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## **REPORT OF THE WORKING GROUP ON THE APPLICATION OF GENETICS IN FISHERIES AND MARICULTURE (WGAGFM)**

**3–6 May 2005**

**SILKEBORG, DENMARK**



**International Council for the Exploration of the Sea**  
**Conseil International pour l'Exploration de la Mer**

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## Executive summary

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The Working Group on the Application of Genetics in Fisheries and Mariculture (WGAGFM) met at the Danish Department of Inland Fisheries Lab at Silkeborg, Denmark from 3–6 May 2005. Attendance was good with nineteen present, twelve official representatives of their countries, and seven Chair-appointed experts. A new WG Chair for 2006–2008 was elected. Dr. E. Eg Nielsen of the Danish Fisheries Institute for Fisheries Research at Silkeborg replaces outgoing Chair, Dr. E. Kenchington of the Department of Fisheries and Oceans, Canada.

Five terms of reference were addressed at the meeting. The first dealt with the issue of climate change and the evolutionary ability of fish stocks to respond. The current and predicted rates of change greatly exceed any previous periods of climatic warming over evolutionary time. Faced with rapid temperature increases species can either move to higher latitudes or adapt to prevailing conditions. In the latter case the rate of change may exceed capacity to adapt genetically, with the problem being more severe for species with limited thermal tolerance. Biodiversity, which is fundamentally genetic diversity, will be reduced due to the loss of populations on the southern limits. Evolutionary processes will only slowly restore lost among-population diversity where a species is able to extend its range northward. With regard to phenotypic traits, the impacts are less predictable but, in general, a reduction in abundance and changes in traits would be expected. The WG proposed five recommendations related to this ToR.

Marine species are often characterised by high dispersal potential and annual migration to common feeding areas. These aggregations are often the target of high intensity fishing activities. Harvesting of mixed stocks can lead to overexploitation and risk of extirpation of minor population components when harvest rates are high. Information on spatial and temporal variations in stock composition in mixed-stock fisheries is therefore essential for effective fisheries management and conservation, and generation of stock estimates has long been an important tool in fisheries management. Genetic mixed stock analysis is a powerful tool for establishing differential individual population contributions to many mixed-stock fisheries. For these cases, it is likely to present the only way to address questions about specific stock contributions to fisheries. These techniques can be applied to both adult and juvenile aggregations yielding useful information even where levels of population structure among contributing populations is low. This information can be used to define exploitation rates of different populations in the mixed groups as well as helping to elucidate adult movement and juvenile dispersal patterns in numerous important fisheries species. The WG reviewed the various statistical methods commonly used in mixed stock analyses, and their applications to date. We then compared and evaluated the properties of the different methods, giving examples from Baltic salmon and Atlantic herring and discussed which are likely to perform the best in MSA in marine species. With the likelihood of increased usage and application of MSA to marine fisheries questions and problems, a number of specific recommendations are made with reference to the implementation and analysis of such studies.

Local adaptation in marine fish populations is a crucial topic and of utmost relevance to fisheries management and conservation biology. The topic is very complicated, as it encompasses theoretical and empirical information from a number of different disciplines, including general fish biology, ecology, evolutionary biology, physiology, population genetics, quantitative genetics, molecular biology and genomics. Further, we are at a point in time where novel conceptual, statistical and methodological developments have the potential to provide numerous ways to target the issue of local adaptation. The WG considered that the scope of ToRc was too complex to deal with in a single year. Rather than provide a cursory treatment, the WG discussed the outline in detail, providing the scope for further treatment of the topic. The WG recommends putting this ToR on the agenda for the 2006 meeting. We also recommend that

we modify the justification to include shellfish. The WG will work intersessionally to undertake this comprehensive review.

The WG considered the usefulness of Probabilistic Maturation Reaction Norms (PMRN) as an Ecological Quality Objective metric, including appropriate reference points, and provided some useful discussion for consideration by ACE. The principle of PMRN analysis is rather simple. When observing changes in life history traits, the challenge is to be able to disentangle variation due to phenotypic plasticity (the capacity of a genotype to express different phenotypes according to the environment experienced) and variation due to modifications in the genetic basis of the life history trait considered. Reaction norms allow disentangling these two components in the sense that they describe variation in the trait considered as a function of the environment, the genotype being fixed. A life history trait's reaction norm is thus a genotype's property and temporal trends in reaction norms are evidences of genetic evolution for the traits considered. This methodology is theoretically applicable to any life history trait as soon as one can access the related reaction norm. However, in practice, accessing the reaction norm requires being able to measure environmental variation affecting the life history trait considered, which is far from easy in the field. One exception is maturation, because growth (or size-at-age) is (supposedly) a proxy accounting for environmental variation affecting the maturation process.

Finally, the WG evaluated the evidence for genetic erosion and changes in life history characteristics of local stocks due to mariculture activity. Since the topic was last addressed (2003) there has been very little new data to evaluate. However, a new EU Concerted Action project has just been announced which should provide information about genetic impact of mariculture activities on wild populations, specifically on their genetic interaction. This project, entitled GENIMPACT, includes many WG members, and will deal with important marine species such as Atlantic cod, European sea bass, gilthead sea bream, turbot, halibut, scallops, mussels, oysters and European lobster. In the current document we discuss the topic and provide recommendations on the types of data that are needed to fully evaluate this potential impact.

