Status and trends in genetic resources of capture fisheries

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1. SUMMARY

Genetic diversity encompasses three hierarchical levels: differences between species, differences among conspecific populations and genetic differences among individuals in a population. While the protection of each of these levels of genetic diversity is essential for achieving sustainable harvests, overfishing, habitat degradation and climate change generally overshadow concerns for genetic integrity. Capture fisheries for freshwater and diadromous species are marginally increasing globally, but capture fisheries for marine species have leveled or are declining. The demand for fishery products remains unabated and will increase as the economies of developing countries improve.

The continuing development of new molecular genetic tools provides high-resolution markers for assessing genetic population structure, for estimating demographic parameters and for providing insights into breeding biology. A growing body of population and evolutionary theory, and new statistical and computer procedures greatly assist in the interpretation of genetic data. Presently, genetic variables are generally not incorporated into ecological or economic models. Future models incorporating genetic data will be tailored to particular situations.

Fisheries in rivers and lakes are largely focused on species with naturally fragmented populations. These species are prone to inbreeding depression in small populations and to hybridizations with introduced divergent strains. Hence, genetic concerns are usually addressed under the framework of conservation biology and theory relating to inbreeding and unintentional hybridization.

Diadromous species support large commercial fisheries in the North Pacific and North Atlantic. These species are especially vulnerable to ecological disturbances because of their complex life-history cycle, which spans freshwater and marine habitats. The loss of between-population genetic diversity through population extinctions in some species is especially acute in areas of human development. The failures of numerous transplanting programmes for many species indicate that local populations are adapted to particular habitats and seasonal events and cannot be easily moved to other habitats.

In the marine realm, the greatest genetic threats appear to be the extinction of genetically unique subpopulations and loss of genetic diversity through declines in abundance by overfishing and climate change. For species or stocks supplemented with cultured individuals, genetic swamping with artificially propagated individuals can reduce the fitness of wild populations.

Numerous international conventions and agreements recognize the importance of maintaining biological diversity, but generally treat genetic diversity indirectly as a component of biodiversity. Four steps provide a framework for conserving genetic

diversity: 1) identification of objectives, 2) assessment of genetic risk, 3) identification of reference points and 4) monitoring of progress toward objectives.

2. INTRODUCTION

Biological diversity encompasses three components: 'the variety of living forms, ecological roles they perform and the genetic diversity they contain' (Wilcox, 1984). Capture fisheries are faced with several problems that tend to erode these fundamental components of diversity. The most important problem in many environments is overfishing (Pauly *et al.*, 1998, 2003; Allan *et al.*, 2005), but habitat changes from human development, pollution and physical degradation from trawling are also substantial. The increasing demand for fish and weak enforcement of fishery regulations in many regions have led to serious depletions of once abundant stocks. These problems are especially acute in coastal and estuarine areas close to human development. In addition to these direct human impacts on wild populations, natural (North Atlantic Oscillation, Pacific Decadal Oscillation) and induced (climate warming from greenhouse gases) shifts in climate greatly influence the abundances of local populations (Attrill and Power, 2002; Benson and Trites, 2002).

The chief focus for achieving sustainable harvests of capture fisheries has been on the preservation of species abundances and ecosystems with little attention given to intraspecific diversity (Ryman *et al.*, 1995). The reasons for this are twofold. First, management policies are heavily influenced by economic demand and the sustainable use of particular species. Second, the task of characterizing intraspecific diversity for each species is immense and often beyond the will or research capabilities of management agencies, especially those in developing countries. However, the maintenance of intraspecific genetic diversity may be key to preventing species extinctions (e.g., Ehrlich, 1988). The erosion of intraspecific diversity is not limited to small and geographically isolated populations but can also occur in seemingly abundant marine species.

Genetic resources can be viewed as genetic differences at three hierarchical levels of organization: 1) species, 2) populations and 3) individuals. At the highest level, species consist of populations that are reproductively isolated from populations of other species. Genetic isolation occurs because of geographic (allopatric) or behavioural isolation and, together with local adaptation, leads to the appearance of novel genetic traits (Otte and Endler, 1989). Hence, each species harbours a unique set of genetic material. Biologists agree that the process of speciation usually occurs on timescales of several hundreds of thousands of years. However, once species are lost, the fossil record indicates that several million years are required for species diversity to recover (Briggs, 1995).

At the population level of organization, the identification of discrete stocks has been a major theme in fisheries research. The definition of a stock can vary, as the motivations of fishery managers may be influenced by political, economical or biological mandates (Carvalho and Hauser, 1994). As a result, management boundaries are sometimes set at national borders because of issues of jurisdiction, even though a biological perspective may be of far greater importance in promoting the viability of a stock. The problem of managing "straddling stocks" is of particular importance for many highly mobile marine species (Meltzer, 1994).

Finally, the largest store of genetic variability in most species exists as genetic differences among individuals within a population. This variability arises from the physical assortment of genes among offspring during reproduction. Of great importance for the conservation of this genetic variability is the theoretical concept of effective population size, which is usually much smaller than census size. Both theory and empirical results show that the loss of genetic variability is greater in small populations than in large populations. Hence, the goal of preserving genetic variability in a population coincides with the goal of maintaining large ecologically sound natural populations.

In agriculture, the problem of conserving genetic diversity has been largely framed as the preservation of domesticated plant cultivars and animal breeds, which have adapted to local environments over thousands of years of selective breeding. Technical advances have led to a greater availability of cheaper grains, and this has produced a shift from pastoral grazing to more capital-intensive methods of farming. Intensive farming methods are more productive and more predictable than traditional methods of farming. Consequently, farmers have abandoned many indigenous breeds, and this shift has led to the loss of genetic diversity. Much less attention has been directed toward the conservation of genetic resources in natural, free ranging capture species. The development of domesticated breeding lines for aquatic organisms is still in its infancy and depends on the availability of wild strains to a much greater degree than does the present-day development of breeds of plants and animals for agriculture.

The chief goal of this study paper is to survey the status of genetic resources in freshwater and marine capture fisheries and to develop an argument for conserving genetic resources in these species. These arguments parallel those developed for the conservation of plant and animal genetic resources. A second goal is to outline trends in the development of these methodologies and the concepts used to manage genetic variability in capture fisheries. The methodologies used to describe genetic variability and to assess its value in inland and marine capture species differ somewhat from those used to assess genetic resources in domesticated plants and animals. A third goal is to summarize institutional mandates focused on preserving genetic diversity and to present a framework of action for conserving genetic diversity.

2.1 Why conserve genetic diversity?

Several arguments have been developed to support the notion that the conservation of genetic resources is important in various settings. Biological and normative justifications for conserving genetic diversity are:

1. to ensure the future adaptability of natural populations;
2. to preserve life-history, behavioural and morphological traits that ensure sustainable fisheries;
3. to promote the use of genetic resources in commerce and medicine; and
4. to conserve genetic diversity for cultural reasons.

Although these arguments have been developed for agricultural resources, they are a starting point for developing analogous arguments for the conservation of diversity among and within species supporting capture fisheries.

In agriculture, indigenous breeds have value for the creation of new breeds, even though individually they may not be of high economic value (Mendelsohn, 2003). Locally adapted breeds, for example, may harbour genes that promote disease resistance, which may have been lost in highly selected production strains. Other arguments focus on societal choices. A society may be willing to maintain economically inferior breeds, because these breeds may be part of a local landscape that is valued by society, or because society finds value in maintaining historical activities and traditional livelihoods. The decline of indigenous breeds is often tied to biological and environmental conservation issues in developing countries.

Much less attention has been given to evaluating the importance of genetic resources in species supporting capture fisheries. The chief reason is that little is known about the genetic components of production in wild populations. These populations lack the recorded breeding histories that are maintained for plant cultivars and domesticated livestock. Although many inland and some diadromous species can be bred in captivity, only a few marine species have been bred in captivity. A compelling reason for conserving genetic diversity in wild populations is to provide a large base for developing strains for aquaculture. Wild populations of plants and animals are now no longer used to a large extent to develop new agricultural strains. However, the development of strains for aquaculture is ongoing and depends on the availability of genetically diverse wild populations.

2.2 Trends in capture fisheries production

Inland and marine capture species together make up the bulk of fishery products, although production from aquaculture is increasing rapidly. Fisheries provided about 140 million tonnes of food and fish products in 2001. Most of this production comes from marine waters (about 85 million tonnes; 59.8%) and almost half consists of small pelagic fishes. The remaining capture production comes from inland waters (8.7 million tonnes; 6.1%) (FAO, 2003). A growing amount of production comes from marine and freshwater aquaculture (48.4 million tonnes; 34.1%). The size of the marine capture fishery has leveled in the last few years and may be declining (Pauly *et al.*, 2003), while inland fisheries have been relatively stable, or marginally increasing (Figure 1). Inland capture fisheries are largest in Asia (5.8 million tonnes) and Africa (2.1 million tonnes), with important fisheries also in Europe (0.3 million tonnes), South America (0.3 million tonnes), North America (0.2 million tonnes) and Oceania (0.02 million tonnes). About 7 million tonnes (80 % of inland fisheries) are produced in countries with low average incomes and food deficits. Inland capture fishery production is the sole source of fish in many of these countries.

2.3 Trends in demand for fishery products

Trends in the consumption of fish suggest continued increases in the demand for fish. A sample of 132 nations indicates that the consumption of fish is greatest in countries with high standards of living, as measured by per capita gross domestic product (York and Gossard, 2004). However, demand differs among regions and among nations. Several developing countries have high fish consumption, including Bangladesh, Cambodia and China (FAO, 2003). The demands for fish products in the nations of Africa, the Middle East and western countries of North and South America and Europe are similar (Figure 2). The largest rate of increase occurs in Asian countries, because of the traditional emphasis on fish consumption, population increases and economic

FIGURE 1
Marine, inland capture fishery production, and aquaculture production (FAO)

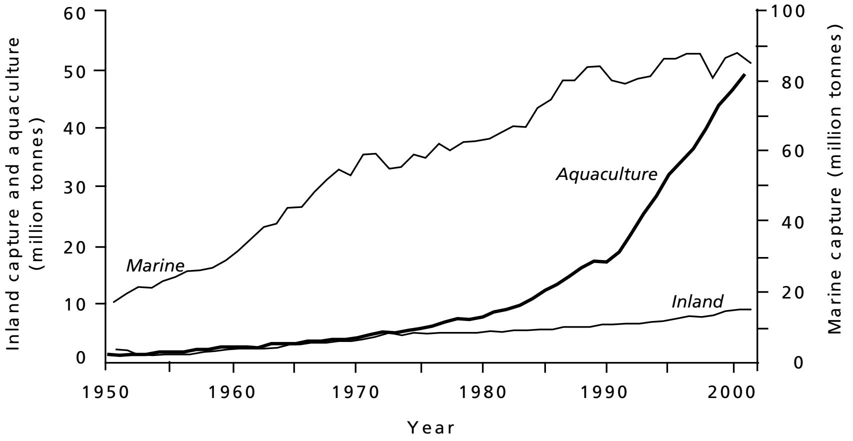
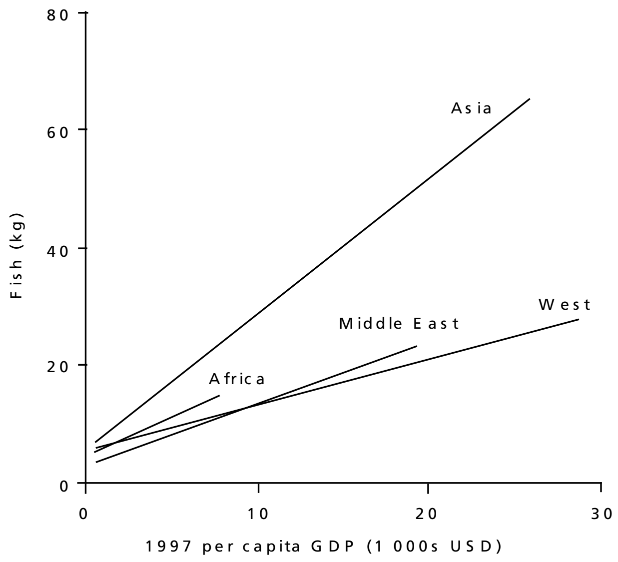


FIGURE 2
Association between per capita annual fish consumption (kilograms) and per capita gross domestic product (GDP) among regionally grouped countries. From York and Gossard (2004)



improvement. The shift of rural populations into cities, which often accompanies economic development, also leads to the increased consumption of fish. These trends indicate that the demand for fish will increase globally, but will increase most in Asian countries as they develop economically.

3. USE OF MOLECULAR MARKETS TO SURVERY GENETIC RESOURCES

The use of molecular genetic markers to survey genetic variability and to infer population processes has advanced on two fronts in recent years. New technologies have been developed to assay DNA polymorphisms directly, and these methods have produced a range of DNA markers with complementary characteristics to address various questions (Annex 1). These advances provide a means of generating large amounts of data as a basis for statistically testing research and management hypotheses.

