International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report **IR-03-005**

Maintenance of Genetic Diversity: Challenges for Management of Marine Resources

Ellen Kenchington (Kenchingtone@mar.dfo-mpo.gc.ca)
Mikko Heino (mikko@imr.no)

Approved by

Ulf Dieckmann
Project Leader, Adaptive Dynamics Network

February 2003

Contents

Abstract

There are three general classes of threat to biodiversity at the gene level: 1) extinction, which results in complete and irreversible loss of genes; 2) hybridization, which may cause re-arrangement of co-adapted genes and loss of adaptability to local conditions, and 3) reduction of genetic variability within populations. While extinction avoidance is a fundamental management objective and hybridization can usually be dismissed in marine populations, the reduction of genetic variability within populations is a plausible threat and can occur in two ways. First, a decrease in population size may result in inbreeding. Normally, marine fish have very large population sizes, and commercial extinction is likely to occur long before populations are reduced to the level required for losses of genetic diversity due to inbreeding. However, when populations are very severely over-fished to small numbers, concerns associated with small population sizes and disruptions of migration between populations may become prominent. In particular, undetected populations within management units may be fished to this level before the situation is properly evaluated and remedied. Second, a reduction of genetic variability within populations may occur in a directed way, due to, e.g., selective fishing. Fishing is expected to generate selection on life history traits such as age and size at maturation; changes in life history traits influence the dynamics of fish populations, energy flows in the ecosystem, and ultimately, sustainable yield. We discuss management objectives designed to ameliorate genetic complications associated with small population size and fisheries-induced selection, and outline a management approach that may be useful when developing advice for maintaining genetic diversity.

About the Authors

Ellen Kenchington
Centre for Marine Biodiversity, Bedford Institute of Oceanography,
1 Challenger Drive,P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2

Mikko Heino
Institute of Marine Research Scholar P.O. Box 1870 Nordnes, N-5817 Bergen, Norway
and
International Institute for Applied Systems Analysis,
Schlossplatz 1, 2361 Laxenburg, Austria

Acknowledgments

We thank the members of the WGECO and WGAGFM in 2002 for the discussions and feedback on the issues formulated here, and K. Brander, U. Dieckmann and O.R. Godø for discussions on "Management of Adaptive Responses to Fishing". MH acknowledges the financial support by the Academy of Finland (Project 45928). EK wishes to thank the Norwegian Research Council for the opportunity to apply for travel assistance.

Maintenance of Genetic Diversity:
Challenges for Management of Marine Resources

Ellen Kenchington
Mikko Heino

1. Introduction

For many countries, the legal mandate for the preservation of biological diversity, including genetic diversity, follows from the acceptance of the Rio Declaration, thereby creating a demand for developing management strategies that recognize this issue. Scientific justification for conserving genetic diversity within and among populations stems from the need to: 1) maintain adaptability of natural populations in the face of environmental change; 2) preserve the potential future utility of genetic resources for medical and other purposes; and 3) minimize changes in life history traits (e.g., age- and size-at-maturation, growth) and behaviour (e.g., timing of spawning) that unpredictably influence dynamics of fish populations, energy flows in the ecosystem, and ultimately, sustainable yield.

The impacts of commercial fisheries on genetic diversity have received considerable attention in recent years in a wide variety of media, including journals, books, reports, conferences and workshops. Within ICES, the genetic effects of fishing have been included in the terms of reference for the ICES Working Group on the Application of Genetics in Fisheries and Mariculture (WGAGFM) in one form or another from 1995-2000, and were briefly discussed in the ICES Working Group on Ecosystem Effects of Fishing Activities (WGECO) report in 2000. This paper is derived from work the authors conducted during the 2002 meeting of the WGECO (ICES 2002, chapter 10).

Section 2 provides a background and assessment of the problems associated with the loss of genetic diversity through fishing practices using Northeast Arctic cod as an example of a species that experienced a loss of genetic diversity within a population. Section 3 suggests an appropriate course of action to protect genetic diversity based on the best available scientific evidence, and Section 4 provides conclusions and recommendations for establishing a process for protecting genetic diversity of exploited stocks and those suffering fishery-induced mortality.

2. Background

A gene is the fundamental hereditary unit that determines (or partially determines) a trait. The DNA sequence of a specific gene may not always be exactly the same among individuals. There may be some differences in the sequence, resulting in different variants of that same gene. Such alternate variants of a specific gene are called alleles and the number of different alleles can be used as measure of genetic variation. The different alleles of a specific gene often occur in different frequencies in different populations (allele or gene frequencies). The genetic variation of a species is therefore distributed both within populations, expressed as the different allele combinations between individuals (so called genotypes) and between populations (in the form of differences in occurrence and frequency of alleles between populations). Each measure provides an indication of the genetic diversity of a population. Natural selection acts within populations, while the genetic potential of the species to adapt to environmental changes depends on the total genetic diversity represented among populations.