## **1 Introduction**

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The Working Group on the Application of Genetics in Fisheries and Mariculture (WGAGFM) met at the Danish Department of Inland Fisheries Lab at Silkeborg, Denmark from 3–6 May 2005 to address its Terms of Reference (ToRs) for 2005 (Annex 1). The ToRs were decided in Council Resolutions adopted at the ICES Statutory meeting held in Copenhagen, Denmark in 2004. Dr. E. Kenchington (Canada) chaired the meeting, which opened at 0900 h on Tuesday, 3 May and closed at 1730, Friday, 6 May 2005.

### **1.1 Attendance**

Nineteen persons from ten countries were in attendance (Annex 2). Twelve were official members for their countries and seven were Chair-appointed members for 2005. The latter were registered with ICES prior to the meeting. Apologies were accepted from Filip Volckaert (Belgium), René Guyomard (France), Jean-Marie Sevigny (Canada), Marja-Liisa Koljonen (Finland), Sheila Stiles (USA), Svein-Erik Fevolden (Norway), Jochen Trautner (Germany), Roman Wenne (Poland), Gary Carvalho (UK), Jarle Mork (Norway) and Anna Kristin Danielsdottir (Iceland).

### **1.2 Venue**

The meeting was held at the Danish Department of Inland Fisheries, Danish Institute for Fisheries Research at Silkeborg, Denmark. The WG wishes to express our appreciation to Danish WG members Dorte Bekkevold and Einar Eg Nielsen, our hosts, for their kind hospitality. The

meeting venue was ideal with accommodation available at the Fisheries Centre itself and at a nearby hotel/conference centre.

### **1.3 Meeting format**

WGAGFM has an established framework for completing its ToRs. Prior to the meeting, small *ad hoc* working groups, under the leadership of one person, are established to prepare position papers related to specific issues in the Terms of Reference. The leader of the ToR is responsible for presenting the position paper in plenary at the meeting and chairing the discussion. Thereafter, volunteers undertake the task of editing and updating position papers according to points raised in the plenary discussions. The ToR leader is responsible for preparing the final report text from their sessions. Prior to the meeting an agenda is circulated to all members.

The 2005 WGAGFM meeting proceeded under the following direction: E. Kenchington chaired the business and general scientific session, including presiding over the election of the new chair; P. McGinnity chaired ToRa and d, D. Bekkevold chaired ToRb, E. Kenchington chaired ToRc, and G. Dahle chaired ToRd.

An election for the next Chair of the WG was held on 3 May. Prior to the meeting nominations were sought from the membership resulting in two candidates coming forward. Running for the position were Einar Eg Nielsen (Denmark) and Geir Dahle (Norway). Two other members expressed an interest in running in future years which bodes well for the WG. All official (Delegate-appointed) members of the WG were given an opportunity to vote, either through email prior to the meeting or at the meeting. The Chair oversaw the collection of votes and did not vote herself. The new Chair of WGAGFM for 2006–2008 is Dr. Einar Eg Nielsen of the Danish Institute of Fisheries Research at Silkeborg, Denmark.

## **2 Terms of Reference 2005**

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### **2.1 Document the evolutionary ability of fish stocks to respond to climate change by reviewing the information on the nature and rates of environmental change (ToR a)**

This text was based on a working paper prepared by P. McGinnity, E. Verspoor, B. Ernande, A.-B. Florin, R. Hanel and adopted by WGAGFM at Silkeborg, Denmark in 2005.

#### **2.1.1 Climate change**

The rates and characteristics of climate change have been well documented in the most recent Intergovernmental Panel on Climate Change report (2001), which outlines the magnitude and rate of contemporary and future climate change. Mean global temperature has increased by 0.5°C over the last 100 years and is expected to increase by a possible 3 °C over the next century. However, the increase is unlikely to be even across the world and is expected to be greater in boreal and arctic regions.

The North Atlantic Oscillation (NAO) is the dominant mode of recurrent atmospheric variability over the North Atlantic (Hurrell, 1995). A substantial fraction of the recent warming in this area is linked to the behaviour of the NAO. In particular there has been a trend in the NAO index from large amplitude anomalies of one phase in the 1960s to large amplitude anomalies of the opposite phase since the 1980s (Hurrell *et al.*, 2003). The existence of a deterministic relationship between greenhouse gas forcing and the NAO is strongly supported, and continuing major changes in the NAO can be expected in the future as greenhouse gas levels increase.

Trends in sea surface temperatures in the Northeast Atlantic, Northwest Atlantic, North Sea and Baltic Sea show a warming trend. However, as is the case globally, there is also spatial variation in the impact within the North Atlantic region, with some areas showing warming

trends (e.g., Barents Sea) and other areas becoming colder (e.g., Labrador Sea). A comprehensive review of the NAO and its influence on oceanic conditions in the North Atlantic is provided by Drinkwater (2003), Hurrell *et al.* (2003), and Visbeck *et al.* (2003).

### 2.1.2 Climate change and species

Climate is a major determinant of species distribution. Application of global meta-analysis to a large number of mostly terrestrial species has shown substantial range shifts averaging 6.1 km per decade toward the poles and significant mean advancement of spring life-history events by 2.3 days per decade over the last 40 years (Parmesan and Yohe, 2003). Numerous studies link the NAO index and the climate dynamics associated with NAO to the biology of the North Atlantic fauna (Drinkwater *et al.*, 2003). This suggests the observed changes are likely to also have a major impact on the majority of North Atlantic fisheries.