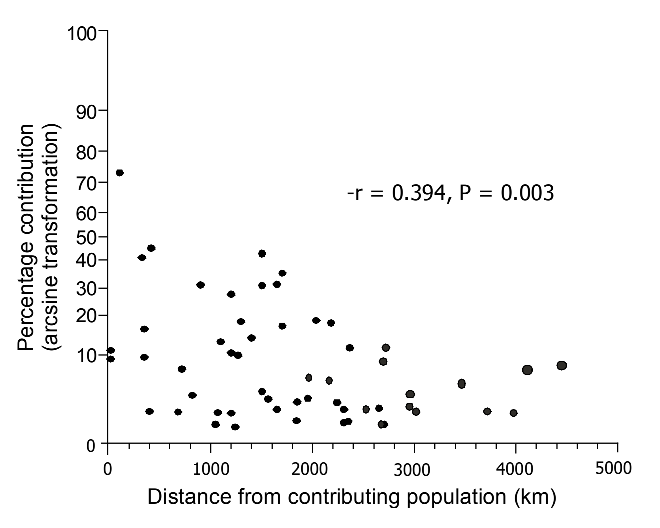
3.1 Applications

Assessments of genetic variability in species in capture fisheries are important for several reasons. Molecular genetic markers occur naturally, are inherited in a predictable way, provide a basis for rigorous statistical analysis, and thus are ideally suited to assessing genetic variability in wild populations. Molecular markers have been used to discover morphologically cryptic species (Shaklee and Tamaru, 1981; Knowlton, 1993; Bernardi and Goswami, 1997; Knowlton *et al.*, 1997), define population boundaries (Ruzzante *et al.*, 1998; Waples, 1995), estimate population components in areas of population mixing (Hansen *et al.*, 2001; Nielsen *et al.*, 2001; Hauser *et al.*, 2006) or origins of juveniles during life-history migrations (Teel *et al.*, 2003; Bowen *et al.*, 2006). Box 1 illustrates the use of mitochondrial DNA markers to infer migration patterns of juveniles of endangered hawksbill sea turtles (*Eretmochelys imbricata*).

One promising use of molecular data is to estimate population parameters such as population size (Nunnery and Elam, 1994; Bagley *et al.*, 1999; Turner *et al.*, 2002) (Annex 1) or to reconstruct demographic histories of population growth or

BOX 1

Genetic mixed-stock analysis of Caribbean juvenile hawksbill sea turtles, a CITES listed species. (Bowen *et al.*, 2006)



Genetic stock identification has been especially useful in the management of species that are harvested in areas of stock mixing. In these areas, less abundant stocks may be threatened with overfishing. The method was developed to estimate the proportions of component stocks in harvests of Pacific salmon as they returned to rivers to spawn (Grant *et al.*, 1980), but has proved useful for other species.

Hawksbill turtles (*Eretmochelys imbricate*) are specialized sponge feeders, which migrate between nesting beaches and feeding habitats on tropical reefs. The colourful "tortoiseshell" scutes of this species are especially valued in the production of artisan products. Harvests of this species have brought it close to extinction. A pressing question has been the extent that harvests of juveniles on feeding grounds influence spawning site abundances in other areas, a perennial problem in 'straddling stock' species. The migration biology of juveniles is largely unknown because the physical tagging of nestlings is impossible. A survey of mtDNA variability showed strong haplotype frequency differences among female nesting sites that could be used to identify the origins of juveniles on shallow reefs (Bowen *et al.*, 2006). Bayesian estimates of the origins of 629 juveniles from seven feeding congregations demonstrated that juveniles tend to return to feeding areas close to their birth sites. A significant correlation appeared between the percentage contribution to a feeding area and the distance from the contributing population (Figure). The magnitude of these distances indicates that harvests in one part of the Caribbean will impact nesting sites throughout the region.

of bottlenecks in population size (e.g. Luikhart *et al.*, 1998a). An understanding of responses to past environmental or climate disturbance can give clues to how populations might respond to future challenges. Molecular genetic data have been especially useful for estimating kinship among individuals in natural populations (Bernatchez and Duchesne, 2000; Bentzen *et al.*, 2001; Garant *et al.*, 2001; Banks *et al.*, 2003), for measuring reproductive success (Fiumera *et al.*, 2002) or for forensic identifications (Birstein *et al.*, 2000).

The development of high-resolution population markers provides a means of testing models of population structure. Populations of inland species are largely isolated from one another by terrestrial barriers to movement and the construction of population models is straightforward. These populations generally act as collections of subpopulations (a metapopulation), in which subpopulations are tied to each other by various levels of gene flow. Local extinctions and colonizations also appear to be a general feature of inland (e.g. Bernatchez and Wilson, 1998; Lafferty *et al.*, 1999).

The structures of marine populations, on the other hand, are less well known. As expected, near shore species with both limited larval and adult dispersal (or homing behaviour to spawning areas) tend to have subdivided population structures (McQuinn, 1997; Robichaud and Rose, 2001). However, many species in capture fisheries have high dispersal abilities and occur in oceanic areas without firm barriers to movement. These species tend to show much less genetic population structure with populations occupying much larger areas than do populations of inland species (see below). How these populations are structured is of considerable importance to their management in capture fisheries. Surveys of molecular population markers continue to be important for testing the various models of population interconnection and structure.

These applications generally assume that molecular markers are not directly influenced natural selection and that the distributions of the markers reflect such parameters as effective population size and gene flow. However, genetic diversity itself is also an important component of ecological and evolutionary health of a species. A rapidly growing field of research focuses on the development of molecular markers linked to quantitative trait loci (genes that affect the ecological fitness of individuals). "Genomic" methods are used to survey portions of the genome directly influenced by selection (Reid *et al.*, 2005; Slate, 2005), to monitor genotoxic pollutants (Newton *et al.*, 2004, Rockett and Dix, 1999) and to study the effects of hybridization (Dowling and Childs, 1992; Rhymer and Simberloff, 1996) and population crashes on gene organization (Luikart *et al.*, 1998a, b; Garza and Williamson, 2001).

Market or production traits, including growth rate, flesh characteristics and disease resistance, are generally influenced by the actions of several genes, which can be evaluated only by breeding experiments (e.g. Law, 2000). In addition to experimental breeding manipulations, information on breeding lines and pedigree analysis form the basis for evaluating genetic resources in domestic livestock and agricultural plants. However, laboratory experiments on most populations targeted in capture fisheries are not possible, so alternative methods are required to assess the genetic status of natural populations.

3.2 Statistical analysis

The development of statistical methodologies and computer programmes has kept pace with laboratory progress in providing a means of analyzing genetic data (Annex 2). A variety of statistics can be used to assess genetic diversity within and among populations. Genetic data for a sample of individuals can provide information about genetic diversity within and among populations (Nei, 1987; Hedrick, 2005) and can be used to infer phylogenetic relationships among species (Felsenstein, 2004). Three measures of diversity are widely used in conservation and population studies (Box 2). The first, average heterozygosity, H, (also called gene diversity) measures the level of genetic variability in a population and is routinely estimated with allozyme and microsatellite DNA data (Nei, 1987). Nucleotide diversity, Θ_π, extends the concept of gene diversity by adding a measure of sequence divergence between haplotypes. These statistics can be used to detect the erosion of genetic diversity from historical reductions in population size. A third statistic, F_{ST}, measures diversity among subpopulations in a species.

BOX 2

Statistics used to measure genetic diversity within and among populations

Average heterozygosity or gene diversity: Average heterozygosity can be estimated in two ways. The first way is to count the number of heterozygous individuals in a sample of diploid genes. This is known as observed heterozygosity, H_E. These counts are usually presented as a proportion of all genotypes. A second way of estimating heterozygosity is to assume that the sample of genes from a population does not deviate significantly from Hardy-Weinberg proportions and calculate the proportion of expected heterozygotes from gene frequencies. For a single locus expected heterozygosity, h, can be calculated as:

$$h = 1 - \Sigma p_i^2$$

where p_i is the frequency of the ith allele in a sample. This formula is used to also estimate gene diversities for haplotypic loci such as mitochondrial DNA in animals or plastid DNA in plants. When data for a sample of several loci are available, such as for allozyme and microsatellite DNA data, heterozygosities are averaged,

$$H = \Sigma h/R,$$

Where R is the number of loci sampled. Average heterozygosities estimated from allozyme data usually also include monomorphic loci and are taken as an estimate of genome wide variation when samples sizes of loci are large ($R > 20$). Average heterozygosities based on microsatellite DNA usually only include polymorphic loci and are, therefore, not comparable with allozyme heterozygosities.

Nucleotide diversity: Sequences of DNA provide a basis for estimating divergences between alleles, which is not possible for allozyme or microsatellite data. The amount of sequence divergence between haplotypes in a sample provide information about the age and historical size of a population. Other variable equal, older populations are expected to accumulate more mutations and show larger divergences between haplotypes. One the other hand, larger populations of the same age are also expected to accumulate a greater number of mutations. The loss of low frequency haplotypes in a large population is less than in small populations because the loss of haplotypes through genetic drift is less. These haplotypes, however, are expected to be closely related to each other. These characteristics form the basis for estimating several demographic parameters of populations (Rogers and Harpending, 1992;).

Nucleotide diversity can be estimated from the average number of nucleotide differences between haplotypic sequences, π. The number of nucleotide differences per nucleotide site, $d_{xy,}$ is used to account for differences in the lengths of sequences in different studies. Nucleotide diversity, Θ_π, is the sum of the product of divergences between haplotypes and the frequencies of haplotypes

$$\Theta_\pi = \Sigma\Sigma d_{xy} p_x p_y,$$

Where p_x and p_y are frequencies of haplotypes in a sample.

BOX 2 *(cont.)*

F_{ST}: This statistic is the standardized variance of gene frequencies among populations and is estimated by

$$F_{ST} = \mathrm{var}(p)/p(1-p)$$

where $p(1-p)$ is the binomial variance. This statistic ranges from 0.0, indicating identical gene frequencies between populations, to 1.0, indicating fixed gene frequency differences between populations. F_{ST} values are usually averaged over loci when data for several loci (allozymes and microsatellites) are available. The co-distribution of H and F_{ST} can be used to test for the effects of natural selection on gene frequency divergence between populations (Beaumont and Nichols, 1996).

The maximum value of F_{ST} is limited by high heterozygosities, as are commonly found for microsatellite loci. The upper limit of F_{ST} is $(1 - H_S)$, where H_S is the average within subpopulation heterozygosity (Hedrick, 1999). Hedrick (2005), therefore, suggests that F_{ST} be modified

$$F'_{ST} = F_{ST}\,(1 + H_S)/(1 - H_S)$$

These adjusted values provide a better estimate of differentiation among populations when estimate with microsatellite DNA.

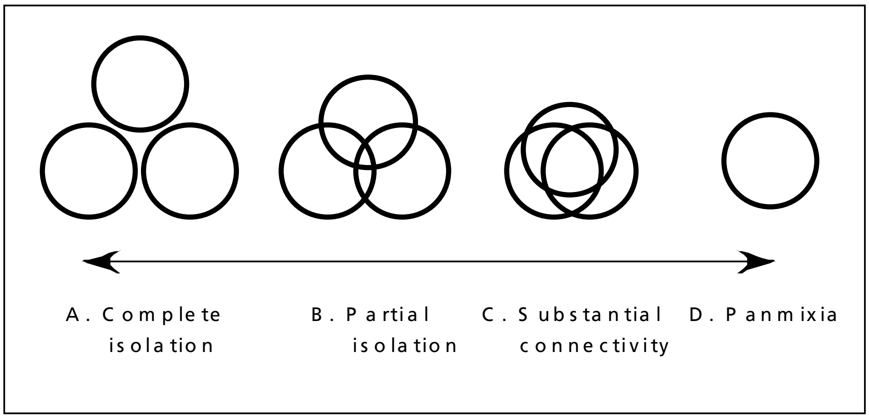
4. PATTERNS OF GENETIC VIABILITY IN NATURAL POPULATIONS

Species generally are divided into a few to numerous populations depending on the dispersal ability of individuals and on the availability of dispersal corridors. At one extreme, some marine fishes with highly mobile adults and with unimpeded movements of planktonic eggs and larvae, consist of only a single global population (Figure 3). At the other extreme, some species are highly subdivided into genetically unique subpopulations because of physical barriers to movement, or because of strong natal and site spawning fidelity. As a consequence, many marine species, such as tunas, tend to be "population poor", while inland and anadromous species tend to be "population rich" with numerous small populations. How populations react to physical and biological variables is a subject of ongoing debate (Sinclair, 1988; MacCall, 1990; Sherman *et al.*, 1993).

Various isolating mechanisms produce different levels of population subdivision among inland, anadromous and marine populations (Table 1). Although the relative amounts of allozyme and microsatellite DNA gene diversity are similar among these groups, how this diversity is partitioned among populations differs among groups. The largest amount of genetic subdivision appears among conspecific populations of freshwater species (mean F_{ST} = 0.222, median F_{ST} = 0.144), because of the physical isolation of lake and riverine habitats. Anadromous species (salmonids) show large amounts of population subdivision (mean F_{ST} = 0.108, median F_{ST} = 0.081). In this group, subdivisions reflect not only geographic isolation between freshwater spawning sites, but also homing to natal spawning sites. Populations of marine fishes show the least amount of genetic subdivision (mean F_{ST} = 0.062, median F_{ST} = 0.020), because of fewer restrictions to the movement of eggs, larvae and adults in marine waters. These statistics have been used to infer the number of migrants between populations each generation. However, the models used to make these estimates are over-simplifications

FIGURE 3

A continuum of population models showing different degrees of differentiation (based on Waples and Gaggiotti, 2006). The circles represent populations with different degrees of geographical overlap or migration between them



A. Independently, self-sustaining population that do not exchange individuals. These populations are expected to show substantial life history, demographic, morphological or genetic differences.
B. Partially isolated populations with some geographic overlap or exchange of individuals, or both. These populations may show small life history, demographic, morphological or genetic differences. Genetic differences are often used to define genetic stocks. Theoretically genetic differences appear between populations over long periods only when migration is limited to 1-5 individuals each generation.
C. Substantial geographical overlap or mixing of individuals. Although life history or demographic differences may still appear between populations, genetic differences are not expected to appear. Genetic methods are incapable of detecting these populations, however, from a fishery management perspective each population may still merit recognition.
D. Panmixia. Only a single population exists with individuals (or gametes) freely moving between areas.