There are three general classes of threat to biodiversity at the gene level: 1) extinction (population or species), which results in complete and irreversible loss of genes; 2) hybridization which may cause re-arrangement of co-adapted genes and loss of adaptability to local conditions, and 3) reduction in genetic variability within populations. This third threat can occur in a directed manner, due to fisheries-induced selection (e.g., Heino and Godø, 2002), or due to decrease in population size resulting in inbreeding (Laikre and Ryman, 1996).

Normally, marine fish have very large population sizes and the concern for loss of genetic diversity can appropriately be directed to the loss of variation within populations through selection caused by fishing. In most marine species, parents produce large numbers of offspring and there is large scope for local selection. However, when populations are very severely over-fished to small numbers, concerns associated with small population size (e.g., number of actual breeders, inbreeding etc.) and disruptions to migration between populations become prominent.

From a population perspective, it is immaterial whether or not the mortality induced by fishing is incidental. Many by-catch and other non-target species are subject to substantial fisheries-induced mortality, given the vast areas of seabed trawled each year, and the unselective nature of most fisheries (Alverson *et al.*, 1994). Consequently, fishing activities may also affect the genetic composition of non-target species.

The population structure of a species will determine what if any genetic impact results from a fishing-induces loss of spatial components. More subtle changes, inferred from phenotypic changes that are occurring irrespective of population abundance may be more difficult to demonstrate empirically, but can be estimated through modelling approaches. Consequently, objectives can be identified at a macro-level (e.g., number of spawning components, relative abundance of components, percent change in life history trait) to maintain genetic diversity under the Precautionary Approach. However, it will be more difficult to assign biologically meaningful reference points for these objectives. Unlike population dynamics models for which all parameters can be reasonably estimated and predictions evaluated, we cannot predict which aspects of genetic diversity will be important in the future or which losses in the past have influenced present day conditions.

Genetic variation among populations

Fishing is known to affect the spatial structure of populations. The result of this spatial alteration on genetic diversity will depend upon the migration patterns between populations. New animals may migrate from one population to another, and if they mate within the new population, they have the potential to contribute new alleles to the local gene pool. This is called gene flow. There are many theoretical types of genetic population structure (cf. Smedbol *et al.*, 2002); these range from complete *panmixia* where each individual has an equal probability of reproducing with any other individual, to highly structured populations with complete reproductive isolation. Complete panmixia was postulated for the European eel, but has since been refuted (Wirth and Bernatchez, 2000), and it is unlikely that panmixia occurs in marine species (although it is the null hypothesis for all genetic tests of population distinctness – see below). At the other extreme, subdivided populations with reproductive isolation are also not typical, except in situations of rare and very localized species with limited possibilities for larval dispersal (cf. Nielsen and Kenchington, 2001; Smedbol *et al.*, 2002). While the genetic structure of marine species is generally unknown, the *stepping-stone model* and its variants (Kimura and Weiss, 1964) are likely to be more relevant. In this model, a number of genetically distinct populations exist and are linked by gene flow. However, unlike Wright's *island model* (1931), the probability of gene flow from one population to another is dependent on the degree of geographic separation between populations. It is expected that genetic distance (a metric of differentiation) between populations will increase with geographic distance, i.e. there will be isolation by distance. A variant of this model is the source-sink situation, where a stable population (source) contributes migrants to smaller populations (sinks) that only exist due to the recurrent contributions from the source population (cf. Smedbol *et al.* 2002). It is critical to evaluate the genetic structure of a species in order to infer the genetic implications of the loss of components. Unfortunately, complex population structure is occasionally associated with species that demonstrate no obvious population discontinuities. Therefore, careful consideration of genetic data is often necessary to elucidate population interactions. For populations linked by gene flow, the organization of populations in time and space in conjunction with the ratio of within and among population variation are important to preserve to avoid negative genetic effects (Altukhov and Salmenkova, 1994). Fishing may result in the decimation of populations producing fragmentation, disruption of gene flow and local extirpation.

Taylor and Dizon (1999) describe the statistical approach commonly used to test for genetic structure among populations and discuss how this can result in management failure through loss of local populations. Typically, these tests are designed to test the null hypothesis, H_o, that populations have equivalent gene frequencies (panmictic), while the alternative hypothesis, H_A, is that populations are structured (not panmictic). A standard critical value (α = 0.05) is applied, emphasizing the importance of not concluding incorrectly that populations are genetically isolated, when, in fact, they are panmictic (a low Type I error). However, application of the precautionary approach might support the argument that it is a more serious error to incorrectly conclude that populations are panmictic when, in fact, they are reproductively isolated. In such cases the statistical goal should be a low Type II error rate, even if this comes at the cost of a higher Type I error rate. These authors advocate calculating β, the probability of failing to reject the Null Hypothesis of panmixia when populations are actually isolated, as well as setting the more traditionally controlled α. Their intent is to avoid an implicit prioritization of one type of error at the expense of the other. In an example given in their paper, Taylor and Dizon (1999) illustrate that by choosing an $\alpha = 0.05$, a $\beta = 0.60$ is unintentionally accepted, giving a result that is 12 fold (β/α) more likely to result in incorrectly pooling populations than an error that will incorrectly split them. In some cases it might be appropriate to equalize these errors ($\alpha = \beta$), although this will inevitably require large sample sizes and/or an increased number of markers. As many genetic studies are undertaken without consideration of management questions, a careful evaluation of the methodology is needed to fully appreciate the applied implications of these studies.