Drinkwater *et al.* (2003) and colleagues include studies of changes in biomass, distribution and growth of several commercial species of fish, as well as in the abundance of benthos, the spread of marine diseases, cetaceans, and sea birds. Their review spans the North Atlantic, and includes deep ocean basins, the continental shelves and coastal embayments. A recent report by Beaugrand *et al.* (2002) is fairly indicative of the biological response of keystone species which can be expected in the North Atlantic. They showed that strong biogeographical shifts in all copepod assemblages have occurred with a northward extension of more than 10° latitude of warm water species associated with a decrease in the number of colder water species. They conclude that these biogeographical shifts are consistent with recent climate changes in the spatial distribution and phenology detected for many taxonomic groups in terrestrial European ecosystems. They are also related to both the increasing trend in northern Hemisphere temperature and the North Atlantic Oscillation.

Overall, six major types of climate change effects on biological systems are identifiable (Parmesan and Galbraith, 2004):

- phenological changes (timing of important events in an organisms life cycle);
- physical and physiological changes;
- evolutionary changes;
- range shifts;
- community changes;
- ecosystem process changes.

In all categories, biological effects will involve genetic processes and have genetic implications, particularly those effects manifest across generations. Consideration of population genetics theory and the broad-based body of genetic evidence in the literature provides considerable insight into what these genetic processes and implications might be. As genetic processes underpin recruitment and fishery characteristics, as well as productivity and resilience over the long-term, it is important to understand the nature of these processes and implications, so that these can be taken into account in the strategic planning process associated with present and future fisheries management. Two key areas of management application are likely to be *in situ* local stock conservation and reintroduction programmes where stocks have been extirpated.

### 2.1.3 Genetic responses to climate change

#### 2.1.3.1 Overview

The potential impacts of climate change on fisheries can be expected to involve the character, abundance, and distribution of species; changes with implications for the level and distribution



of their exploitation. As such, these affects need to be taken into account in how fisheries are managed.

The potential impact of climate on fish character has implications for both intra-specific biodiversity and for phenotypic trait expression. Biodiversity, which is fundamentally genetic diversity, will be reduced due to the loss of populations on the southern limits and general reductions in abundance elsewhere through increased genetic drift. Evolutionary processes will only slowly restore lost among-population diversity where a species is able to extend its range northward. With regard to phenotypic traits, the impacts are less predictable but, in general, a reduction in abundance and changes in traits would be expected. Detailed consideration of existing information may allow identification of the probable nature of some of these changes, particularly expected geographical shifts.

Overall, fisheries productivity is expected to be depressed, though some fisheries will decline while others will expand. This scenario offers management both challenges and opportunities. It represents a challenge where fisheries are in decline, and an opportunity to bring in more sound management regimes where new fisheries emerge.

Within management timeframes, the overall genetic capacity and environmental range of a species (i.e., thermal niche – a trait determined by its evolutionary history) can be expected to remain the same. No overall evolutionary genetic response can be expected and the only possible response by a species can be to shift its range. If anthropogenic factors have reduced abundance and increased fragmentation the capacity of species, it may be more difficult for species to readjust their distributions to their new distributional optima, i.e., the normal evolutionary and demographic response to climate change may be impaired or slowed down. Where isolated populations exist on the colder limits of species' distributions, these can be expected to be lost or integrated into the advancing centre of the distribution. The result will be a loss of the unique biodiversity they represent. This will only gradually be restored over evolutionary timescales as new fringe populations at the new northern limit are established.

### **2.1.3.2 Ecosystem and community levels**

Species are fundamentally genetic entities, and genetic changes at these levels will relate to the loss or gain of species at the ecosystem or community level. The consequences of such changes will be the development of new community complexes with new and altered species interactions. Species responses to climatic change in a given biogeographical circumstance can be expected to be individual, depending on their biology with regard to factors as dispersal capacity and degree of thermal niche specialisation. Some species will benefit from climate change and others will be negatively affected, altering community structure. While ocean warming is likely to facilitate non-indigenous species invasions in the marine environment, there are few studies to evaluate the effects of climate change on this type of invasion. Studies by Stachowicz *et al.* (2002) on sessile marine invertebrates suggest that the greatest effects of climate change on biotic communities may arise from changing maximum and minimum temperatures rather than from changes in annual means. Consequently, global warming may facilitate a shift of dominance by non-native species by giving introduced species an earlier start, and increasing the magnitude of their growth and recruitment relative to native species.

### **2.1.3.3 Species level**

A species' range is defined and constrained by its genes and gene interactions at the genome level, and by the habitat to which it has access. The former determine the range of environmental conditions under which a species is able to develop and survive to reproduce successfully. At the same time, a species range will only include suitable habitat to which it has had historical access.

At the species level, there are two possible genetic responses to climate change. The first is the evolution of the species as a whole to adapt *in situ* within its existing distributional range to the new climatic regime. The second is to shift the species distribution to areas with conditions to which it is pre-adapted, i.e., its existing species niche. A review of the literature indicates the second option is more likely. Species establish in new regions more readily than they evolve a new range of climate tolerances (Davis and Shaw, 2001). The rate of climatic change occurring and predicted will be too great for evolutionary change to allow for a niche shift. Therefore the dominant genetic response at the species level will be for species to shift their ranges rather than adapt quickly enough where they are to the new circumstances. Support for this view comes from short-term observations of contemporary situations (Root *et al.*, 2003). However, long-term historical (paleoclimatic) studies can be even more insightful. Hewitt (2000) provides a good review of research in this area. Given global climate has fluctuated widely in the past 3 million years, with dramatic periods of global cooling and warming, an inescapable consequence for most living organisms is great changes in their distributions. These changes are expressed differentially in boreal, temperate and tropical zones, and can be expected to have consequences for the genetic character of affected species. Evolutionary in nature, they will involve the distribution of variation within and among a species' constituent populations. Though species are not expected to change (extend or shift) their niches, genetic changes will occur at the population level within a species and may lead to overall species' niches becoming more limited. In some situations where there is no new suitable habitat for a species to shift into (e.g., a shelf-constrained species), the range of a species may contract in the absence of any niche change.