TABLE 1

Components of gene diversity in freshwater, anadromous and marine fishes (summarized from Ward *et al.*, 1994 and Waples, 1998). H_T is the total amount of genetic diversity in a species, and F_{ST} is the variance of allozyme frequencies among subpopulations. H for microsatellite DNA is based on a single or only a few populations (DeWoody and Avise, 2000)

Group	Number of Species	Mean number of populations in sample	H_T	F_{ST}	
				Average	Median
Allozymes					
Freshwater	49	5.9	0.062	0.222	0.144
Anadromous	7	13.1	0.057	0.108	0.081
Marine	57	6.4	0.064	0.062	0.020
Microsatellite DNA					
Freshwater	13		0.54		
Anadromous	7		0.68		
Marine	12		0.66		

of real populations. Hence, these estimates should be used cautiously (Bossart and Prowell, 1998; Whitlock and McCauley, 1999).

4.1 Inland species

Even though inland capture fisheries are much smaller than marine capture fisheries, freshwater fisheries are an important source of protein in many countries. About 7 million tonnes (80 % of inland fisheries) are produced in countries with low average incomes and food deficits (FAO, 2003). Fisheries are the sole source of animal protein in many of these countries. Freshwater habtitats are much more fragmented than marine habitats and experience greater seasonal extremes in temperature and desiccation. Hence, freshwater populations of fishes are expected to be smaller in general, show greater fluctuations in abundance and be genetically more subdivided than marine fishes. The problems facing populations of freshwater species tend to be addressed largely by principles in conservation biology, rather than in fishery management. Even though the problems facing inland aquatic species are most severe in developing countries, aquatic species in developed countries have best been studied with genetic methods.

4.1.1 Habitat degradation and genetic population structure

The greatest problem facing inland aquatic species is habitat degradation from human activities. Aquatic habitats are often modified by deforestation and watershed erosion, pesticides and agricultural and industrial run-off. Canalization of streams for agriculture, or direct use by humans, destroys riparian zones and impairs natural ecosystem processes that maintain water quality and produce food for aquatic species. Habitat degradation can have important genetic consequences for aquatic populations.

1. Habitat-related reductions in population size inevitably lead to the loss of genetic diversity and often to inbreeding depression. Genetic diversity can decline rapidly in small populations through random genetic drift (Crow and Kimura, 1970). The detrimental effects of inbreeding are well known from agriculture and aquaculture and inbreeding itself can lead to the demise of a population (e.g., Gall, 1987; Leberg and Vrijenhoek, 1994).
2. Habitat degradation often leads to habitat fragmentation and the loss of important connections between populations. The loss of habitats increases genetic isolation and reduces the possibility of genetic rescue of endangered populations and the probability of colonization of empty habitats in a metapopulation (Hanski and Gilpin, 1997).

4.1.2 Genetic risks from introduced species and non-native stocks

Another important threat to inland species is the introduction of non-native species, or of stocks of the same species adapted to different environments. Introductions can produce a variety of effects.

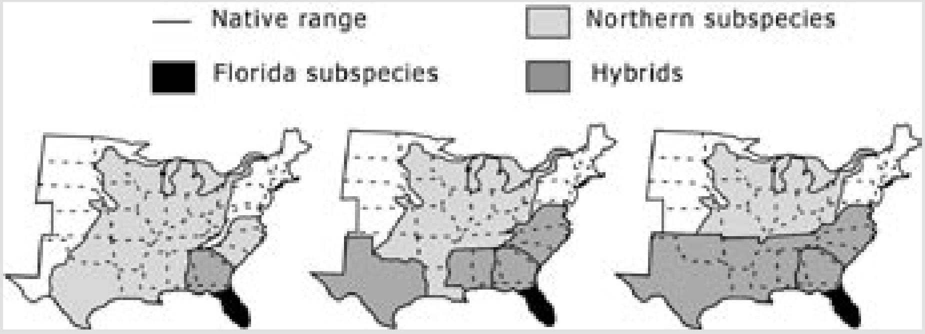
First, introductions of non-native species can lead to ecological imbalances. For example, the introduction of the predatory Nile perch (*Lates niloticus*) into the Great Lakes of Africa led to a population explosion that caused the extirpation of about 65% of Lake Victoria's endemic cichlid fish species diversity (Witte *et al.*, 1992; Goldschmidt *et al.*, 1993). The large populations of Nile perch then supported a large fishery in Lake Victoria and the production of choice filets for European and Asian markets (Kitchell *et al.*, 1997). In recent years, the burgeoning fishery has in fact reduced predation pressure on native species to about 10% of its 1970 levels and has allowed the rebound of some of the remaining cichlid species (Kitchell *et al.*, 1997).

Second, fish are sometimes transferred to other areas out of their native range. If the transferred fish are genetically different from local fish, hybridization between the two may lead to outbreeding depression and the loss of fitness (e.g. Morizot *et al.*, 1991; Carmichael *et al.*, 1993). Box 3 gives a case history of stock supplementation and mixing of two subspecies of largemouth bass across North America. Alternatively, if the introduced individuals are competitively superior to local individuals, local native populations may be hybridized to extinction.

Third, introduced individuals of the same species may be genetically compatible with local populations, a condition assumed in most stock supplementation programs and hatchery operations. Great caution, however, is needed to ensure that artificially propagated individuals have not also been genetically modified by adaptation to hatchery conditions. Selection in hatcheries can potentially occur with some feeding methods, the selection of broodstock, or other procedures that modify behaviour. Supplementation of wild populations by hatchery reared individuals can potentially lead to genetic 'swamping' and the loss of genetic diversity in wild populations, even

BOX 3

Introductions of non-native populations of largemouth bass (Philipp, 1991: Philipp *et al,* 1993)



A programme of stock introductions for largemouth bass (*Micropterus salmoides*) illustrates how genetic diversity can be lost through hybridizations with non-native individuals. Largemouth bass originally ranged across central and southeastern United States and consisted of two subspecies. The range of *M. s. floridanus* was formerly restricted to the Florida peninsula, while the range of *M. s. salmoides* extended northward over most of eastern of the United States of America. The two subspecies initially met in a narrow hybrid zone (purple).

A vigorous stocking program of the southern subspecies was initiated in 1949, because the southern subspecies was larger and preferred by fishers. By the 1970s, a study of allozyme population markers indicated that the hybrid zone had expanded northward (Philipp *et al.*, 1983). Continued introductions of *M. s. floridanus* have spread the genes of this subspecies across the entire southern range of largemouth bass. Natural levels of gene flow also helped to spread introduced genes.

As a result of these introductions, populations of the northern subspecies have lost much their distinctiveness because of the loss of between-population diversity that accompanies the homogenization through stock introductions. These two subspecies have different life history patterns and the stock transfers had led to outbreeding depression in hybrid individuals. In northern areas, "common garden" experiments showed that hybrid offspring were less fit than offspring from pure northern parents (Philipp and Whitt, 1991). These results prompted the Minnesota Department of Natural Resources to prohibit further stocking of the southern subspecies.

if hatchery individuals have not be genetically altered in captivity (Ryman and Laikre, 1991).

4.2 Diadromous species

Diadromous fishes include species that spawn in either fresh or marine waters, but spend part of their life cycle in the other habitat. Diadromous species exhibit several life history traits that make them vulnerable to extinction (Jonsson *et al.*, 1999) (Box 4). About 18% of diadromous fishes are considered to be endangered, threatened, rare or vulnerable, whereas only about 5% of fish species in general are considered to be of conservation concern (Barbault and Sastrapradja, 1995; McDowall, 1999).

4.2.1 Catadromous species

These fishes spawn in marine waters, but migrate into fresh or brackish water. The best studied of these species are North American (*Anguilla rostrata*), European (*Anguilla*

anguilla), Asian (*Anguilla japonica*) and shortfinned (*Anguilla australis*) eels, which spawn in the marine waters, but mature in rivers and lakes. In North America, allozyme markers showed significant differences among river populations (e.g. Williams *et al.*, 1973), whereas mtDNA markers indicated a lack of geographic differentiation (Avise *et al.*, 1986; Lintas *et al.*, 1998). Recent studies with high-resolution molecular markers have detected weak, but significant, differences among freshwater populations of European eels (Daemen *et al.*, 2001; Maes and Volckaert, 2002; Wirth and Bernatchez, 2003), but not among North American populations (Wirth and Bernatchez, 2001). Species consisting of a single large breeding population are particularly vulnerable to environmental changes and require international cooperation in their conservation and management.

4.2.2 Anadromous species

Anadromous fishes, on the other hand, spawn in freshwater, but mature in marine waters before returning to freshwater to spawn. The problems facing these species are particularly severe because, in addition to harvest mortality, individuals are tied to aquatic habitats that are often heavily impacted by human activities. One group of special concern includes anadromous and freshwater resident species of sturgeons, which exhibit many of the life history traits predisposing species to extinction (Williot *et al.*, 2002) (Box 4). They occupy different habitats during their life cycle, are large, long-lived, slow growing and late maturing. Habitat degradation, dams and exploitation for caviar have produced alarming population declines (Birstein, 1993). Genetic studies of sturgeons indicate complex population structures (Doukakis *et al.*, 1999; Campton *et al.*, 2000; Wirgin *et al.*, 2000) and confused taxonomies (Phelps and Allendorf, 1983; Birstein *et al.*, 2000; Birstein *et al.*, 2002; Krieger *et al.*, 2000).

Anadromous salmonids, which are distributed across temperate regions of the Northern Hemisphere, are also vulnerable to many of the same threats facing sturgeon (Nehlsen *et al.*, 1991). Considerable effort has been spent on the life history and genetic analyses of these species, because these fishes support substantial commercial, traditional or recreational fisheries. A variety of genetic population structures appear in salmonids that reflect ecological and life history differences, not only among species, but also among some stocks of the same species. For example, Waples *et al.* (2001) found that among seven species of Pacific salmon in the genus *Oncorhynchus* a strong correlation appeared between ecological and life history diversity. Species inhabiting a greater number of ecological provinces tended to exhibit a greater number of life history types as evidenced by degree of anadromy, spawning run timing, time to adult maturity (marine phase duration) and juvenile freshwater residence time (Figure 4). This correlation reflects the direct influence of environmental factors such as temperature and food availability on the expression of life history traits.

An understanding of the nature of adaptive traits is of fundamental importance in the conservation and management of fishery resources. Both rate and mechanism determine the extent to which life history diversity and diversity generating eco-processes should be conserved. Adaptations in many salmonids occur rapidly (Hendry, 2001; Koskinen *et al.*, 2002) and over short distances (Taylor, 1991). Life history characters shifted in only a few decades after introductions of Chinook salmon (*Oncorhynchus tshawytscha*) to New Zealand (Quinn *et al.*, 2000) and into the North American Great Lakes (Kwain and Thomas, 1984). Rapid rates of life history diversification on contemporary time scales have also been documented in sockeye salmon (*Oncorhynchus nerka*) (Hendry 2001) and grayling (*Thymallus thymallus*) (Koskinen *et al.*, 2002). The failures of many stock transfers of salmon between rivers and streams along the west coast of North America indicate

BOX 4

Population or biological traits that predispose stocks or species to depletion and extinction. Declines in effective population sizes can lead to the loss of genetic diversity

1. *Slow growing and long lived*: Species with these traits are vulnerable to the effects of overfishing because standing biomass after harvest is replaced very slowly. These traits are often associated with large body size, late maturity and small numbers of offspring.

2. *Several years to reproductive maturity*: Many species of fish have market value before they reach reproductive maturity. Unless a significant number of individuals are allowed to reproduce the viability of a stock is great reduced. Another component of this problem is that older, larger individuals often have reproductive potentials far larger than younger, mature individuals.

3. *Few offspring per year*: Producing only a few offspring per year is part of a continuum of reproductive strategies. Many fish and invertebrates produce millions of eggs with little or no parental care of larvae. Even though the probability of survival to maturity for individual eggs is very small, at least some of larvae are expected to survive. Other species invest more parental care by producing larger, but energetically more costly eggs, or by guarding offspring. These latter species are most at risk from the effects of overfishing, because fewer offspring are produced.