Genetic variation within populations

Physical and life history traits (phenotype) are generated by the genetic makeup of the individual, by the environment in which it lives (e.g., temperature, food availability) and by the interaction between the genes and the environment. Data on fish populations from many parts of the world have shown that removing large fish generally appears to favour the promulgation of slow-growing, early maturing fish (see reviews by Smith, 1999; Law, 2000). The challenge is to ascertain whether these changes are irreversible and a consequence of genetic alteration of the population or whether they are due to selected removals or a suite of other environmental factors such as temperature and prey fields. Put simply, is there a genetic difference between the fish removed and those left behind (Law, 2000)? Law and Grey (1989) and Heino (1998) have modelled the impact of a decline in age-at-maturation in Arctic cod and conclusions of work in progress (Dieckmann *et al.* 2002) suggests that the phenotypic response is consistent with selection-induced deterioration of genetic diversity. However, empirical data for these conclusions are generally lacking in marine species, despite the fact that the evolution of life history traits is a field of great interest, both in population biology and genetics.

However, a recent paper by Haugen and Vøllestad (2001) clearly documents evolution of grayling in Norway (*Thymallus thymallus*) in response to 48 years (8 generations) of intense and consistent selection caused by size-selective fishing (gill nets). The authors conclude that size-selective fishing has caused a rapid evolution towards earlier age-at-maturity, reduced length-at-maturity, faster early growth and slower late growth, and increased size-specific fecundity. Further, significant changes occurred over a 10-year period, well within the time scales of relevance to fisheries management. In this case, when the selection intensity was relaxed, age and length at maturity and length-at-age increased, indicating that the genes were still present in the population.

Population modelling is a powerful tool both for exploring the expected consequences of current exploitation regimes, and for experimenting with different management measures that might be adopted to mitigate unwanted selection pressures. It can also be used to assess the scope of these problems, which can in turn be used in risk assessments. One of the areas in which we are data deficient is in the estimation of the proportion of phenotypic variance which is inherited. In terms of quantitative genetics, this proportion is referred to as the heritability of a trait (h^2), and traits with low values of h^2 change more slowly than those with higher values. Mean values of h^2 have been determined from broad surveys of both traits and species (Mousseau and Roff, 1987), and salmonids produce estimates consistent with these values (cf. Law, 2000). However, extrapolation from culture conditions to the wild can only be indicative, because the specific environment defines the heritability of a trait. Calculations of heritability from the wild are dependent on identifying kinship structure, an elusive property in most marine species due to the large population sizes. Roff (1997) suggests that in the absence of better information, heritabilities for life history traits in the range 0.2-0.3 can be assumed, which means that 20-30% of the observed variation is due to the genes, while the remaining 70-80% is largely due to effects of the environment interacting with expression of those genes. To compensate for the lack of information on heritability, sensitivity analyses can be done using a range of heritabilities when modelling quantitative genetics and phenotypic data.

In the absence of direct genetic evidence, the dependence of phenotypes on environment can be characterized by a metric referred to as “reaction norms”. The reaction norm predicts the phenotype that follows from a single genotype as a function of the condition of the environment. The reaction norms themselves are presumed to be genetically determined. Thus, change in a reaction norm is indicative of genetic change. The idea of using maturation reaction norms can be traced back to Stearns and Crandall (1984), Stearns and Koella (1986) and Rijnsdorp (1993). Probabilistic extension of the methodology is necessary to make the reaction norm approach fully operational (Heino *et al.*, 2002a). Identification of traits under genetic selection using reaction norms may facilitate the identification of quantitative trait loci (QTLs) which could then be used to validate the models.

The special case of small populations

In all populations of a restricted size the frequency of particular alleles changes randomly from one generation to the next. This process, called genetic drift, may also result in loss of genetic variation. By chance some of the alleles that exist in the parent generation may not be passed on to their offspring. The smaller the population, the more dramatic the fluctuation of allele frequencies, and the faster the loss of genetic variation. Another consequence of small population size is inbreeding, i.e., the production of offspring from matings between close relatives. If a population is small and isolated, inbreeding is inevitable. In many species, inbreeding is coupled with reduced viability and reproduction, reduced mean values of meristic traits, as well as increased occurrences of diseases and defects, so called inbreeding depression.

The rate of genetic drift and inbreeding is not determined by the actual (census) population size, N, but by a parameter denoted "effective population" size or N_e. Typically, estimates of N_e are surrounded by large confidence intervals especially when inferred from gene frequency data. In certain situations, N_e can be quite precisely estimated from abundance surveys, e.g., with the breeding population of Atlantic right whale. Effective population size is nearly always less than N because generally not all individuals in a population are reproductive at spawning time. N_e depends on such factors as sex ratio, variance in family size (i.e., variability in numbers of offspring per individual), temporal fluctuations in numbers of breeding individuals, overlapping generations, etc. For example, for some species genetic variation will be reduced if the sex ratio of breeders departs from 1:1. It is much better (genetically) to have a population of 50 males and 50 females than to have one of 10 males and 90 females, yet both have 100 breeders. Similarly, the maximum genetic variation is produced in the population when all mating pairs produce equal sized families. In the case of the northern elephant seal, dominant bulls establish a harem and monopolize females, skewing the sex ratio through mating behaviour (Hoelzel 1999). Fishing practices that select one sex over the other also may, over time, cause a reduction of genetic diversity within populations.