With regard to fish, few longer-term historical studies have been carried out. The few, mostly unpublished, that have, give useful insight and more research on the historical responses of species distributions to climate change in the past is needed. Such studies would help to understand in specific detail the likely responses of particular fish species to future global climate change.

#### **2.1.3.4 Intra-specific evolutionary level (population level)**

Most, if not all, species are composed of multiple, distinct genetic populations. These will respond individually to the particular changes in their local climatic conditions. These responses may, or may not, lead to changes in the overall genetic character of a species, and the niche this defines. However, as stated previously, it may lead to niches becoming more constrained and the overall range of a species being reduced. Theory and available evidence provide a good perspective on genetic changes expected at the population level and their biological implications. Though a detailed review of the literature is not presented, the reader is referred below to some key references. Only a basic outline of what genetic consequences can be expected is provided.

A species genetic response will be determined by the way it is structured into genetic populations and each population will respond differently depending on its specific genetic character and its location within the overall species' range. For example, smaller populations with less variation may respond differently from large populations which are more variable. Populations at the warming trailing edge of a species' distribution, which is shifting in response to a warming climate, will have no more capacity to adapt and they will be deprived of gene flow from pre-adapted populations as none of these exist. This latter point is supported by observations from the fossil record (Davis and Shaw, 2001). Although examples of persistence through repeated periods of unfavourable climate are documented in the fossil record, the record of extirpations suggest that limits to adaptation are greatest during periods of rapid change, such as predicted for the future. Thus populations at the warmer margins will be lost while the species' range expands at the colder end of the existing distribution.

In the centre of the distribution, many local populations are likely to have genetic variation that will allow an evolutionary response, at least in the short- to medium-term, through the adjustment of gene frequencies. Thus in this situations many populations should be able to compensate for the climate changes they experience. However, if climate change is too rapid then the adjustment may not be quick enough and significant depression of population abundance may still occur. Where populations are already depressed or small, extinction could occur, though the habitat may in the longer term be re-colonised from the larger regional meta-population complex, assuming such a complex exists. This may or may not be the case.

At the northern edge of the distribution, migration is expected to lead to the introduction of adaptive genetic variation from central parts of the distribution. At least a component of this variation will be suited to warmer conditions and once integrated be able to help these populations to evolve to cope with the new conditions. However, again, this may not occur sufficiently quickly where climate change is rapid relative to the dispersal capacity of the species in question. In this regard, the abundance of the species in the source populations will also be an important factor (Gomulkiewicz and Holt, 1995). This may be depressed by anthropogenic factors such as over exploitation or habitat degradation leading to a slower adjustment. Following the genetic input in these previously isolated populations, there may initially be some outbreeding depression (Kirkpatrick and Barton, 1997) prior to fitness increases due to natural selection on the new spectrum of genetic variation. At the same time, migration from populations at the colder edge of the distribution in many cases should lead to the colonisation of emerging suitable habitats.

Species distributions can be expected to shrink where there is no scope for expanding species distributions into newly emerging habitat. This will be the case for arctic species which are already widely distributed in this climatic region. Also, genetic diversity found in these populations that is important to adaptation in these extreme cold environments can be expected to be lost through natural selection. They will not be transferred to populations in new arctic habitats. Where species have a very narrow thermal niche and no suitable new habitat emerges, they can be expected to go extinct, e.g., species currently confined to the high arctic.

Mean population fitness will be reduced and lead to population reductions as climate changes and populations become less well adapted. Loss of genetic variation from a species will be accelerated due to increased genetic drift as well as the extinction of populations at the trailing edge of the distribution. In the northern hemisphere some species show a decline in genetic variability from the centre to the leading edge of the shifting range of the species. This is believed to reflect stochastic loss of variation due to repeated founder events during the course of post-glacial range expansion (Hewitt, 2000). At the same time, different types of genetic variation may be affected in different ways during this process, for example where some variation is affected by epistasis (Hard *et al.*, 1993). A loss of genetic variation among populations will also occur on a species wide basis where a species is unable to shift its range and only suffers range reductions.

Lande and Shannon (1996) have discussed the role of genetic variation in supporting adaptation and population persistence in changing environments. They point out that long-term preservation of biodiversity requires understanding not only of the genetics and demography of small populations but also of the ecology and evolution of abundant species. In their paper, they show that in constant or unpredictable environments genetic variance reduces population mean fitness and increases the risk of extinction. In predictable, or highly variable, environments genetic variance appears essential for adaptive evolution and population persistence. As such, it is worth considering whether levels and patterns of distribution of within and between population variation in species of fish can serve as a useful indicator of their ability to cope with climate change.

Anthropogenic factors have reduced abundance and increased fragmentation of many species. This may impair or slow down as the normal evolutionary and demographic response to climate change and thus affect the capacity of a species to readjust its distributional range. Where they exist, isolated populations on the colder limits of species' distributions can be expected to be lost or integrated into the advancing centre of the distribution with a loss of the unique biodiversity they represent. This will only gradually be restored over evolutionary time scales as new fringe populations at the new northern limit are established and existing population evolve new genetic variation.