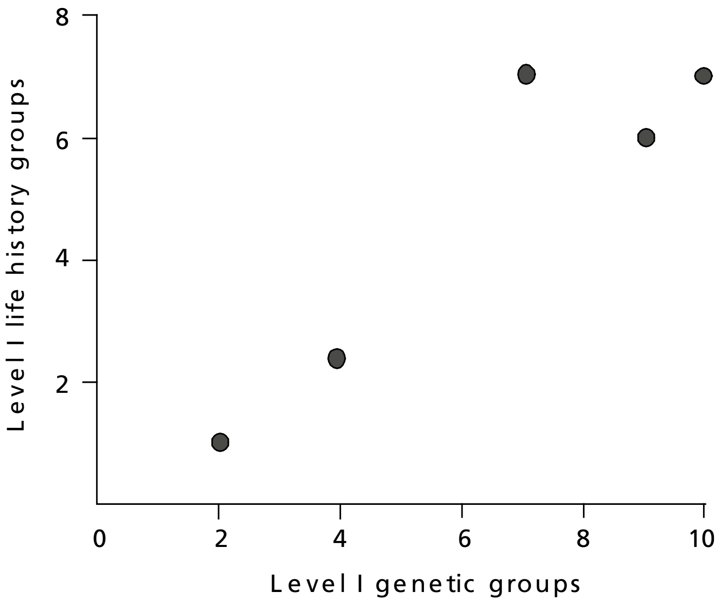
4. *Large body size*: Species with large body sizes are in jeopardy for two reasons. 1) Large, conspicuous animals may be easier to find and harvest than small animals. Visibility is especially detrimental when these species inhabit confined embayments and estuaries. 2) Large animals are inevitably at the top of the food chain and are particularly sensitive to shifts in abundance of species in the food web. Species with large body size are often slow growing, produce few offspring annually and consist of few individuals.

5. *Small natural population numbers*: These species are at particular risk when a large part of their habitat is degraded or destroyed. When core populations become depleted, recovery is hindered by reductions in the number of reproductively active individuals. These species may also be vulnerable to the loss of genetic variability and to such genetic effects as inbreeding depression.

6. *Live in confined habitats*: Species inhabiting confined spaces, such as lakes, estuaries or coastal embayments are much easier to capture than similar species inhabiting the open ocean. Many confined habitats are also associated with human activities, thus increasing the exposure to fishing and habitat changes.

7. *Specialized habitat or life history requirements*: Species with special requirements are at particular risk when only a few suitable habitats are available, or when populations of suitable prey species have been reduced. Species using rivers as migratory pathways may be at risk from the construction of dams and shoreline development. Other species with specialized diets may be at risk when particular items of food are no longer available.

FIGURE 4
Relationship between genetic and life history variability in five species of Pacific salmon (from Waples et al., 2001)



a general lack of ecological inter-changeability between most subpopulations (Utter, 2004).

4.3 Coastal marine species

Most of the World's capture fisheries focus on marine species, some of which support annual harvests of several million tonnes. Species supporting the largest harvests generally occur over the continental shelf in areas with high levels of productivity driven by upwelling. Nutrient rich areas in the eastern boundary currents of North and southern Africa, and North and South America, for example, support large fisheries of pelagic fishes, including hakes, mackerel, anchovies and sardines. Even though many species of marine fishes occur in very large populations, the combination of overfishing and climate change make them susceptible to extinction (Musick *et al.*, 2000; Myers and Ottensmeyer, 2005)

4.3.1 Genetic population structures of marine species

Most marine fishes and invertebrates are broadcast spawners and hence have large potentials for movement between areas by larval drift in currents. Additionally, adults of many species are capable of making long distance migrations. In contrast, adult homing to spawning areas, larval behaviour and hydrographic barriers to movement tend to isolate populations from one another, but not to the same degree as with freshwater fishes. The problem of unraveling demographic and genetic components of stock structure from gene frequency data is especially acute because of ill-defined geographical boundaries and decadal shifts in distributions. For example, early genetic studies of marine fishes indicated that they generally had moderate levels of gene diversity and little population subdivision, often over several hundred kilometers (e.g. Grant 1985; Mork *et al.*, 1985). However, recent studies with high-resolution markers, such as microsatellite DNA and mtDNA, have revealed fine-scale spatial differences (e.g. Ruzzante *et al.*, 1998) and unsuspected deep genetic lineages (e.g. Magoulas *et al.*, 1996).

How populations of marine fishes are structure is a subject of some debate. A persistent problem has been the lack of models that satisfactorily incorporate both ecological and genetic concepts of populations (Annex 3). Ecological models generally assume that populations are highly adapted to local environmental conditions (Sinclair, 1988). The genetic prediction of this model is that species should consist of genetically differentiated, locally adapted populations. This prediction is borne out by genetic data for freshwater and riverine species, but not for many marine species. Other models postulate that contemporary levels of gene flow or historical range expansions and contractions (MacCall, 1990) imprint genetic gradients on populations (e.g. Lecomte *et al.,* 2004). The different implications of these two models are important to formulating management policies and planning locations of marine protected areas.

Genetic estimates of gene flow are high in most marine species (Table 1), implying the movements of tens and hundreds of individuals between subpopulations. Mitochondrial DNA data appear to support the basin model for California anchovy (Lecomte *et al.*, 2004), but support a mosaic model for European anchovy (Grant, 2005; Magoulas *et al.*, 2006). However, finer-scale differences have been detected among populations that are not isolated by obvious physical or hydrographic barriers (Hedgecock *et al.*, 1994; Ruzzante *et al.*, 1999). This chaotic variability is likely due to large reproductive variances among families (Hedgecock, 1994), rather than to isolation or to adaptations to particular open-water habitats. The instability of marine waters on annual, decadal and millennial time scales likely prevents adaptations to specific areas. On a decadal scale, anchovy populations, for example, respond rapidly to small climate changes with range contractions and expansions (e.g. Cushing, 1982; Beare *et al.*, 2004).

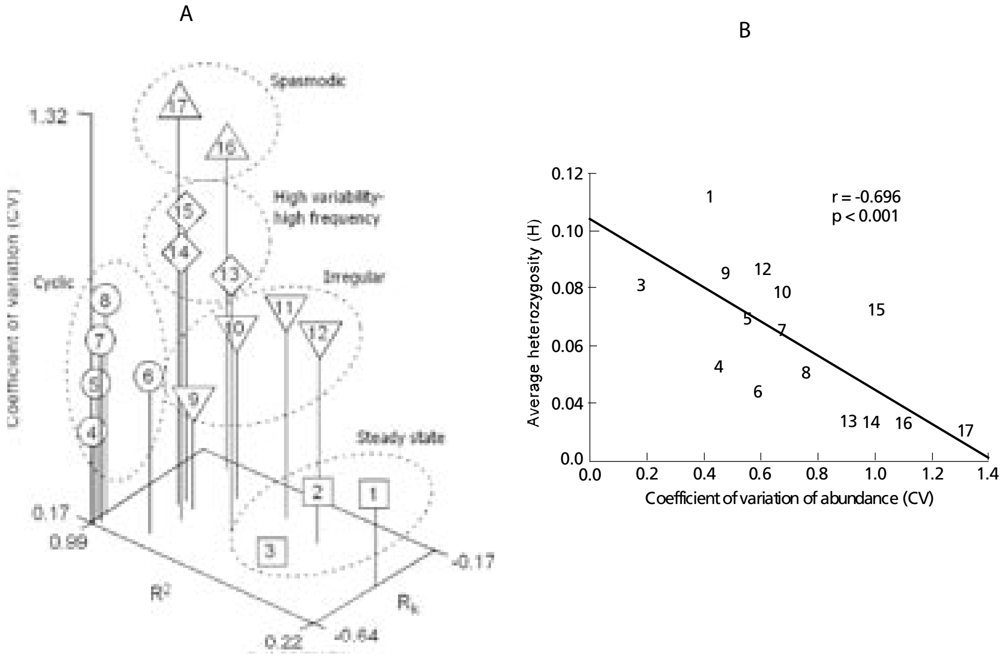
4.3.2 Effects of fishing on genetic variability

Populations of marine fishes, especially species supporting harvests of millions of tonnes, are generally thought to consist of large effective population sizes, and hence to be immune to the same genetic problems facing small populations of inland and anadromous species. Effective sizes of marine populations, however, may be much smaller than previously thought, because large fecundities can lead to large variances in family success. Only offspring spawned during a narrow window of oceanic conditions conducive to larval survival eventually recruit into the adult population (Hedgecock, 1994). As a result, the genetic effective size of a population may be orders of magnitude smaller than its census size (Nunnery and Elam, 1994; Bagley *et al.*, 1999; Turner *et al.*, 2002). Empirical evidence for this hypothesis, however, is mixed (Ruzzante *et al.*, 1996; Herbinger *et al.*, 1997; Li and Hedgecock, 1998). Nevertheless, available evidence indicates that fishing pressures can alter the genetic and demographic structures of seemingly very large marine populations.

The use of molecular genetic markers to estimate contemporary gene diversities is problematic since diversity is influenced by long-term rather than short-term effective population sizes. Long-term effective population size is the harmonic mean of populations each generation, and this mean is most influenced by small populations sizes. Abundances of most populations of marine species fluctuate on decadal and millennial time scales. For example, the analysis of fish scales in anaerobic sediments in the Santa Barbara Basin indicates large shifts in the abundances of anchovies and sardines over the last 2000 years before the onset of fisheries (Baumgartner *et al.*, 1992). Spencer and Collier (1997) classified population fluctuation patterns of several marine fishes based on historical catch statistics. Three variables, coefficient of variation (CV) in abundance, variable around the long-term mean and temporal autocorrelation in abundance revealed five categories of population behaviour: 1) spasmodic, 2) high variability, 3) cyclic, 4) irregular and 5) steady state (Figure 5a). Allozyme data for many of the species in the Spencer and Collier (1997) study show a negative

FIGURE 5

Effect of population instability on genetic diversity (allozyme heterozygosity) (from Grant and Waples, 2000)



A. Populations ordered by the coefficient of historical abundance (CV), variability around a long-term mean (R^2) and temporal autocorrelation of abundance (R^k) (Spencer and Collie, 1997). Species include: 1. Southern African anchovy; 2. Pacific cod; 3. NE Pacific hake; 4. Pacific halibut; 5. Pacific Ocean perch (Aleutian Island Arc); 6. Japanese anchovy; 7. NW Atlantic herring; 8. Bering Sea yellowfin sole; 9. North Sea herring; 10. California anchovy; 11. N Atlantic haddock; 12. Norwegian herring; 13. South African sardine; 14. Namibian sardine; 15. NW Pacific herring; 16. California sardine; 17. Japanese sardine.

B. Linear correlation of average allozyme heterozygosity and the coefficient of variation of historical abundances.

relationship between heterozygosity and the CV of historical abundance (Figure 5b; Grant and Waples, 2000). These results indicate that even temporary reductions in population size can have a strong influence on long-term population size and, hence, on genetic diversity.

Genetic variability in a stock can also be lost through selection by capture methods, in addition to genetic drift and metapopulation dynamics. Effects of fishing on species are evidenced by shifts in the average sizes of individuals (e.g. Ricker, 1969, 1981; Bigler *et al.*, 1996), changes in inherited life history parameters (e.g. Beacham, 1983a, b), reductions in average heterozygosity (e.g. Smith, 1994; Hauser *et al.*, 2002) and by temporal shifts in gene frequencies (e.g. Lacson and Morizot, 1991). Directional selection can occur more rapidly in large populations than in small populations, because random drift, which tends to counter selection, is much less in large populations (Ryman *et al.*, 1994).

5. GENETIC THREATS TO CAPTURE FISHERIES

Population size is a key variable for maintaining the genetic integrity of species in capture fisheries. Several ecological and genetic factors can converge to reduce population abundances. Most important for the marine environment has been overfishing by large industrial fleets. While external factors may play a role in some stock extinctions, intrinsic genetic factors can also be operating. One risk is the loss of genetic diversity, which declines at a rate that is inversely proportional to effective population size because of random genetic drift. The loss of genetic diversity can limit the ability of a population to adapt to changing environmental conditions and detract from its economic value. Small populations face the risk of inbreeding (mating between close relatives), which increases homozygosity and, hence, the expression of deleterious, recessive genes.

5.1 Overfishing and habitat degradation

Overfishing has been implicated in the collapse of some fishery populations (Jackson *et al.*, 2001; Allan *et al.*, 2005). For example, Dulvy *et al.*, 2003 documented the extinctions of 133 local, regional or global marine populations. Most of these extinctions could be attributed to overfishing (55%) or habitat loss (37%), while the remaining population declines appeared to be due to the effects of invasive species, climate change, pollution or disease. Global fisheries landings are continuing to decline at the rate of about 500 000 tonnes per year from a peak of 80-85 million tonnes in the late 1980s (Watson and Pauly, 2001). The effects of overfishing are not limited to large industrial fisheries. Small subsistence fisheries can also greatly influence species' abundances (Jennings and Polunin, 1996; Friedlander and De Martini, 2002).

These trends are likely to continue because of the increasing demand for fishery products and because of habitat degradation. As fisheries decline in productive waters over continental shelves, fishing is extended into deeper waters aided by the development of new technologies, such as satellite positioning and seafloor imaging. Marine species most vulnerable to stock depletions and extinction have large body sizes, long life spans, late maturities, low reproductive rates, limited geographical ranges, sporadic recruitment and adaptations to unique environments (islands and sea mounts) (Sadovy, 2001; Morato *et al.*, 2006) (Box 4).