Genetically small populations are unlikely to be of concern in marine fish with large census population sizes. For these species, commercial extinction is likely to occur long before populations are small enough to be inbred. However, hidden populations within management units may be fished to this level before the situation can be appreciated. Therefore, it is critical that the population structure of species be defined.

Case study of fisheries-induced selection on the northeast Arctic cod

The northeast Arctic cod (*Gadus morhua*) is one fish stock where consideration of genetic changes caused by fishing-induced selection have attracted attention. This stock is very large, and even when stock abundance reached record-low levels in the 1980s, the spawning stock consisted of tens of millions of fish. This description holds even if substructure is considered (Mork *et al.*, 1985). Thus, in this example, loss of genetic diversity in Northeast Arctic cod is considered in context of fisheries-induced selection (cf. Law, 2000).

During the first quarter of the 20th century, intensive harvesting of Arctic cod took place on the spawning grounds which are some distance from the feeding grounds. Under this scenario, cod with delayed maturation had a reduced mortality risk, while gaining in terms of increased size and, after maturation, increased fecundity. This historical selection pressure for delayed maturation may be responsible for the late maturation traditionally observed in this stock (Law and Grey, 1989) - the age-at-50%-maturity was 10 - 11 yrs before the 1940s (Jørgensen, 1990). Since around 1930 when the modern trawler fishery began, harvesting became size-selective for larger fish, indirectly favouring selection for earlier maturation. Effort was also transferred to the feeding grounds. Borisov (1978) raised the concern that high fishing pressure might select for earlier maturation in this stock. Indeed, the decline in age-at-maturation in this stock has been particularly strong (Jørgensen, 1990), and the year-classes born in the 1980s have a mean age-at-maturation of 6 - 7 yrs (Godø, 2000). Size-at-maturation has declined in parallel, from 89 cm (1940 year-class) to 74 cm (1989 year-class) (Godø, 2000). Assuming a cubic relationship between length and weight, this corresponds to a 42% decrease in weight of the first-time spawning cod (assuming a constant fecundity-to-weight ratio, the same decrease applies to fertility).

Analysis of the reaction norms for age- and size-at-maturation for this stock shows a significant temporal trend towards higher probability of maturation at a certain age and size (Heino *et al.*, 2002b). A quantitative genetics model is currently being developed to determine whether the observed rate of change is consistent with the selection pressures that have been present, and the preliminary results from this model are presented in this theme session (Dieckmann *et al.*, 2002).

Although there may be environmental effects that are not considered in the reaction norm analysis, it is probable that the change in reaction norms of the northeast Arctic cod has a genetic basis. However, the analysis also shows that phenotypic plasticity (in form of the so-called 'compensatory response', i.e., maturation at earlier age correlated with a higher growth rate) also explains an important part of the observed changes in age- and size-at-maturation. Partitioning of response to genetic and phenotypically variable components is not straightforward because these two factors are not fully additive. However, it appears that change in the reaction norm explains a larger proportion of the change in age- and size-at-maturation than change in growth does.

Theoretical studies indicate that decline in age-at-maturation could cause a major decline in sustainable yield from the northeast Arctic cod (Law and Grey, 1989; Heino, 1998). It must be emphasized that these models were designed to make only qualitative predictions and that the predictions of yield should be interpreted cautiously. Nevertheless, annual losses in sustainable yield of the order 10^5 tonnes appear to be possible. Thus, despite the uncertainty, these findings call for increased awareness of the possibility of adverse effects on yield. Earlier maturation will also result in smaller size-at-age after maturation, and, assuming that large fish are more highly valued than small fish, diminish the market value of the catch. In addition, it is possible that earlier maturation may further increase recruitment variability in this stock. The long spawning migration imposes an energetic stress that would be relatively larger for smaller individuals, and may affect egg quality in females. If feeding conditions before the migration are poor, the energetic stress might become too high for the fish maturing at small size, and they might either fail to reach the spawning grounds or delay spawning altogether. Likelihood of recruitment failure under poor conditions could therefore increase. On the positive side, it is unlikely that the stock could sustain the present-day exploitation regime if its maturation reaction norm was similar to its state prior to modern exploitation.