Limitations on a population's adaptive potential are various. For example, for terrestrial species, the extent of land currently committed to urban and agricultural use represents a considerable, novel impediment to range shifts, and in many cases of gene flow among populations (Stockwell *et al.*, 2003). For marine fish, contemporary evolution as a consequence of fishing might have limiting effect (Olsen *et al.*, 2004). To keep pace with current climate change projections for the 21st Century, range shifts at rates of 300 to 500 km per century will be required. This is in contrast to commonly observed migration rates in the past of 20 to 40 km per century. Even the exceptional migration rates documented in the fossil record, of 100 to 150 km per century, are thus far below the rates required to track predicted climate changes in the future.

Transplant and laboratory experiments should be able to provide insight on this point. Opportunistic studies, e.g., on high temperature cooling waters emanating from a nuclear power plants, can provide useful insights into fish ecosystem response to increasing temperature. Studies undertaken by Sandström (1995) have identified ecosystem, species and population changes as a consequence of such opportunistic studies.

The rate of evolutionary response to selection on a specific trait, e.g., a physiological trait involved in heat tolerance, depends on the magnitude of genetic variation present for that trait and on the intensity of selection. Rapid adaptation to changing climate might be predicted from these findings, yet, whenever adaptation depends on change in multiple traits, genetic interdependence among the traits may retard the evolutionary response (Rodriguez-Trelles and Rodriguez, 1998). Thus rapid adaptive responses may have very large genetic costs.

#### **2.1.3.4.1 Intra-specific physical, physiological, and phenological levels (within populations)**

Two important considerations in the assessment of how climate change will impact organisms are:

How close organisms are to their thermal limits in nature;

An understanding of how organisms respond to increasing habitat temperatures, especially the degree to which organisms are able to adjust, or acclimatise, in other words their thermal sensitivity (Portner, 2001).

Populations are composed of different genetic types, whose proportions are determined by gene frequencies, gene linkage and selection processes. In a given population, this distribution can be expected to be optimised for the mean recent historical environmental conditions encountered and influenced by levels of gene flow from other populations. This distribution will be adjusted selectively toward some new more optimal distribution as climate change occurs, in so far as the variation is adaptive with respect to habitat temperature and other correlated environmental variables. However, even if climate change exceeds the rate at which populations are able to adjust evolutionarily, then there will still be non-genetic changes. Including physical, physiological and phenological character shifts, these may appear heritable but simply reflect changes to the genotype-environment interactions of existing genes. For any given genotype, there will be a range of potential phenotypic outcomes which are depend-

ent on the environment in which the genotype finds itself. The possible range of this type of phenotypic plasticity is known as the reaction norm for a given trait.

Most analyses of the biological effects of climate change have been correlative and not examined the underlying causal mechanisms behind the observed effects. To understand cause and effect it is necessary to examine the physiological processes limiting thermal tolerance (Pörtner, 2001). The most critical of such processes are tied to an organism's aerobic scope, i.e., its capacity to deliver the needed oxygen to the cellular machinery to make survival and successful reproduction possible. In terms of thermal adaptation and limitation, the functional capacities of oxygen delivery systems are set to be optimal between the average highs and lows of environmental temperatures, along the lines of the idea of symmorphosis presented by Taylor and Weibel (1981), i.e., there is no spare capacity. Temperature adaptive shifts in gene expression serve as a foundation for physiological acclimation, e.g., thermal tolerance. Losses in the capacity for temperature mediated gene expression, including the absence of heat shock response, may reduce the ability of populations (and species as a whole) to acclimate to increased temperatures.

For a population whose environment moves beyond its historical environmental limits or capacity, this means that existing genotypes will increasingly become dysfunctional and generate new phenotypic responses in an effort to cope. This response will lead to the changes in population character and reductions in abundance, something, which will continue until evolution is able to bring the population to a new genetic optimum for the new environmental context. Thus if the environmental change continues to outstrip a population's capacity for evolutionary change, these impacts will be an ongoing, unresolved issue.

An overview of thermal tolerance ranges of tropical, temperate and polar bivalves and other ectotherms, compiled by Peck and Conway (2000) suggests that tolerance windows are wider in tropical and temperate species than in polar stenotherms, indicating that adaptation to permanently low temperatures in polar areas leads to a narrowing of the tolerance window. Despite the likely occurrence among species (and populations) of generally similar requirements for temperature-adaptive shifts in gene expression (Gasch *et al.*, 2000), species or populations that fall into different regions of the stenotherm to eurytherm spectrum may have distinctly different capacities for acclamatory regulation of transcription (Somero 2005).

#### **2.1.4 Climate change and mariculture**

Climate change will have a number of impacts on mariculture. Changes to sea level rise and temperature changes will have a direct impact on the species cultured in a given area and will indirectly influence other factors such as oxygen, disease, and the occurrence of toxic algal blooms. The industry may turn to biotechnology and genetic manipulation, in addition to traditional breeding programs, to produce species better adapted to temperature rises, and even to toxins and diseases. Additionally, the frequency and severity of extreme weather events are projected by global climate models. This may lead to an increase in the frequency of escapes. None of these concerns are novel and many have been addressed previously by the WGAGFM, however, it is likely that managers will be called upon to alter previous risk assessments to incorporate these expected changes.