Once depressed, stocks may not recover for ecological and genetic reasons (Hutchings, 2005). For example, at very low abundances reproductive output falls off in some species (e.g. Shelton *et al.*, 1999), and the removal of top predators may lead to dramatic shifts in ecosystem structure and food-web dynamics (Hansen *et al.*, 1998; Scheffer *et al.*, 2005). Ecosystem shifts resulting from ocean-climate changes may also retard the recovery of a depleted stock (e.g. Shelton *et al.*, 2006). The reduction of population sizes by intense fishing also appears to have led to the loss of genetic diversity in some marine species (Smith, 1994; Hauser *et al.*, 2002).

Declines in the abundances of natural stocks have stimulated aquaculture production. Although many countries have no alternatives, the aquaculture does not efficiently convert primary production into fishery products. Like the production of meat, which consumes about 40% of the world's grain production to feed livestock (Harrison and Pearce, 2000), aquaculture requires large amounts of fish meal. Wastes from aquaculture often threaten nearby habitats and can severely degrade riverine and sensitive coastal ecosystems. Some aquacultural products are sometimes perceived to be inferior to products from capture fisheries (e.g. Hites *et al.*, 2004; Senkowsky, 2004). Society, therefore, has a strong motivation to maintain wild stocks.

5.2 Genetic signatures of declining populations

The development of molecular methods provides an opportunity for identifying genetically distressed and declining populations. When populations become small, they are expected to lose genetic diversity. This loss is a central concern for declining populations threatened with extinction, as genetic factors can hasten extinction. For example, inbreeding depression is thought to be especially detrimental to the well being of small populations (Frankham, 1995; Hedrick and Kalinowski, 2000). Inbreeding between close relatives tends to increase the homozygosity of deleterious, recessive genes that are relatively harmless in the heterozygous condition. Low levels of gene diversity in themselves may not be universal distress signals, as many species with low gene diversities appear to be thriving after historical bottlenecks in population size (Hoelzel, 1999). Conversely, moderate or high levels of gene diversity may mask genetic problems in a population. Hybridization, for example, may produce an artificially elevated level of gene diversity (Ferguson 1986; Leary *et al.*, 1993).

Several biological and genetic indicators can be used to identify declining populations (Box 5). Molecular markers, for example, can be used to monitor levels of genetic

BOX 5
Genetic indicators of declining populations

1. *Reduced gene diversity*. Genetic diversity can be lost in several ways. For a gene not under the influence of natural selection, the loss of gene diversity is inversely proportional to population size. Small populations lose diversity faster than large populations. Theory predicts that the loss of heterozygosity each generation from random genetic drift (reproductive sampling error) is 1/2N, where 2N is the number of gene copies in a population for a diploid gene. A recursion formula predicting the loss of gene diversity, h_t, after t generations is

   $$h_t = h_o\,(1 - 1/2N)^t$$

   where h_o is the beginning level of gene diversity. Demonstrations of the loss of gene diversity in a population have to be made by comparison to un-fished populations of the same species and not to gene diversities in other species. Variability in gene diversity among species may be due to events on long evolutionary time scales and not to recent population events. Gene diversities can be measured with several molecular genetic markers, including allozymes, nuclear DNA (sequences or SNP polymorphisms) and mitochondrial DNA (RFLP or sequence polymorphisms).

2. *Changes in allelic or haplotypic frequency distribution*. The Ewens' (Ewens, 1972) sampling equation can be used to estimate an allele- or haplotype-frequency distribution from sample size and sample heterozygosity. This distribution is sensitive to the effects of population growth and decline and forms the basis of detecting recent bottlenecks in population size (Luikart *et al.*, 1998a, b; Garza and Williamson, 2001).

3. *Genetic discontinuities among populations*. Geographical fragmentation resulting from population extinctions can lead to discontinuities in allelic or haplotypic frequencies. A demonstration of genetic population fragmentation, however, must be based on a comparison with populations inhabiting undisturbed environments.

4. *Altered phenotypic traits*. Low gene diversities, as measured by molecular markers, may not always detect populations in genetic distress. Selection on phenotypic traits, such as size at age, can be effective in large populations where random drift is unimportant. Shifts in average size for some capture species have been attributed to size-selectivity of fishing gear.

5. *Altered life-history traits*. The timing of fishing effort can alter the genetic profile of a population by eliminating some temporal components of diversity. For example, early spawning migrations in some species of Pacific salmon were eliminated because of fishing pressure on early returning adults.

diversity. In Atlantic salmon (*Salmo salar*), microsatellite DNA markers showed a decline in gene diversity in a contemporary population in Denmark, relative to gene diversity in archived scales from the same area (Nielsen *et al.*, 1997). Other genetic profiles can also be used to identify distressed populations, including the distributions of microsatellite DNA alleles (Garza and Williamson, 2001), the distributions of mtDNA frequency haplotypes (Tajima, 1989) and haplotype mismatch patterns (Rogers and Harpending, 1992). One problem in the application of some of these approaches is that the appearance of some genetic profiles often lags behind population declines, especially rapid declines. For example, Lavery *et al.*,1996 found a mtDNA signature typical of an expanding population in a species that has declined in the past several decades.

5.3 Stock enhancement and supplementation

When capture populations decline, population enhancement and supplementation (the release of cultured individuals to boost wild population abundances) are sometimes used to attempt to rehabilitate wild stocks. Hatchery supplementations of salmonid populations have been practiced for several decades and provide lessons for other species (Utter, 2004). Although supplementation programmes for marine species have only recently been established, numerous projects are underway for fishes and invertebrates in several countries. Stock supplementations will likely increase as stocks continue to decline.

As aquaculture, mariculture and stock supplementation activities become more common, escapees and releases of cultured individuals will increase and potentially influence the genetic integrity of wild populations. The logic of supportive stock supplementation is to increase the survival of individuals in a hatchery without changing their genetic make up before release into the wild. However, the history of hatchery supplementation is filled with examples of genetic changes in cultured individuals, especially of salmonids (Reisenbichler and McIntyre, 1977; Allendorf and Phelps, 1980; Ryman and Ståhl, 1980; Verspoor, 1988; Busack and Currens, 1995; Campton, 1995; Norris *et al.*, 1999; Ford, 2002), but also marine species (Iguchi *et al.*, 1999; Sekino *et al.*, 2002).

Life history variables with an additive genetic variance (e.g. Reisenbichler and McIntyre, 1977; Cross and King, 1983; Taniguchi *et al.*, 1983; Hard, 1995), or developmental and morphological traits (Leary *et al.*, 1985) are also subject to change. Captive breeding and hatchery programmes also can lead to elevated frequencies of deleterious alleles that are otherwise kept at low frequencies in wild populations by selection (Lynch and O'Hely, 2001). Hybridization of genetically altered individuals with wild individuals can lower the fitness of offspring (outbreeding depression). Even if cultured individuals have not been genetically altered, supplementation may still pose a genetic threat to wild populations (Box 6).

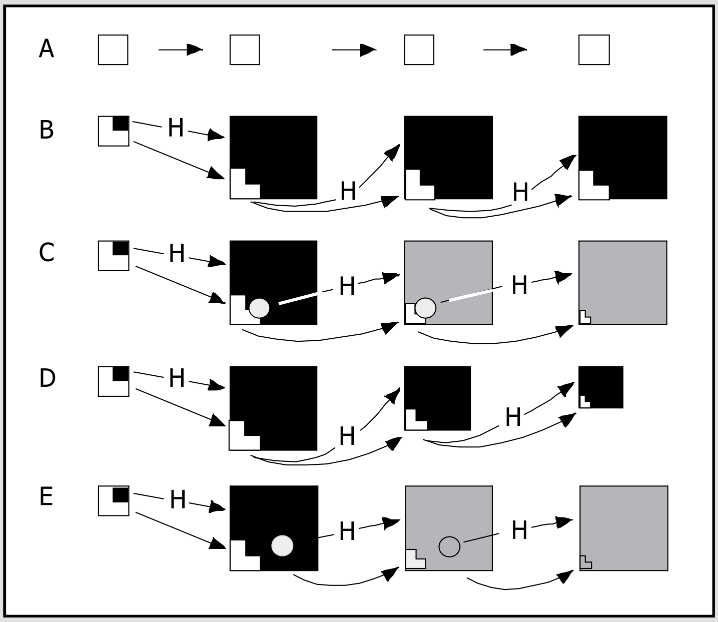
5.4 Hybridization and outbreeding depression

Hybridizations between genetically divergent wild populations can occur for several reasons (Epifanio and Nielsen, 2001). One is the inadvertent or intentional introduction of genetically divergent conspecific individuals into a native population. Non-native individuals can be inadvertently introduced by ship ballast water, or as escapes from mariculture or aquaculture. Less common are natural or intentional habitat modifications that bring previously isolated populations in contact with one another. Ecological or competitive interactions between introduced and native individuals may drive wild populations to extinction. Genetic effects, although less obvious, can be equally detrimental to the survival of a species or stock. Genetic changes are greatest in captive populations closed to wild individuals. These results indicated that releases of

BOX 6
Genetic effects of supplementation

Ryman and Laikre (1991) outlined how stock supplementations can reduce genetic diversity through "genetic swamping", even though the census size of the population in the wild increases. Captive individuals are generally produced from only a small number of parents relative to the number of potential parents in the wild. Releases of cultured individuals increase the parent-offspring variance and reduce the effective population size of the wild population, even though census numbers may be larger. Ryman and Laikre (1991) found that the effective population size equaled the sum of wild (Nw) and captive (Nc) parents only when the fraction of captive progeny was Nc/(Nc + Nw). Effective population sizes at other values of Nc and Nw are smaller. Importantly, supportive breeding in most instances reduces the total effective population size below what it would have been without supplementation. These smaller effective population sizes can lead to a loss of genetic diversity. Genetic swamping is a concern in species with high fecundities and high larval or juvenile mortality rates, a characteristic of most marine species.

Waples and Do (1994) explored this effect in more detail for Pacific salmon. They found that the extent of genetic swamping depended on the number of parents used in culture and not on the fraction of the wild population used for spawning. Genetic swamping can be hastened when individuals of hatchery origin are included a broodstock (Figures C and E). The most important determinant of levels of inbreeding in wild populations is the size of a wild population after supplementation. Even if the supplementation is successful and the wild population remains large, continued supplementation will eventually lead to the complete replacement of wild individuals with hatchery descendents. One of the few attempts to monitor the effects of supplementation showed reductions in genetic diversity in some populations of brown trout *(Salmo trutta)* that are likely due to stocking (Hansen *et al.*, 2000).



BOX 6 *(cont.)*

Genetic effect of supplementing natural stocks with hatchery (H) raised individuals (based on Ryman and Laike, 1991 and Waples and Do, 1994)

Scenario	Result
A. No supplementation to a self-sustaining natural population.	No genetic contamination of natural gene pool.
B. Offspring from captive broodstock are used to supplement a wild population. In this scenario, a portion of the wild population is used as broodstock to produce offspring for release. Hatchery releases are marked so they are not used as broodstock. Also no hybridization occurs between native individuals and releases, and native individuals mate only with other native individuals.	No genetic contamination. However, this scenario is highly unrealistic.
C. Scenario as in B, except hatchery offspring are not marked and both hatchery and native individuals are used as broodstock.	Eventual genetic swamping of native gene pool with genes of hatchery origins.
D. Scenario as in B, except that population abundance declines because of overfishing, or because supplementation exceeds environmental carry capacity.	Natural gene pools are still intact, but native individuals now represent only a small fraction of the population.
E. Scenario as in B initially, but native and hatchery individuals mate in the wild, so broodstock consist of a mix of native and hatchery genes.	Genetic swamping of native gene pool.

captive individuals can pose a genetic risk to wild populations through hybridization (Box 7).

In a survey of the literature on hybridizations in fish, Utter (2001) found several generalizations (modified here).

1. Freshwater species are more susceptible than anadromous species to introgression from distinct lineages. Anadromous species are adapted to a greater number of life history variables (freshwater migration timing, marine migration, natal homing, run timing) than are freshwater species. Hence, introgression may be prevented by outbreeding penalties against hybrids in anadromous species.
2. Genetic distances between lineages of freshwater fishes are poor predictors of introgressive hybridization. Hybrids have occurred between highly diverged lineages and even between species.
3. Anadromous populations may be more prone to displacement than to introgression between major lineages. However, introgression commonly occurs between subgroups within major lineages.
4. Persistent disruption of subgroup adaptation through hybridization with non-native individuals retards the full potential for productivity of natural populations.

When selective pressures on captive populations are not managed, or when introgressive hybridizations are recurrent from long-term supplementation releases, genetic transformations of wild populations can potentially lead to the inability of a wild population to sustain itself without supplementation (Lynch and O'Hely, 2001).

BOX 7

Genetic effects of hybridization

The major genetic risk of hybridization is the disruption of adapted gene complexes and loss of fitness (outbreeding depression) (Rhymer and Simberloff, 1996). In one form of outbreeding depression, native individuals are better adapted to particular habitat conditions than are either the introduced or hybrid individuals. For example, experimental hybrids between even- and odd-year run pink salmon *(Oncorhynchus gorbuscha)* showed much lower survival rates than either of the two control groups (Gharrett and Smoker, 1991). Outbreeding depression can also occur in hybrids between geographically separated groups of the same year type (Gilk *et al.,* 2004). A second form of outbreeding depression occurs when non-native genes are introduced into the genomes of wild individuals after the first generation of hybridization (introgression). Introgression disrupts the genes influencing a particular adaptation. Depending on the mode of expression of the genes, first generation hybrids may not be affected, but genetic recombination during reproduction separates co-adapted genes on parental chromosomes and reduces fitness in the introgressed individuals.