Management measures that would be necessary to mitigate selection pressures towards earlier maturation in northeast Arctic cod are, at the broad level, theoretically well understood (Law and Grey, 1989; Heino, 1998). The origin of this change in selection pressure is the shift of exploitation pattern: from selective removal of mature cod to unselective (with respect to maturity status) removal of both immature and mature cod. Increasing fishing pressure on mature fish and decreasing fishing of immature cod would diminish — and eventually revert — the selection on maturation given the large population size of the stock. However, the exact levels of selective and non-selective fishing mortality that would eliminate the selection pressure are not known, although the existing modeling results indicate that the emphasis should be strongly on selection for mature cod (Law and Grey, 1989; Heino, 1998). Size-selective harvesting strategies, which allowed undersized fish to escape, could potentially prove to be an alternative way of mitigating selection pressures towards earlier maturation. This possibility currently remains unexplored, although the evaluation would be technically possible and practically feasible, e.g. with the quantitative genetics model mentioned earlier (Dieckmann *et al.*, 2002).

One further consideration is that selection pressures are not necessarily symmetric. Fishing can create a very strong selection gradient for early maturation, whereas in the absence of fishing, late maturity is only weakly selected for (Law and Grey, 1989; Rowell, 1993; Heino, 1998). Decreasing fishing pressure assists in decreasing the selection pressures but may not easily reverse them. Thus, trying to restore genetic stock properties by reverting selection pressures is inherently more difficult than trying to slow changes by decreasing the selection pressures. Thus, considerable uncertainty surrounds the management implications. However, under precautionary approach to fisheries (FAO 1996), "where there are threats of serious or irreversible damage, lack of full scientific complexity shall be not used as a reason for postponing cost-effective measures to prevent environmental degradation" (excerpt from the Principle 15 of the

Rio Declaration of the UN Conference on Environment and Development, Rio de Janeiro, 1992). Therefore, there appears to be a strong case for incorporating consideration of genetic effects of fishing into the management of the northeast Arctic cod.

3. Managing genetic diversity

In this Section, a scientific framework for the provision of advice on genetic diversity is outlined. We propose a three-phase approach to the development of this advice: identification of management objectives, identification of appropriate reference points and/or definition of acceptable risk and development of a monitoring program (Fig. 1). Considerations for defining management objectives for maintaining genetic diversity within a species include:

1) genetic diversity among populations
2) population structure and relative abundance
3) within population genetic diversity
4) the current status of the species (endangered, threatened etc.)

The last consideration can be used to prioritize decision-making, which will become important because the management actions required when viable population sizes are intact are different from those needed when populations are small.

Management objectives

Any management regime requires clear management objectives that can be operationalized. When drawing examples from the literature, genetic diversity itself (e.g., number of alleles or genotypes) is not directly “managed” but the elements that influence it are. Thorpe *et al.* (1995) have suggested that the first priority of management plans should be to maintain populations in a natural setting to which adaptation may have occurred, and in which evolutionary forces may continue to act. Taylor and Dizon (1999) describe two similar objectives used by the US Southwest Fisheries Science Centre in La Jolla, California which are to: (i) maintain populations, and (ii) maintain the full geographic range of a species. Both of these examples address Consideration (1) and to a certain extent Consideration (3), however, they do not directly address the potential loss of genetic diversity within populations due to selective fishing or the relative abundance of populations. The latter is important in maintaining migration patterns (gene flow) and population structure, both potential consequences of exploitation. Examples of management objectives, which match those considerations, are provided in Table 1.

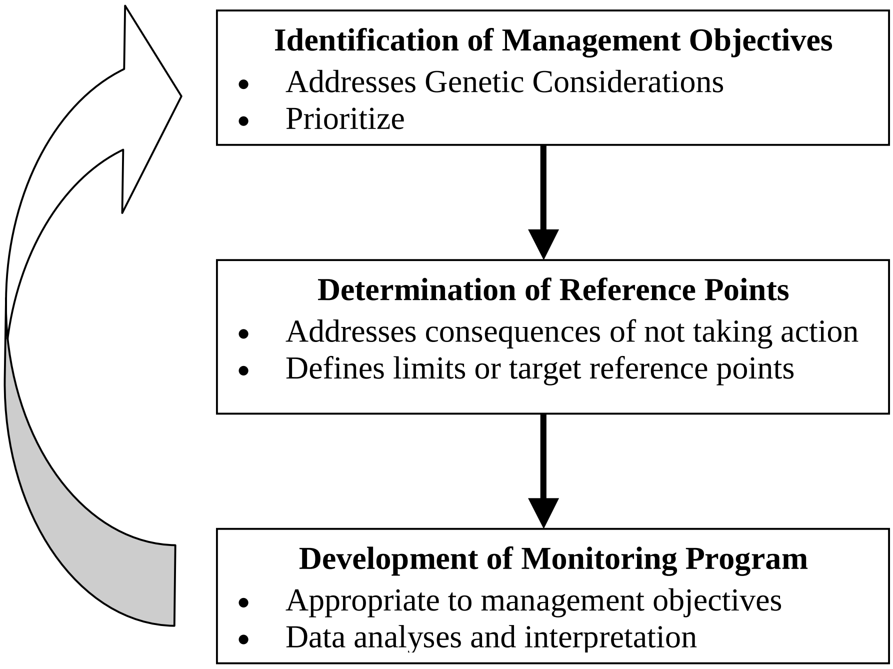

Figure 1. Three phases of approach to the development of advice for maintaining genetic diversity.