#### **2.1.5 Recommendations**

- 1) Synthesize existing information on species distribution, ecological and physiological limits (niche), population structure and population variation in phenotypic traits to model the probable changes to fish species distributions for various climate change scenarios. This should also encompass modelling of historical change in fish abundance and distribution related to historical climate change. For example, this work is already underway for cod in the northeast Atlantic. This exercise would provide information pertinent to future fisheries management. At the same time keystone or

indicator species should be identified which can be used to monitor actual responses to climate change.

- 2) Identify genetic responses to anthropogenic impacts that are likely to influence distribution and abundance dynamics suggested in models developed in the above. Also as non-climatic influences dominate local short-term biological changes it is important to account for these, in order to understand biological trends due to climate change.
- 3) Include genetic studies in ongoing and future temperature tolerance experiments. Undertake research to identify Quantitative Trait Loci (QTLs), as opposed to just markers, important in temperature response. This will be important in monitoring genetic response in populations to temperature change.
- 4) Incorporate data provided in the first recommendation into future single species and multi-species long-term stock assessment projections. There is an assumption in species stock assessment that the environmental processes that underlie the relationship between stock and recruitment are stable over long time periods (termed, stationarity). In a period of rapid climate change this will not be the case (non-stationarity).
- 5) Take into account understanding of contemporary evolution in response to climate change in the areas of *in situ* local stock conservation and reintroduction programmes where stocks have been extirpated.

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## **2.2 Evaluate methods and provide recommendations on the application of mixed-stock and assignment analysis to elucidate stock components, with an emphasis on marine fishes and fisheries (ToRb)**

This text was based on a working paper prepared by D. Bekkevold, M.-L. Koljonen (inter-sessionally), J. Coughlan, E. Dillane, M. O’Sullivan and O. Vasin and adopted by WGAGFM at Silkeborg, Denmark in 2005.

### **2.2.1 Introduction**

Marine species are often characterised by high dispersal potential and annual migration to common feeding areas. These aggregations are often the target of high intensity fishing activities. Harvesting of mixed stocks can lead to overexploitation and risk of extirpation of minor

population components when harvest rates are high. Information on spatial and temporal variations in stock composition in mixed-stock fisheries is therefore essential for effective fisheries management and conservation, and generation of stock estimates has long been an important tool in fisheries management (Begg *et al.*, 1999; Shaklee *et al.*, 1999). These estimates have commonly been based on analysis of variance in morphological and meristic characters, such as scale patterns (Marshall *et al.*, 1987), otolith characteristics, variance in vertebrae numbers (e.g., ICES, 1991), and from artificial tags (Ihssen *et al.*, 1981). In marine species however, the resolution of such markers is commonly low and estimates are accordingly associated with high statistical uncertainty. With the development of high through-put genetic marker analysis tools, such as microsatellite DNA analysis, estimates can, however, now be generated using genetic mixed stock analysis (hereafter abbreviated MSA). Various statistical methods are available, and several have proven highly successful in applications to salmonid mixed stock fisheries, both in the Pacific and in the Atlantic. In spite of the great potential of the approach, applications in marine species are still rare.

Here, we first review the various statistical methods commonly used in MSA, and their applications to date. We then compare and evaluate the properties of the different methods, giving examples from Baltic salmon and Atlantic herring and discuss which are likely to perform the best in MSA in marine species.

### 2.2.2 Statistical MSA models

MSA approaches are based on comparing allele frequencies in samples of individuals from the mixed stock (hereafter referred to as the ‘mixture sample’) with allele frequencies observed in baseline samples from the populations assumed to contribute to the mix (hereafter referred to as ‘baselines’). Limitations to genetic mixed stock analysis are set only by limited genetic differentiation among baseline populations contributing to the harvest. Several statistical models have been developed to estimate relative stock contributions. Three main types of approach are described and compared here, two of which are based on mixture modelling, and one that is based on an individual assignment approach: 1) Maximum-Likelihood based models, 2) Bayesian models, and 3) Assignment methods. The recommendations provided are based on the capabilities of three software packages associated with each of these three methods (although it should be noted that a range of packages are currently available).

MSA has traditionally been based on **maximum likelihood estimation** (MLE) using allozyme data (Fournier *et al.*, 1984; Pella and Milner, 1987). This method determines the relative contributions of baseline stocks with the highest likelihood of providing the observed multilocus genotypic frequencies in the catch sample. The genotype frequencies in the separate baseline stocks are estimated from the baseline samples, assuming Hardy-Weinberg/Linkage-Equilibrium conditions, and using the observed allele frequencies. Confidence intervals for stock proportions are generated via a bootstrapping method, namely, by generating empirical distributions of the maximum likelihood stock composition estimates for many re-sampled baseline and mixture samples. The bootstrap evaluation accounts for multinomial sampling variation in stock composition of the mixture sample, uncertainty in the genotype frequencies because of sampling error in estimates of allele frequencies, and uncertainty in sources of individuals because of overlap of genotype distributions among baseline stocks. The software SPAM (Devebec *et al.*, 2000) is a commonly applied tool for MLE based MSA.

The software BAYES using **Bayesian statistics** has more recently been developed for stock composition estimation by Pella and Masuda (2001). Following this method, posterior distribution combines the information on baseline stocks with that on the stock-mixture sample to estimate both the stock composition of the mixture sample and the genotypic composition of the baseline stocks. The stock group proportion estimates are expressed in terms of probability distributions, which can be included in the fisheries management assessment model. This approach also allows for inclusion of non-genetic baseline information, such as spawning time



and morphology. Okuyama and Bolker (2005) also recently developed an alternative Bayesian model which also allows for inclusion of other information, such as baseline population sizes and hydrography.