Reduced hybrid fitness has been documented experimentally in 'common garden' experiments for numerous freshwater (e.g. Dowling and Moore, 1985; Philipp *et al.*, 2002; Neff, 2004) and anadromous fishes (e.g. Ferguson, 1986; Hawkins and Foote, 1998; Leary *et al.*, 1985; McGinnity *et al.*, 2003). A much longer list of species shows evidence of introgression from molecular markers (see Utter, 2001). However, virtually no examples exist of outbreeding depression in marine fishes, even though hybridizations are well documented with molecular methods. One reason for the apparent lack of outbreeding depression in marine fishes may be that it is difficult to demonstrate outbreeding experimentally. Another reason may be that local adaptations are not as prevalent in marine species because high levels of gene flow may prevent local adaptations. Generally, the lower levels of genetic divergence between populations of marine fishes and many invertebrates as detected by molecular genetic methods indicate high levels of gene flow. In marine species, substantial supplementation efforts have not always resulted in the expected increases in population abundance (Larkin, 1991; Masuda and Tsukamoto, 1998). These failures could in part be due to undocumented introgressive hybridization with long-term releases of cultured individuals.

6. MAPPING THE POLICY ENVIRONMENT

Numerous national and international initiatives have been proposed to explore ways of reversing declining abundances of the world's biological resources (Table 2). Chief among these is the 1992 Convention on Biological Diversity (CBD, 1993), which calls for the conservation of biological diversity at three levels: genetics, species and ecosystems. Kenchington *et al.* (2003) noted that most initiatives focus on the conservation of species and ecosystems with little attention to genetics. Although ecosystem-based fishery management promotes the preservation of ecosystems and represents a major step toward achieving sustainable uses of natural resources, ecosystem management may not always protect genetic diversity within a species.

In addition to international initiatives, many countries or national organizations have outlined specific national problems and have attempted to implement policies intended to protect biodiversity at several levels. Parts of these policies have been formulated to address genetic issues directly. For example, the Fisheries Society of the British Isles recently published a briefing paper (FSBI, 2004) outlining the effects

TABLE 2

International initiatives on the conservation of aquatic biodiversity and the extent of focus on genetic issues. Modified from Cochrane and Doulman (2005)

Programme or Declaration	General intent	Statements or implications for genetics
Agreement, Convention or Declaration		
1973 Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)	Prohibit international trade of endangered and threatened species.	Indirect: Reduce risk to endangered species.
1982 UN Convention on the Law of the Sea (UNCLOS)	Provides legal framework to strengthen fisheries management.	Indirect: 1. Reduce risk to endangered species; 2. Promote ecosystem-based management; 3. Implement precautionary approach.
1992 UN Conference on Environment andDevelopment (UNCED)	Promote eco-efficiency as a guiding principle 'Earth Summit' for businesses and governments; Agenda 21, comprehensive programme of action for global action to promote sustainable development; Rio Declaration on Environment and Development, principles defining rights and responsibilities of States. Resulted in Convention on Biological Diversity	Indirect: 1. Development of sustainable resources. 2. Conservation and sustainable use of biodiversity 3. Benefit sharing of genetic resources
1993 FAO Compliance Agreement	Promote compliance with international conservation and management measures by fishing vessels on the high seas.	Indirect: Reduce fishing pressure on harvested species.
1995 FAO Code of Conduct for Responsible Fisheries (CCRF). Several subsequent conferences.	Provide holistic framework for developing regulations of inland and marine fisheries and aquaculture.	Indirect: 1. Long-term preservation of fishery resources; 2. Habitat protection; 3. Call for research to support scientific decision making. Direct: 1. Call for management of genetic resources in aquaculture; 2. Management of alien species
1995 Kyoto Declaration	Underscore importance fisheries to food security in developing countries.	Indirect: Sustainable fisheries.
1995 UN Fish Stocks Agreement	Implement provisions of the UNCLOS relating to straddling fish stocks and highly migratory fishes. Developed in response to failure of 1982 UNCLOS to achieve goals.	Indirect: 1. Management of straddling stocks and stocks of highly migratory species. 2. Reduce impacts of fishing on marine environment. 3. Preserve marine diversity. 4. Maintain integrity of ecosystem.

TABLE 2 *(Cont.)*

Programme or Declaration	General intent	Statements or implications for genetics
1995 Jakarta Mandate on Marine and Coastal Biological Diversity (CBD-JM)	Global consensus on conservation of marine and coastal biological diversity;	Indirect: 1. Marine and coastal protected areas; 2. Sustainable use of marine and coastal living resources; 3. Mariculture and introductions of alien species; 4. Ecosystem processes approach to development.
2001 Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem	Recognizes fisheries impact on ecosystem, and hence, on fishery productivity.	Indirect: Preservation of ecosystem services and integrity of fishery populations.
2002 Plan of Implementation adopted by World Summit of Sustainable Development	Reinforce and consolidate existing plans and concepts to achieve sustainable development. Set a deadline (2010) to implement ecosystem approach and the maintenance or restoration of stocks to maximum sustainable levels (2015).	Indirect: Preservation of ecosystems and sustainable use of populations.
Organizations		
1923 International Pacific Halibut Commission	Conduct research and management of the stocks of Pacific halibut in the waters of Canada and the USA.	Indirect: Population management incorporating genetic information.
1945 FAO established as specialized agency within United Nations	Provide forum to address issues relating to development and sustainable use of living marine resources. Provide fishery databases to support formulation of fishery management policies.	Direct: Numerous publications on importance of genetic processes in management and sustainable use of marine resources.
1948 World Conservation Union (IUCN). World's largest conservation network, bringing together 82 States, 111 government agencies, more than 800 non-governmental organizations (NGOs).	Influence, encourage and assist societies throughout the world to conserve the integrity and diversity of nature and to ensure that any use of natural resources is equitable and ecologically sustainable.	Direct: Genetic diversity is one of the three forms of biodiversity recognized by the World Conservation Union (IUCN) as deserving conservation.
1950 Inter-American Tropical Tuna Commission (IATTC)	Conservation and management of fisheries for tunas and other species taken by tuna-fishing Vessels in the eastern Pacific Ocean.	Indirect: Population management and reduction of by-catch.
1969 International Commission for the Conservation of Atlantic Tunas (ICCAT)	Conservation of tunas and tuna-like species in the Atlantic Ocean and adjacent seas.	Indirect: Population management and reduction of by-catch.
1982 Commission for the Conservation of Antarctic Marine Living Resources (CCAMLAR). Part of Antarctic Treaty System	Balance the conservation of Antarctic marine living resources and their rational use.	Indirect: Early focus on harvests of krill. Population management.
1983 FAO Commission on Genetic Resources for Food and Agriculture	Permanent forum where governments discuss and negotiate matters relevant to genetic resources for food and agriculture.	Direct: Discussion of policies and practices influencing genetic diversity in plant and animal resources.

TABLE 2 *(Cont.)*

Programme or Declaration	General intent	Statement or implication for genetics
World Resources Institute (WRI)	Promote sustainable use of living resources through dissemination of information.	Indirect: 1. Reverse ecosystem degradation. 2. Protect global climate system.
1994 Convention for the Conservation of Southern Bluefin Tuna (CCSBT)	Conservation and management of fisheries for southern bluefin tuna	Indirect: Harvest management and reduction of by-catch.
1995 UNEP Global Programme of Action (GPA)	Protection of marine habitats from land-based activities	Indirect: Ecosystem protection
1994 International Coral Reef Initiative (ICRI)	Protection and restoration of reef ecosystems.	Indirect: Recognition that reefs are important fish nursery areas.
Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection (GESAMP)	Provides advice on impact of human activities on marine ecosystems.	Indirect: Population health through sustainable use.
Global Oceans Observing System (GOOS) Created by Intergovernmental Oceanic Commission (IOC) in 1991. Living Marine Resources (LMR) module created in 1998.	Improve information for management of seas and oceans and climate forecasts.	Indirect: Effects of fisheries on living marine resources.
Marine Protected Areas (MPAs) initiated by World Bank, World Conservation Unions (IUCN), Great Barrier Reef Marine Park Authority (GBRMPA) and Global Environmental Facility (GEF).	Establishment of marine protected areas to aid in habitat and species restorations.	Indirect: Restoration of populations through protected marine areas.

of fishing on biodiversity in the North Sea and highlight specific threats to genetic diversity. Elsewhere, endangered species legislation in the United States (Endangered Species Act) has been interpreted by government conservation agencies to protect genetic diversity within and among intraspecific population groups (Waples, 1991). Box 8 gives an example of the use of this legislation to extend protection to threatened population groups of Chinook salmon (*Oncorhynchus tshawytscha*) in western North America.

7. DEVELOPING A FRAMEWORK FOR CONSERVING GENETIC DIVERSITY

It is clear from the arguments presented here that preserving genetic diversity in natural populations subject to capture fisheries is important for maximizing harvests and achieving the sustainable use of fishery resources. Four steps can be taken to develop a framework for conserving genetic diversity in capture fisheries (modified from Kenchington *et al.*, 2003):

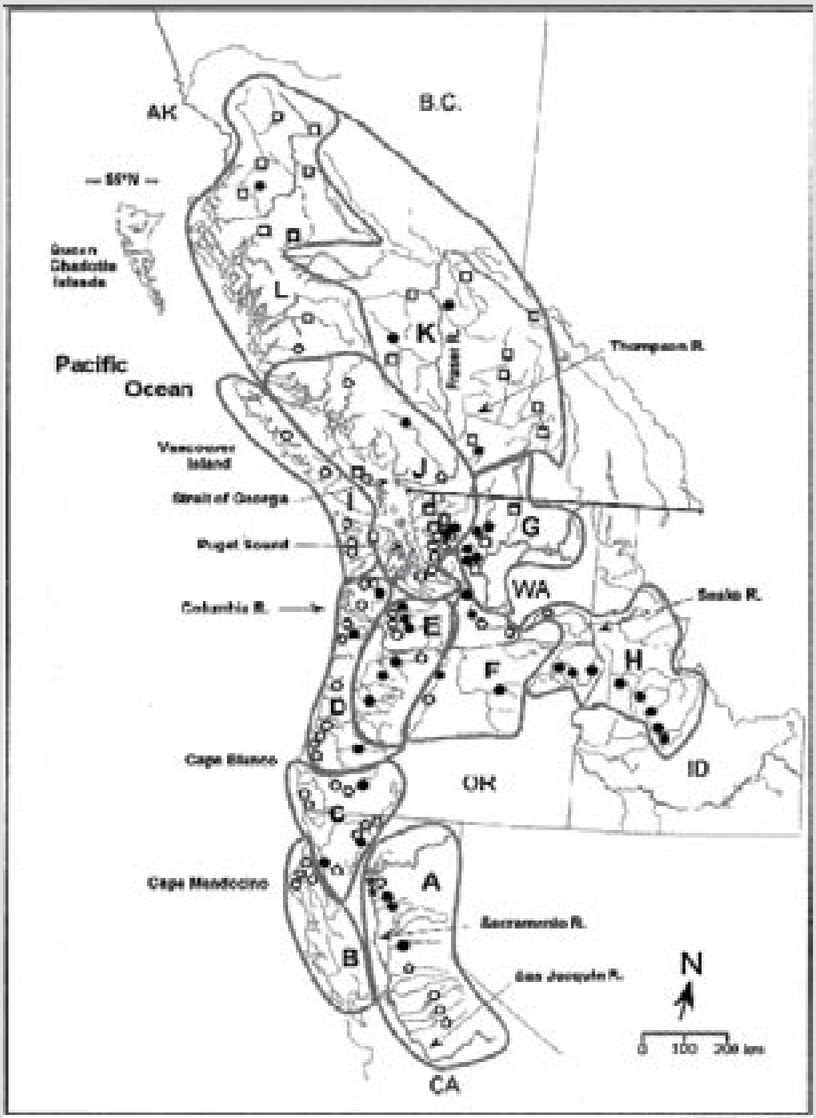
Step 1: Identify management objectives

The rationale for developing the objectives of a conservation or management programme differs among disciplines and determines the directions of management efforts. Goals can be evaluated by arguments from several broad disciplines representing perspectives from the past, present and future (Bowen and Roman, 2004). A systematist may argue that a major goal should be the conservation of species representing the heritage of past evolutionary diversifications (Forey *et al.*, 1994; Wheeler and Cracraft, 1996; Vecchione *et al.,* 2000; Bowen, 1999).

From a contemporary perspective, an ecologist might argue that preserving functional ecosystems is the best way to conserve the components of genetic diversity among species and among conspecific populations. Changes in one component of an ecosystem by overfishing, for example, can ripple through an entire system and threaten the stability of species not targeted by a fishery. The loss of an ecological component in an ecosystem can have often unpredicted effects on other parts of an ecosystem (Brodziak and Link, 2002). A sociologist might argue more narrowly for the preservation of genetically influenced traits in a species or population that is valued by society. An economist might argue for the preservation of specific genes with potential pharmaceutical or commercial value.

