1983).

### Genetic changes due to drift

Genetic drift affects small populations and some rare and endangered freshwater species show low levels of genetic diversity. There is no evidence for loss of diversity due to drift in marine populations, but most populations have not been reduced to near extinction levels. Populations of marine bivalves that have been severely reduced in numbers have not been tested for genetic diversity. There is no evidence that collapsed stocks have suffered a loss of genetic diversity, but evidence is restricted to a comparison of electrophoretic data collected after the collapse. Although the stocks have collapsed from a commercial perspective most have maintained large population sizes even at their lowest state and thus may not be expected to lose genetic variation due to drift.

The increasing use of enhancement techniques to rebuild depleted stocks could have a genetic impact on coastal resources. Inappropriate choice of broodstock and loss of diversity in the hatchery seed could change the genetic composition of the wild population.

### Recommendations

Recommendations that follow from this report fall into three areas:

1. Experimental studies are required to determine the heritability and response to selection of life history characters of exploited species, and to determine if relaxation of fishing pressure allows the recovery of

“fast growing” and “late maturing” genes or gene complexes in populations. While it is unlikely that an open marine fishery would be allowed to recover to some early exploitation level, it would be desirable to use an experimental population (lake or laboratory) to test for genetic changes under heavy and relaxed levels of exploitation. Experiments have been designed for the pink salmon *Oncorhynchus gorbuscha* fishery to test the heritability of growth rate and the effects of size selective fishing on a natural population, and it has been shown that there would be no economic disadvantage to conducting such experiments (McAllister and Peterman 1992).

2. It would be desirable to collect and record data on levels of genetic diversity levels in exploited species, especially recently exploited or lightly exploited species. To date most genetic studies have focused on stock identification. The skills and resources developed for these studies could be refocused on intrapopulation studies and use both life history characters and molecular markers to examine genetics of recruitment and genetic changes in stocks. A combination of experimental and field studies would permit a more rigorous testing of genetic changes in exploited populations.
3. Changes to management controls should be considered to increase the minimum size in heavily exploited stocks. Raising the size limit, provided that it is not achieved by higher discard rates of undersize fish, would reduce the selection pressure for early maturity. Controls may take the form of gear restrictions or modifications to avoid the capture of juveniles and/or extensive closed areas to protect juveniles from fishing. To date most marine reserves are small and concentrate on the immediate sub littoral zone with a focus on recreational interests rather than scientific principles of conservation. For enhancement programmes it is recommended that the released seed should be produced from local broodstock and from a minimum effective number of parents ( $N_e = 50$ ).





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<sup>1</sup> The references are presented as submitted by the author