Some studies have applied **individual assignment analysis** (IA) to estimate relative compositions in mixture samples (e.g., using the software GENECLASS; Cornuet *et al.*, 1999)). Following the procedure each mixture individual is assigned to the baseline stock in which the frequency of its genotype is the greatest (Cornuet *et al.*, 1999; Luikart and England, 1999). The individual assignment tests partition the possible genotypes into assignment classes corresponding one-to-one with the baselines, such that each class is composed exclusively of the genotypes whose frequencies are highest in its associated baseline. Regardless of assignments made of other mixture individuals, each mixture individual is assigned to the baseline of its genotype's assignment class. Because their genotype distributions overlap, mixture individuals include genotypes of incorrect assignment classes, and such individuals are misclassified to another baseline in which these genotypes are most frequent. After each individual has been assigned to a baseline, the genotype frequencies among mixture individuals are not used further and their uncertain baseline sources are treated as if known and correct. A further discussion of why assignment methods are inappropriate for most MSA applications is given in Koljonen *et al.* (2005). As the approach is widely used we evaluate and compare some of its features together with MSA applications.

### 2.2.3 Evaluation of model performance

The three commonly used MSA paradigms can all be used in certain 'perfect' situations such as may occur among highly differentiated freshwater or terrestrial species. However, there are a number of problems associated with MSA applications to marine fish and shellfish. These are related to their species characteristics (large population sizes, large geographical ranges, massive dispersal potential) and a lack of complete and detailed genetic and biological information.

Before embarking on MSA of marine fish species it is important to clearly define the specific objective in terms of addressing particular fisheries questions or problems. Whereas in some cases there is a requirement for information merely on presence or absence of particular populations within mixed aggregations, in other instances proportional contributions of various populations may be needed for effective management. The definition of the fisheries question will drive both sampling strategies and analysis approaches. If individual origin is of concern, assignment analysis should be applied, whereas if composition of mixed stock is of concern, mixed stock analysis should be applied. In terms of sampling strategies, in an ideal situation, all individuals would be sampled from all potentially contributing populations and the mixed aggregation. These would then be screened with sufficient genetic markers to allow discrimination of populations and unambiguous assignment of individuals and proportions. In reality this is often not achievable. Because of incomplete sampling and ambiguous population structuring, Bayesian MSA paradigms will be more appropriate in many situations. Table 2.2.3.1 summarises the most common scenarios in marine fish MSA applications, and a discussion of these follow below.

**Table 2.2.3.1. Summary of appropriate applications of the different methods**

IS METHOD APPROPRIATE WHERE:	MLE METHODS	BAYESIAN METHODS	ASSIGNMENT METHODS
There are low levels of population differentiation?	No	Yes	No
There is incomplete sampling of baselines?	No	Yes	No
Estimates for low contributing populations are of interest?	No	Yes	Yes
Presence or absence of a particular population needs to be established?	Yes (but with low confidence)	Yes	Yes (but with low confidence)
The genetic marker being used is characterised by few alleles?	No	Yes	No
There are rare alleles?	No	Yes	Yes
Non-genetic information can be incorporated?	Sometimes	Yes	No

In the first case, marine species are often characterised by low levels of population differentiation. Whereas as MLE, and to some extent assignment methods, work well in situations involving highly structured species, Bayesian methods can still identify population contributions in the absence of significant differentiation among baseline populations. Similarly, where not all baseline populations have been identified or sampled, the Bayesian approach appears to give the best contribution estimation based on the available baseline data. When some baselines contribute relatively low proportions of individuals to the mixed stock, or where there is large variance in population contribution, CML methods will tend to overestimate the proportion of less important stocks in the mixture. All three approaches will give at least some information as regards presence or absence of particular stocks in a mixed fishery; however both MLE and assignment methods have low confidence levels associated with the statistical output.

The choice of genetic marker will largely be dictated by available technology in particular laboratories. Although highly variable microsatellites are the preferred markers for all MSA applications at the present time, Bayesian methods are the most suitable for analysing data produced from lower variability loci such as allozymes and mtDNA. Assignment analysis and MLE can produce erroneous results when dealing with markers characterised by low variability. Similarly, the presence of rare alleles in contributing populations and mixtures can cause significant problems for MLE methods which are not apparent when Bayesian or IA approaches are used.

A large amount of existing data on population structure and migrations in marine species comes from non-genetic studies. It may be of significant value to include such information in MSA applications. At present the only viable option for incorporating non-genetic information are Bayesian methods.

Bayesian methods of MSA generally appear to have the fewest shortcomings when addressing questions relating to marine species. They are capable of dealing with lower levels of population differentiation than either maximum likelihood or assignment methods. This was illustrated recently by Koljonen *et al.* (2004) who compared conditional maximum likelihood (CML) estimation and the Bayesian method using the same microsatellite data in self-assignment tests. The mean percentage of correct estimation over the baseline stocks improved by 10%, from about 87% for CML to 97% for the Bayesian method. The maximum downward bias for an individual baseline stock was 23% for CML estimation and only 8% for the Bayesian method. The mean error for CML was 12.9% and for the Bayesian method 3% (Koljonen *et al.*, 2004). Self-assignment tests are optimistic with respect to the bias and precision of estimation as compared with test samples drawn independently from the baseline stocks. Nevertheless, they provide valid comparisons of estimation methods. The Bayesian

method improved the estimates notably in the most difficult cases, i.e., in stock pairs of high similarity. For instance, the proportion of correct estimation for one Baltic salmon stock was 70% with CML and 91% with the Bayesian method (Koljonen *et al.*, 2004).