With an eye to the future, an evolutionary biologist might argue for preserving the breadth of genetic diversity in a species to ensure its capacity to adapt to future environmental changes (Crandall *et al.*, 2002; Bowen and Roman, 2004). The rationale many conservation efforts is the preservation of genetic diversity to allow future adaptive shifts (e.g. Waples, 1995). Ecological and evolutionary considerations, however, are views of the same events on different temporal scales (Frank and Leggett, 1994). All these arguments must be weighed openly by society to set conservation priorities and to provide a foundation for setting management objectives.

In practice, conservation and management goals are often forged by the contradictory demands of industry, politicians, economists, ecologists and conservationists. Unlike conservation efforts, which are often directed at preserving components of genetic diversity, the goals of managing large fisheries are not usually directed at preserving genetic diversity itself, but at the population processes influencing this diversity. An underlying objective might be to maintain populations in a natural setting that allows 'normal' ecological and evolutionary processes to occur and to maintain the full geographical range of a species (Thorpe *et al.*, 1995; Taylor and Dizon, 1999). Other management objectives might include an increase in recruitment or a reversal of the effects of selective fishing on average size, maturation age or spawning timing.



Run timing: closed circles, spring; open square, summer; open circle, fall; asterisk, winter. Twelve geographic provinces (A–L) were delineated with allozyme frequencies and life-history information, such as spawning migration timing and the length of juvenile freshwater residence (Waples *et al.*, 2004).

The "Endangered Species Act" (ESA) of 1973 in the United States of America mandated that endangered or threatened species be identified for special conservation efforts. Waples (1991) developed a framework to identify "distinct population segments", which could be considered to be "species" under the ESA and receive the same protections as an endangered species. This framework invoked two criteria based on genetic and evolutionary considerations. A population represented a distinct population segment if it was reproductively isolation from other populations in the same species and if it represented an important component of the evolutionary legacy of a species. Genetic, ecological, geographical and life-history information was used to evaluate the statuses of populations in seven species of anadromous salmonids inhabiting western of the United States of America. While coastal fisheries can potentially limit the abundances of salmon populations, spawning biology and early life-history stages appear also to be important limiting factors.

Step 2: Assess genetic risk

This step is related to the first step. A clear understanding of the risks associated with the loss of genetic variability through inbreeding and stock extirpations, or the disruption of genetic structure through hybridizations, will help to guide the development of management goals. One important research agenda addresses the extent and rapidity of adaptation in local populations and the extent that human activities disrupt local adaptation (e.g., Taylor, 1991; Miller and Kapuscinski, 1994; Currens and Busack, 1995;

Sheridan, 1995; Conover, 1998; Law, 2000). Answers to these questions bear on the extent that evolutionary processes should be factored into management objectives. A growing body of evidence indicates that fish are often finely adapted to local habitats (Gilk *et al.*, 2004; Utter, 2004), and that genetic changes can occur rapidly after transplantation (e.g. Kinnison *et al.*, 1998), in culture (e.g. Hindar *et al.*, 1991) or in response to fishing selectivity (e.g. Heino, 1998; Stokes and Law, 2000). Other genetic risks may come from intraspecific hybridizations between wild and fish that have been genetically modified in captivity (e.g. Leary *et al.*, 1985; Philipp *et al.*, 2002).

Step 3: Identify reference points

Setting benchmarks to evaluate progress toward fulfilling management objectives is a critical step in the process. Reference points have been defined by an ICES working group (ICES, 2001) as “specific values of measurable properties of systems (biological, social, or economic) used as benchmarks for management and scientific advice”. The purpose of setting benchmarks is to increase the awareness of the consequences of inaction on a particular problem. Two kinds of reference points can be distinguished (ICES, 2001). The first are ‘target reference points’, which are properties of stocks, species or ecosystems that help to achieve biological, social and economic goals. The second are ‘limit reference points’, which are threshold values of resource variables that trigger a conservation concern of unacceptable risk or irreversible harm. The setting of reference points for the preservation of genetic diversity depends on defining particular genetic risks to short-term goals such as maintaining stock abundance, economic return and species survival, and to long-term goals of preserving the capacity to adapt to environmental change.

The challenge in setting reference points is to understand what facets of genetic diversity are important for achieving particular goals. Only an integrated research agenda that includes genetics, ecology and economics can provide this understanding. Even a basic understanding of some genetic mechanisms is lacking. For example, little is known about what levels of genetic diversity are needed for a species to thrive and adapt. Generally, the wisdom is that as much gene diversity should be conserved as possible and that the loss of diversity leads to reductions in production. Theoretical considerations indicate that populations should not drop below 1 000-5 000 individuals to minimize the loss of gene diversity through random drift (Lynch and Lande, 1998). Yet, counter examples show that species can thrive after experiencing bottlenecks in population size that eliminated nearly all genetic diversity (Hoelzel, 1999).

Step 4: Monitor progress

Patterns of genetic variability within and among populations of a species can be monitored directly with molecular genetic methods or indirectly with models and population baseline data. Surveys of molecular genetic variability are costly, but have been vital for estimating levels of connectivity among and gene diversity within populations. Temporal sampling is needed to monitor the effects of management actions, after an initial survey establishes a baseline. One constraint on genetic monitoring is the lack of historical data. Major declines in stock abundances from fishing occurred several decades before molecular methods were first used to survey genetic variability on a large scale in the 1970s. Hence, a pre-fishing baseline is difficult to establish for most species. Temporal datasets have been instrumental in showing gene-frequency shifts in some species that appear to be due to fishing intensity (Hauser *et al.*, 2002). Another constraint in using molecular genetic markers to monitor the effectiveness of management on short time scales is that genetic profiles may not respond rapidly to environmental and demographic events. The development of high throughput methods of surveying genetic diversity (e.g., SNPs, Smith *et al.*, 2005; DNA microarrays, Cossins and Crawford, 2005) will make genetic monitoring more feasible in the future.

Avise (2001) outlines how cyto-nuclear signatures of genetic variability can be used to detected hybridizations and introgressions. Dowling *et al.,* 2005 provide an example of monitoring the genetic effects of supplementing over 11 years populations of endangered Catostomid fish.

Genetic parameters can also be monitored indirectly with theoretical models and data for population abundance, population demography and geographical distribution. For example, population models indicate that strong reductions in population size, metapopulations extinction dynamics and population fragmentation can lead to the loss of genetic variability.

8. CONCLUSIONS

The relative importance of genetic processes in species supporting capture fisheries differs among ecosystems and species. Fisheries in rivers and lakes are largely focused on species with naturally fragmented populations. Dams and land transformations further isolate some populations by destroying migration corridors between populations. Inland species are therefore vulnerable to the loss of genetic diversity through the metapopulation processes of extinction and colonization and through random drift in small populations. Hence, genetic concerns are largely addressed under the framework of conservation biology and theory relating to inbreeding and inadvertent hybridization.

Anadromous species support large commercial fisheries in the North Atlantic and North Atlantic. These species are especially vulnerable to ecological disturbances because of their complex life-history cycle, which spans freshwater and marine habitats. The loss of between-population genetic diversity through population extinctions in some species is especially acute in areas of extensive human development and degraded habitats. Native salmonids appear to be particularly at risk from hybridizations with genetically divergent conspecific individuals.

In the marine realm, species supporting capture fisheries also face genetic threats. Marine species in open waters can experience the loss of genetic diversity through the extinction of local subpopulations, genetic swamping through stock enhancements with artificially propagated individuals and intentional or inadvertent introductions of related species. The loss of genetic variability through random genetic drift appears to be less important for marine species than for inland and anadromous species. Even so, shifts in gene frequencies from drift induced by overfishing have been documented in some marine species and imply reductions to small effective population sizes.

Overfishing, habitat degradation and climate shifts appear to be far more important threats to stocks of most species than are genetic risks. This assessment is illustrated by a recent collection of papers from a symposium, entitled "Fisheries, past, present and future" (Philosophical Transactions of the Royal Society B, 2005, vol. 360), which did not include a single article dedicated to genetic issues in the management of capture fisheries. Although genetic processes were briefly discussed in some of the 14 major articles, highlights of genetic issues were absent from the introductory summary of the conference (Beddington and Kirkwood, 2005). Genetic processes appear to be perceived as far less important than ecological and life history processes influencing stock abundances.

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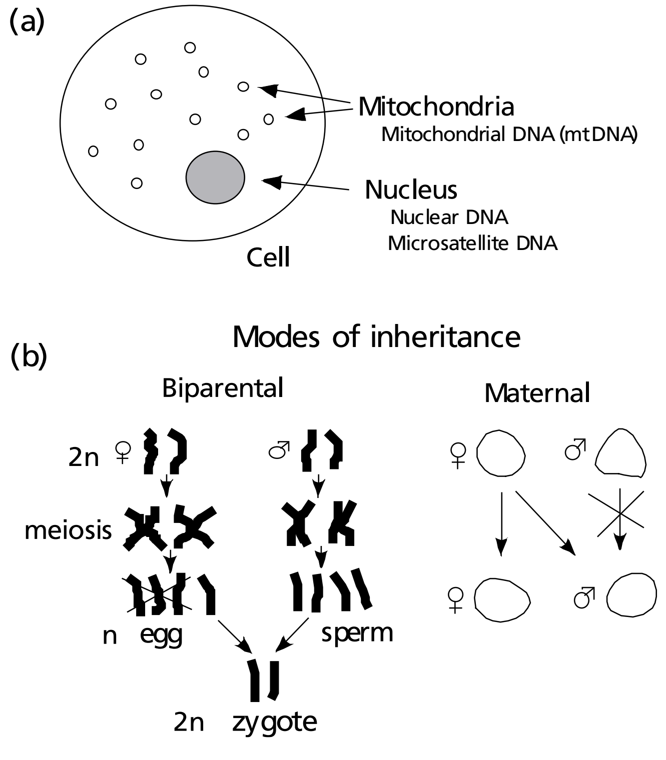
ANNEX 1

METHODS AND CONCEPTS FOR SURVEYING GENETIC RESOURCES

1. GENETIC BASIS FOR MOLECULAR VARIABILITY

The genetic information needed for the development and physiological maintenance of an individual is stored in a long polymeric molecule called DNA. DNA is found in two organelles in a cell: over 99% of DNA is located in the nucleus, but a small fraction occurs as a plasmid-like circular structure in mitochondria (Figure a). Genes encoded by nuclear DNA are inherited from both parents, and hence occur in pairs to form a diploid genotype (Figure b). Genes encoded by mitochondrial (mt) DNA, however, are maternally inherited in most species and hence occur as a single haplotype in an individual. The analysis of mtDNA, which also lacks recombination, can provide unique insights into population structure that is not possible with nuclear DNA (Avise, 1994). The entire complement of DNA is denoted by the term genome, and various parts of the genome serve different functions.

One important function is to encode information that can be translated into proteins. The coding parts (exons) of many genes are often interspersed by noncoding (introns) sections of DNA. Introns are less constrained by natural selection and hence mutate at a higher rate than the protein coding portions of a gene. Other parts of the genome encode regulatory information, important in development and gene expression. A large portion of the genome appears to serve no coding function, but may be important in the physical arrangement of DNA in the nucleus. These sections of DNA often have large numbers of short repeats called microsatellites.



2. TRENDS IN THE DEVELOPMENT OF MOLECULAR GENETIC MARKERS

Early methods of surveying genetic variability, such as immunological assays and allozyme electrophoresis, examined the products of DNA coding genes. A large amount of information on the genetics of natural and cultured populations of aquatic organisms has been produced since the early 1970s, when protein electrophoresis was first used on a large scale to the survey genetic variability in and among natural populations. However, technological developments since the 1980s have produced methods that assay DNA polymorphisms directly (Palsbøll, 1999). The most important population markers include direct sequencing, restriction enzyme fragment length polymorphisms (RFLPs), amplified fragment length polymorphisms (AFLPs) and single nucleotide polymorphisms (SNPs). The application of these methods has been greatly aided by the development of the polymerase chain reaction (PCR), which amplifies targeted DNA sequences from small amounts of tissue. These various techniques provide complementary information about natural populations and are variously suited to answering different questions. When molecular population markers are under natural selection, caution must be used to infer movement between subpopulations from the geographical distributions of allele or haplotype-frequencies. Although selection on allozymes can occur because they encode proteins (Mitton, 1997), DNA cannot always be assumed to be free of selection (Avise, 1994; Bazin *et al.*, 2006; Nielsen *et al.*, 2006). Biogeographical and laboratory evidence indicates that selection may shape the geographical distributions of protein (Powers *et al.*, 1991; Powers and Schulte, 1998), mitochondrial DNA (Árnason, 2004; Bazin *et al.*, 2006; Grant *et al.*, 2006) and nuclear DNA variants (Pogson and Mesa, 2004; Canino and Bentzen, 2004; Case *et al.*, 2005). The nature and intensity of selection must be understood when using selected population markers to infer population structure. Patterns of divergence for adaptive and neutral markers may not coincide (McKay and Latta, 2002). Although selectively neutral molecular markers will continue to be important, Vrijenhoek (1998) argues that adaptive traits should also be examined to help resolve conservation and management problems.