Table 1. Examples of management objectives to address generic concerns related to the loss of genetic diversity in marine species.

Consideration	Example Management Objective
1. Genetic diversity among populations	1. Maintain number of populations
2. Population structure and relative abundance	2. Maintain relative size of populations
3. Within population genetic diversity	3.1 Maintain abundance of individual populations
	3.2 Minimize fisheries-induced selection

With respect to selection-induced genetic impoverishment,, the mitigation options can be broken down further: (slow/stop/reverse) fisheries-induced selection on X. It is necessary to specify which component of selection is being addressed (“X”), e.g., selection on maturation, sex, etc. Also, as discussed in section 2, the management actions need to be specifically targeted if a reversal of selection pressure is desired, as opposed to a slowing. This may involve gear modification such as changes in mesh size, separator panels, or square mesh panels to alter selection and allow fish to escape.

Reference points?

The ICES framework for applying reference points to management objectives also can be applied to genetic diversity objectives. However, while target reference points may be established, reference points and limit reference points, as defined by ICES, are more problematic. ICES defines reference points as “specific values of measurable properties of systems (biological, social, or economic) used as benchmarks for management and scientific advice” (ICES, 2001). Their purpose is to flag decision points and therefore the consequences of not taking an action at a particular reference point should be clear.

One of the difficulties with determining minimum acceptable levels of genetic diversity is that the aspect of genetic variability that will be important for a species to adapt to environmental change in the future is unknown. We can deduce which genes under selection, that is quantitative trait loci, maybe important, and very few of these have been identified for any species. When phenotypic traits are used as a proxy of genetic diversity, it is easier to quantify the outcome of following specific management advice. Modelling has an important role in predicting the consequences of decisions, and in particular models that incorporate population and quantitative genetics are powerful. However, the specific actions, which will lead to a negative effect, are known, and these can be avoided. For example, we know that in most cases, the loss of populations will result in a loss of genetic diversity, although we cannot say that losing 1 of 5 is acceptable but losing 2 is not. Target reference points are “properties of stocks/species/ecosystems which are considered to be desirable from the combined perspective of biological, social, and economic considerations” (ICES, 2001). For genetic diversity, target reference points can be established. The biological target would be no loss, modified by social and economic considerations (Table 2).

Limit reference points are “a value of a property of a resource that, if violated, is taken as *prima facie* evidence of a conservation concern. By “conservation concern”, ICES means that there is unacceptable risk of serious or irreversible harm to the resource…” (ICES, 2001). Loss of *alleles* from a species represents an *irreplaceable* component of genetic diversity. The *irrevocability* of genetic loss combined with our inability to assess the consequences of not taking action, result in greater potential risks associated with any decision making process that allows for loss of diversity. Loss of alleles may qualify as a conservation concern if the risk is judged unacceptable, however determining the limits at which the resource is “harmed” will be problematic for the reasons discussed above. In this case the limit reference point may be very high and close to the target reference point.

Table 2. Example of biological target reference points for proposed management objectives with an example of a limit reference point (others to be determined (TBD)).

Proposed Management Objective	**Example Target Reference Point (Biological Perspective)**	**Example Limit Reference Point**
1. Maintain number of populations	1. Maintain all populations	1. TBD
2. Maintain relative size of populations	2. Maintain relative size of populations within X% of each other	2. TBD
3.1 Maintain large abundance of individual populations	3.1 Maintain abundance of individual spawning population above X%	3.1 $N_e >> 5,000$ spawners
3.2 Minimize fisheries-induced selection	3.2 No fisheries-induced selection	3.2 TBD

Because changes in *allele frequency* may be irreversible or at best very difficult to reverse, limit reference points will likely have to be set very conservatively because the negative consequences of exceeding the limit reference point will be difficult if not impossible to subsequently rectify. Nevertheless, limit reference points could be defined for some objectives, especially those applicable to within population genetic diversity (Table 2). For example, recent theoretical work suggests that successful breeding population sizes of 1,000 to 5,000 are required for long-term population viability (Lynch and Lande, 1998). If limit and/or target reference points can be established, genetic risk assessment (e.g., Currens and Busack, 1995; Allendorf *et al.*, 1997) may provide a framework for decision making in light of uncertainty and consideration of other factors (e.g., biological, economic and social).

Monitoring genetic changes

Methods identified for monitoring genetic diversity will depend upon the management objective. An effective monitoring program requires three phases: Identifying monitoring questions, identifying monitoring methods and the analysis and interpretation of information for integration into management strategies and the refinement of management objectives (Gaines *et al.*, 1999). Examples of monitoring questions include: What is the genetic diversity within a population or among populations? How has habitat fragmentation affected the genetic structure of a population or species (cf. Gaines *et al.*, 1999)?