3. ESTIMATING EFFECTIVE POPULATION SIZE

One promising use of genetic data is to estimate the effective sizes of fishery populations. The genetic concept of effective population size is the number of individuals that actually contribute genetic information to the next generation. Not all individuals in a population produce offspring that reach reproductive maturity. In the marine environment, many species show a large variance in family size because of variability in the physical and biological factors influencing larval survival (Hedgecock, 1994). Fishery resource managers, on the other hand, focus on the actual number of individuals in a population (census size). The difference between these two numbers can be large for the same stock. Census population sizes are generally at least ten times the effective sizes (Frankham, 1995; Nunnery and Elam, 1994). In some cases, census size can be as much as three orders of magnitude larger than effective population size (Turner *et al.*, 2002). The loss of genetic diversity has been detected in some species, even though census numbers may still be large (Hauser *et al.*, 2002). Effective population size can be estimated in several ways. One way is to estimate the drift effective size by examining temporal changes in gene frequencies. The concept behind this approach is that effective population size influences the amount of genetic drift in a population. Small populations experience a greater amount of genetic drift, and hence greater gene frequency changes, than do larger populations. This method requires gene frequencies estimates from different generations. For some species, the analysis of archived fish scales from collections in the last few decades has provided estimates of historical gene frequencies (Miller and Kapuscinski, 1997; Nielsen *et al.*, 1997, 1999). Different statistical approaches have been used to extract unbiased estimates of effective population sizes from gene frequency data (Luikart *et al.*, 1999; Wang, 2001; Berthier *et al.*, 2002), These methods provide estimates of effective population sizes of contemporary or very recent populations. Other methods of estimating effective population size use equations from evolutionary theory that incorporate long-term effective population size. One approach is to use observed heterozygosity, which is expected to be a function of effective population size and the neutral mutation rate (Waples, 1991). Another approach is to estimate the coalescence times for mtDNA haplotypes when recombination is absent (Avise *et al.*, 1988). Coalescence time (the time until haplotype lineages trace to a common ancestral haplotype) is expected to be a function of population size. While these estimates may be reveal long-term features of the population biology of a species, they are not always useful for making management decisions, because they may not represent current population sizes.

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ANNEX 2

1. COMPUTER PROGRAMMES FOR GENETIC ANALYSIS

The development of new technologies to detect molecular variation and automation of several steps in these laboratory analyses have led to the production of large amounts of genetic data. The availability of these data has stimulated the development of new statistics and computer programmes, which provide insights from data not previously possible (Zhang and Hewitt, 2003). The use of computers provides the opportunity to test hypothesis with bootstrapping and coalescent simulations, in addition to standard parametric, non parametric and exact tests.

Most, if not all, the computer programmes available for genetic analysis can be downloaded from the web sites of academic institutions without charge. Several groups of programmes are available. Multipurpose progammes are generally used to examine genotype or sequence data and to describe gene diversities within and among samples. These programs include ARLEQUIN (Excoffier *et al.*, 2005), DnaSP (Rozas *et al.*, 2003), FSTAT (Goudet, 1995); GENEPOP (Raymond and Rousset, 1995), GENETIX (in French only; Belkhir *et al.*, 2000), and MEGA (Kumar *et al.*, 2004), among others. The basic facilities offered in these programs are reviewed in Excoffier and Heckel (2006).

In addition to these basic programmes, many other programmes incorporate algorithms that attempt to assign individuals to particular populations. These include BAPS (Corander *et al.*, 2004), GeneClass (Piry *et al.*, 2004) and GeneLand (Guillot *et al.*, 2005), STRUCTURE (Pritchard *et al.*, 2000), among others. Also in this group are programs written for fishery management to estimate the origins of individuals in areas of stock mixing (BAYES, Pella and Masuda, 2001; WHICHRUN, Banks and Eichert, 2000). Hansen *et al.,* (2001) reviews the utilities of these and other mixed-stock computer programmes for microsatellite DNA markers.

Another group includes specialized programme performing a variety of tests of past demographies (ARLEQUIN; DnaSP; BATWING, Wilson *et al.*, 2003, among others). Algorithms in these programmes search for evidence of population growth or bottlenecks in population size. Molecular markers are often assumed to be neutral to the effects of selection. This assumption can be tested by gene- or haplotype-frequency districtuions (MEGA; FDIST2, Beaumont and Nichols, 1996). Migration is also an important factor shaping the genetic population structure of a species. Estimates of migration between populations (gene flow) are often used in devising conservation and management strategies (COLONISE, Foll and Gaggiotti, 2005; MIGRATE, Beerli, 2006, among others).

Inferring phylogenetic relationships among species can also be important to the management of a multispecies fishery. Phylogenetic trees were first constructed from genetic distances estimated from gene frequencies. The widespread availability of DNA sequences, however, allow more sophisticated approaches to tree construction (see Felsenstein, 2003). These methods include parsimony, maximum likelihood and Baysian algorithms (Nei & Kumar, 2000). Many of the general programmes listed above provide options to use some of these methods. However, several specialized programmes can be downloaded from the internet. Some of the more commonly used programmes include PHYLIP (J. Felsenstein: http://evolution.gs.washington.edu/phylip.html), PAUP* (D. Swofford: Sinauer Associates), MacClade (W. Maddison: http://phylogeny.arizone.edu/macclade/macclade.html) and DAMBE (X. Xia: http://aix1.uottawa.ca/~xxia/software/software.htm), among others.

Many situations encountered by fishery biologists do not easily fit the assumptions of some biological and statistical models, which are often simplified for easier use. For example, equal population sizes and equal migration rates between populations are assumed in several genetic population models, but in nature are seldom equal to one another. A refinement in the use of statistical models to interpret genetic data is the use of simulation programs to model particular situations (e.g. SIMCOAL, Excoffier *et al.*, 2000; EASYPOP, Balloux, 2001; METASIM, Strand, 2002; MESQUITE, Madison and Madison, 2004; among others). Future approaches to DNA data analysis will use maximum likelihood and Bayesian methods tailored to particular situations (e.g. Whitlock and McCauley, 1999; Pritchard *et al.*, 2003; Dawson and Belkhir, 2001; Wilson and Rannala, 2003).

These computer programmes should be used cautiously. The use of some programmes is complicated by the different input formats. This requires reformatting of datasets manually or with programmes designed for data conversion (see Excoffier and Hackel, 2006). Another caution is that different programmes may produced different values of the same statistics for the same set of data. This is likely due to differences in how the programmes are written. Lastly, these programmes offer numerous options for analyzing data and produce a wealth of statistical output. A researcher should always take the time to read the background literature on how a statistic is calculated and its interpretation. User documentation of some programmes (e.g. ARLEQUIN) presents some explanations. However, the successful application of many programmes requires that the user read the original literature.

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ANNEX 3

USE OF GENETIC DATA IN FISHERY MANAGEMENT

1. DEFINING POPULATIONS FOR MANAGEMENT

One problematic issue has been a lack of consensus on the definition of a population, even though the 'population' is a fundamental unit in ecology, evolution and fishery management. In fishery management, few definitions of a population are operational enough to be used objectively by researchers or policy makers (Waples and Gaggiotti, 2006). Yet, how populations are connected to one another through migration has important consequences for devising management plans. Fishery managers usually agree that management units should coincide with natural population partitions, but how natural populations are defined is a subject of continuing debate (Ryder, 1986; Moritz, 1994; Waples and Gaggiotti, 2006; Schaefer, 2006; Palsbøll *et al.*, 2006).

Two contrasting, but overlapping, views appear in conservation biology and fishery management. In one perspective, the conservation of populations representing major evolutionary lineages is thought to be important. Beyond the conservation of evolutionary legacy is the attempt to maintain the population processes that produce deep levels of diversity in a species (Moritz, 2002). Genetic variability has to be conserved to allow a species to adapt to environmental changes taking place on decadal and millennial time scales. On the other hand, the needs of fishery management are short term and require a greater resolution of population structure on smaller geographical and temporal scales. To this end, traits responding rapidly to environmental variability such as morphology, meristic counts and life history patterns have frequently been used most to define populations and stocks.

A major problem arises in the use of genetic methods for conservation and fisheries resource management, because evolutionary and ecological definitions of a population are mistakenly used interchangeably (Figure 4). Both kinds of populations are defined by the degree of connectivity among populations through the exchange of migrants (population structure). However, far less migration is required to maintain genetic cohesiveness among populations on evolutionary time scales than is required to produce demographic homogeneity among populations. The evolutionary population concept predominates in conservation biology, in which a major concern is the protection of genetic lineages, which allows a species to adapt to environmental changes. In fishery management, an ecological population may not be genetically distinctive, but may still show life history differences or geographical isolation requiring separate management.

Ecological definitions of a population, however, focus on interactions between individuals that influence the demographic characteristics of a population, including competition, age structure and birth and death rates. These kinds of variables are used to define stocks for the biomass assessments used to set harvest limits. From this ecological viewpoint, demographic independence between populations can still persist with much large amounts of immigration (Figure 4). A limited amount of data indicates that demographic independence between populations occurs when the proportion of immigrants (m) falls below 10% (Hastings, 1993). The key variable for management considerations, especially of marine species, is the proportion of migrants, m. However, models used to interpret genetic data yield only estimates of Nm, the number of migrants between populations. Another difficulty is that N represents population size integrated over recent evolutionary time and not necessarily the size of a contemporary population. Estimates of census size are also not useful for estimating N, because effective population sizes may be an order of magnitude smaller than census size (see below). Future research will focus on the development of simulation and modelling tools that integrate ecological and genetic data for particular situations.

2. MODELS OF GENETIC POPULATION STRUCTURE

The origins of genetic population structure in freshwater and riverine organisms are fairly well known. Both demographic and genetic populations are usually delimited by lake shorelines and watercourses that represent strong physical barriers to migration. Unexpected genetic similarities between populations can usually be explained by historical events, such as headwater captures, altered river drainages or gene flow in proglacial lakes after the last ice age. Some of the classic models of population structure [e.g. island model of migration (Wright 1940)] have been used effectively to estimate contemporary levels of migration in many species from molecular markers (Neigel, 1997). Populations of marine fishes, on the other hand, are not generally bounded by strong barriers to migration. Nevertheless, the genetic structures of marine populations can be influenced by spawning migrations (Ruzzante *et al.*, 2006), sea surface temperature gradients (Beare *et al.*, 1995; Attrill and Power, 2002) and currents and ocean frontal systems (Rocha-Olivares and Vetter, 1999; Shaw *et al.*, 2004).

Two contrasting models of population structure have been posed for marine fishes. Under a local, self-sustaining model (vagrant-member hypothesis, Sinclair, 1988), populations are adapted to local environmental settings and persist only when conditions allow uninterrupted cycles of spawning, growth and reproduction. The magnitude of gene differences between populations depends on effective population size, which influences genetic drift and gene flow, which tends to reduce population differences. An extension of this model incorporates the ephemeral nature of some populations by recognizing that regional extinctions and colonization occur in marine populations (Smith and Jamieson, 1986; McQuinn, 1997). This model predicts that subpopulation extinctions and recolonizations should lead to a mosaic pattern of genetic diversity and gene frequency heterogeneity.

Under the 'basin model' (MacCall, 1990), the most favourable habitats lie toward the centre of a species' geographical range. During ocean-climate instability, subpopulations at the edges of the species' range disappear by contracting toward the central favourable basin. Abundances in the centre of the range remain constant, even though the species as a whole is declining. This model is also echoed in the classical biogeographical models of Mayr (1970), who found that environmental factors were most important in regulating abundances at the periphery of a species' range. When these species represent 'straddling stocks', international cooperation is especially important in setting harvest limits. Subpopulations following this model might show gradients in gene diversity with the highest diversities in the centre of the range, where populations have been most stable. Considerations of these two models are important to formulating management policies and planning locations of marine protected areas.

Genetic data generally fail to show the high degree of isolation in open-ocean marine fishes predicted by Sinclair (1988). Genetic estimates of gene flow are high in most marine species (Table 1), implying the movements of tens and hundreds of individuals between subpopulations. Mitochondrial DNA data appear to support the basin model for California anchovy (Lecomte *et al.*, 2004), but support a mosaic model for European anchovy (Grant, 2005; Magoulas *et al.*, 2006). However, finer-scale differences have been detected among populations that are not isolated by obvious physical or hydrographic barriers (Hedgecock *et al.*, 1994; Ruzzante *et al.*, 1999). This chaotic variability is likely due to large reproductive variances among families (Hedgecock, 1994), rather than to isolation or adaptations to particular open-water habitats. The instability of marine waters on annual, decadal and millennial time scales likely prevents adaptations to specific areas. On a decadal scale, anchovy populations, for example, respond rapidly to small climate changes with range contractions and expansions (e.g. Cushing, 1982; Beare *et al.*, 2004).

3. LOSS OF GENETIC DIVERSITY

A major concern in conservation biology is the maintenance of genetic diversity (measured by average heterozygosity). Values of heterozygosity, however, are affected most by the frequencies of abundant genes in the general range of 0.10-0.90. Genes at low frequencies contribute little to heterozygosity. Ryman *et al.* (1994, 1995) pointed out that the store of gene variability represented by low-frequency genes may be important in adapting to changing environments. Large populations have a greater capacity for retaining low-frequency genes than small populations, but the relative loss of rare genes during a population crash is much greater in large populations. For example, consider two populations of sizes 10 000 and 100 000 000, which are at mutation drift equilibrium, but which are reduced to 1% of their original size (1 000 and 1 000 000). The loss of heterozygosity is negligible in both populations, but the small population retains 98% of the original gene number, while the large population retains only 1% of its genes.

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