Once these questions are established, the monitoring methodology can be determined. This includes both sampling design and choice of markers as well as consideration of derived indices. Genetic diversity can be measured at many different levels using a variety of markers. Markers that are ideal for identifying population structure (e.g., so-called neutral markers such as nuclear microsatellite arrays) are not generally useful for monitoring traits under selection. However, different types of markers or combinations of markers can be used to monitor temporal changes in genetic diversity to address specific questions related to the management objectives. With the development of high-throughput equipment with low operating costs, genetic monitoring programs have become affordable. An important constraint on addressing monitoring questions is the lack of historical data. Even where tissue exists, it is often preserved in formaldehyde, rendering the extraction of good quality DNA difficult. Given this constraint, it is recommended that tissue samples from research vessel survey catches be archived for future genetic analysis. The amount of tissue needed for genetic work is very small and hair, scales and otoliths (free from fixative) can be used.

In monitoring phenotypic traits, existing biological data from fisheries surveys is generally adequate to identify potential cases where fishing may have caused selection. However, it is important to consider direct environmental effects to disentangle the genetic component of variation. This requires either monitoring quantities that are robust to environmental variations, or monitoring, in addition to phenotypic traits, the relevant environmental variables that have a major influence on the phenotypic traits in consideration. The former option is preferable when possible. Reaction norms are an example of quantities that are robust to environmental variations. In particular, reaction norms for age- and size-at-maturation are expected to be useful for monitoring changes in maturation.

4. Conclusions

It is clear from the above discussion that managing genetic diversity in marine populations requires serious attention. Evidence that fishing-induced selection is causing genetic changes in fish stocks is currently accumulating (see other papers in this theme session), and the conventional wisdom that marine populations are so large that loss of genetic diversity due to small population size is being challenged. Moreover, it is clear that loss of genetic diversity, be it due small effective population size or directional selection, can have consequences that are undesirable from the human perspective. These undesirable consequences range from potential loss of productivity of marine resources (with easily quantified economic value) to loss of aesthetic or cultural commodities.

Table 3. The proposed process for the continued development of a mechanism for ICES to provide for 'genetic diversity' in management advice. ACE = ICES Advisory Committee on Ecosystems.

Task	**Lead party (ies)**	**Example Timeframe**
1. Review and development of considerations for maintaining genetic diversity	WGAGFM	March 2003
2. Review and development of management objectives to address genetic considerations	WGAGFM; WGECO	spring 2003
3. Evaluation of reference points and/or consequences of not addressing management objectives	WGECO; WGAGFM	spring 2003
4. Development of a list of quantifiable variables who values, individually or in combination, identify a significant threat to genetic diversity	WGECO; WGAGFM	spring 2004
6. Case studies reviewed under the proposed framework and strengths and weaknesses determined	WGAGFM; WGECO	spring 2004
7. Assessment of possible management responses for protection of genetic diversity and provision of commentary to ACE	WGECO; WGAGFM	spring 2004
8. ACE formulates advice to ICES customers	ACE	September 2004

Although the appreciation of conserving local populations is widespread in management of certain freshwater fisheries (i.e. migratory salmonid fishes), these ideas have not yet spread to management of marine resources. Similarly, concerns for the consequences of fisheries-induced selection were first raised in the context of freshwater fisheries, and the quasi-domesticated nature of many salmonid populations makes the issue of selection much more immediate than in marine fish populations. However, we believe that sustainable management of living marine resources requires management of genetic diversity. While the first steps of the process, to develop management advice in the ICES framework for preservation of genetic diversity, have already been taken in the Working Groups on the Application of Genetics in Fisheries and Mariculture (WGAGFM) and Ecosystem Effects of Fishing Activities (WGECO), this strategy is still very much in its infancy. Possible further steps to advance the process are outlined in Table 3.

References

Allendorf, F., Ryman, N., and Utter, F. 1987. Genetics and fishery management: Past, present, and future. In Population Genetics and Fishery Management. Edited by N. Ryman, N. and F. Utter. Washington Sea Grant Publications/ University of Washington Press, Seattle and London, pp. 1-19.

Altukhov, P., and Salmenkova, E.A. 1994. Straying intensity and genetic differentiation in salmon populations. Aquaculture and Fisheries Management 25 Supplement, 2: 99-102.

Alverson, D.L., Freeberg, M.H., Murawski, S.A., and Pope, J.G. 1994. A global assessment of fisheries bycatch and discards. FAO Fisheries Technical Paper 339, FAO, Rome.

Benton, T.G., and Grant, A. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. Trends in Ecology and Evolution, 14: 467-471.

Borisov, V. M. 1978. The selective effect of fishing on the population structure of species with long life cycle. Journal of Ichthyology, 18: 896-904.

Currens, K.P., and Busack, C.A. 1995. A framework for assessing genetic vulnerability. Fisheries, 20: 24-31.

Dieckmann, U., Heino, M., and Godø, O.R. 2002. A quantitative genetics model for the evolution of maturation reaction norms in age- and size-structured populations. ICES CM 2002/ Y:08.

FAO. 1996. Precautionary approach to capture fisheries and species introductions. Elaborated by the Technical Consultation on the Precautionary Approach to Capture Fisheries (Including Species Introductions). Lysekil, Sweden, 6-13 June 1995. FAO Technical Guidelines for Responsible Fisheries 2. FAO, Rome.

Gaines, W.L., Harrod, R.J., Richy, J., and Lehmkuhl, J.F. 1999. Monitoring biodiversity: quantification and interpretation. Gen. Tech Rep. PNW-GTR-443. Portland, Oregon: US Department of Agriculture, Forest Service, Pacific Northwest Research Station, 27 pp.

Godø, O.R. 2000. Maturation dynamics of Arcto-Norwegian cod. IIASA Interim Report IR-00-024. International Institute for Applied Systems Analysis, Laxenburg, Austria.

Haugen, T.O., and Vøllestad, L.A. 2001. A century of life-history evolution in grayling. Genetica, 112-113:475-491.

Heino, M. 1998. Management of evolving fish stocks. Canadian Journal of Fisheries and Aquatic Science, 55: 1971-1982.

Heino, M., and Godø, O. R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. – Bulletin of Marine Science, 70: 639-656.

Heino, M., Dieckmann, U., and Godø, O.R. 2002a. Measuring probabilistic reaction norms for age and size at maturation. Evolution, 56: 669-678.

Heino, M., Dieckmann, U., and Godø, O.R. 2002b. Reaction norm analysis of fisheries-induced adaptive change and the case of the Northeast Arctic cod. ICES CM 2002/ Y:14.

Hoelzel, A.R. 1999. Impact of population bottlenecks on genetic variation and the importance of life-history; a case study of the northern elephant seal. Biological Journal of the Linnaen Society, 68: 23-39.

ICES. 2001. Report of the Working Group on Ecosystem Effects of Fishing Activities, ICES CM/ACME: 09.

ICES. 2002. Report of the Working Group on Ecosystem Effects of Fishing Activities, ICES CM/ACME: xx.

Jørgensen, T. 1990. Long-term changes in age at sexual maturity of northeast arctic cod (*Gadus morhua* L.). J. Cons. Cons. Int. Explor. Mer., 46: 235-248.

Kimura, M., and Weiss, G.H. 1964. The stepping-stone model of population structure and the decrease of genetic correlation with distance. Genetics, 49: 561-576.

Laikre, L., and N. Ryman 1996. Effects on intraspecific biodiversity from harvesting and enhancing natural poppulations. Ambio, 25: 504-509.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science, 57: 659-668.

Law, R., and Grey, D.R. 1989. Evolution of yields from populations with agespecific cropping. Evolution and Ecology, 3: 343-359.

Lynch, M., and Lande, R. 1998. The critical effective size for a genetically secure population. Animal Conservation, 1: 70-72.

Mork, J., Ryman, N., Ståhl, G., Utter, F., and Sundnes, G. 1985. Genetic variation in Atlantic cod (*Gadus morhua*) throughout its range. Canadian Journal of Fisheries and Aquatic Science, 42: 1580-1587.

Mousseau, T.A., and Roff, D.A. 1987. Natural selection and the heritability of fitness components. Heredity, 59: 181-197.

Nielsen, E.E., and Kenchington, E. 2001. Prioritising marine fish and shellfish populations for conservation: A useful concept? Fish and Fisheries, 2: 328-343.

Rijnsdorp, A.D. 1993. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. Oecologia, 96: 391-401.

Roff, D. A. 1997. Evolutionary Quantitative Genetics. Chapman and Hall, New York.

Rowell, C. A. 1993. The effects of fishing on the timing of maturity in North Sea cod (*Gadus morhua* L.). In The exploitation of evolving resources. Edited by T. K. Stokes, J. M. McGlade and R. Law. Springer-Verlag, Berlin. Pp. 44-61.

Smedbol, R.K., McPherson, A.A., Hansen, M.M., and Kenchington, E. 2002. Myths and moderation in marine ‘metapopulations’? Fish and Fisheries, 3: 20-35.

Smith, P.J. 1999. Genetic resources and fisheries: policy aspects. In Towards Policies for Conservation and Sustainable Use of Aquatic Resources. Edited by R.S. V. Pullin, D. M. Bartley and J. Kooiman. ICLARM Conference Proceedings, 59: 43-62.

Stearns, S. C., and Crandall, R.E. 1984. Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. In Fish Reproduction. Edited by G. Potts and R. J. Wootton. Academic Press, London. Pp 13-33.

Stearns, S. C., and Koella, J.C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution, 40: 893-913.

Stephenson, R.L., and Kenchington, E. 2000. Conserving fish stock structure is a critical aspect of preserving biodiversity. ICES CM 2000/Mini:07.

Taylor, B.L., and Dizon, A.E. 1999. First policy then science: why a management unit based solely on genetic criteria cannot work. Molecular Ecology, 8 (Suppl. 1): S11-16.

Thorpe, J.E., Gall, J., Lannan, J.E., Nash, C., and Ballachey, B. 1995. The conservation of aquatic resources through management of genetic risks. In Conservation of Fish and Shellfish Resources: Managing Diversity. Edited by J. Thorpe, G. Lannan and C. Nash. Academic Press, San Diego. Pp. 33-46.

Wirth, T., and Bernatchez, L. 2001. Genetic evidence against panmixia in the European eel. Nature, 409: 1037-1040.

Wright, S. 1931. Evolution in Mendelian populations. Genetics, 16: 97-159.