Limitations to genetic mixed stock analysis are set mainly by lack of detectable genetic differentiation among baseline populations contributing to the harvest. Past MSA studies have been based on both allozyme and mtDNA haplotype data, but analysis of more variable markers like microsatellites are likely to significantly increase attainable precision for most marine species. In Atlantic salmon from the Baltic Sea, Koljonen *et al.* (2004) for example found that numbers of alleles were generally only 2 or 3 for allozyme loci, whereas the number of alleles ranged from 8 to 32, with a mean of 17.8, alleles per microsatellite locus. In simulation studies these authors found that the precision was over three times as high for microsatellite data (3.8%) as for allozyme data (13.7%) when assessed as the mean standard error in MLE (Koljonen *et al.* 2004).

In some cases, detailed information is available about genetic markers exhibiting high population resolution. In Atlantic cod, variation in a single locus with two alleles has for instance shown to offer good distinction between populations of north-east Arctic cod and Norwegian coastal cod (Sarvas and Fevolden, 2005), and the locus would, despite low levels of polymorphism, be a good candidate marker for MSA, when attempting to generate estimates for contributions from the two populations in mixed-stock situations.

Despite initial set-up costs, genetic MSA methods offer several advantages for the estimation of stock proportions compared to non-genetic methods. Compared to tagging approaches, there are no costs associated with the actual tagging, tags are not lost, and there is no need to consider the possible effects of the external tags on the viability and catch ability of the fish. Moreover, all fish are tagged for life, and studies can therefore be conducted on fishes that cannot be tagged by other methods, e.g., wild fish in remote areas or newly hatched fish in releasing programmes. Wild stocks in particular can be studied on an equal basis with hatchery stocks. Most importantly, it is recognised that physical tags cannot be passed on to progeny. With genetic stock identification, the time and place of sampling can be chosen more freely and precisely than with external tagging, as these are not dependent on preceding tag and release programmes. Further, there is no need to consider changes in the probability of the tags being returned by fishermen. Most MSA analyses based solely on morphological traits use information for characters which are highly environmentally determined, and hence are likely to be influenced by phenotypic plasticity, and to a lesser degree specific population origin.

#### **2.2.4 Applications**

Mixed stock analysis and individual assignment have been widely applied in genetic stock identification of salmonid populations (e.g., Beacham *et al.*, 2004; Galvin *et al.*, 1995; Potvin and Bernatchez, 2001; Primmer *et al.*, 2000; Vasemagi *et al.*, 2001). As stated above, IA methods are more appropriate for the validation of population structure rather than evaluating the composition of mixtures. This is because such methods deal only with individual multilocus genotype data when assigning individuals to baseline populations. Therefore they should only be used when one is interested in traits associated with the individual. MSA provides a more dynamic approach to the partitioning of mixed stocks, by building upon estimates of the probability of a fish observed in the mixed fishery having the same genotype of a fish in one of the baseline populations (Kalinowski, 2004).

While all these methods have been widely used in salmonids, their application to marine fish stocks have remained limited to date. Ruzzante *et al.* (2000) used a maximum likelihood method to estimate putative stock components of a mixed stock fishery for Atlantic cod (*Gadus morhua*) near the Gulf of St. Lawrence. Wirgin *et al.* (1997) used mitochondrial DNA

haplotypes to investigate mixed stock composition of Atlantic coast striped bass (*Morone saxatilis*) in Chesapeake Bay. However with regard to the other commercially important ICES quota species few examples are yet available.

Preliminary results from a microsatellite based, Bayesian MSA study in Atlantic herring demonstrate that even in marine fishes exhibiting modest differentiation (Pairwise  $F_{ST} < 1\%$ ) the statistical power associated with stock estimates can be very high, and that the MSA approach can contribute detailed information about migratory behaviour of individual populations and about mixed stock compositions. Due to the relatively low differentiation among individual spawning components, statistical power was too low to determine contributions from individual spawning components. However, the analyses could be carried out on a regional basis (i.e., performing the analysis for contributions from respectively the North Sea, Skagerrak, inner Danish waters and Western Baltic components). Simulation studies showed that individual stock composition estimates could be estimated with more than 90 % precision, even for population components contributing individuals in low proportions (<10%). Analyses of effects of mixed stock sample size further indicated that in herring, and presumably other marine fishes exhibiting modest levels of differentiation, fairly large sample sizes (>100) are required to successfully demonstrate contributions from less important populations (Figure 2.2.4.1). Analyses of mixed stocks from the Skagerrak further demonstrated strong temporal and spatial variation in contributions from individual populations that was hitherto unknown to managers.

The potential for management strategies using MSA is extremely high. Another obvious application of MSA methods is related to monitoring success in stocking or ranching of species of mixed population origin in mariculture or areas uninhabited by wild conspecifics (e.g., Ruzzante *et al.*, 2004). Even where population boundaries are not clearly defined, MSA methods have been shown (in non-marine species) to have enormous potential for the correct discrimination of stock components as long as sufficiently variable genetic markers, such as microsatellites, are employed. Evolving statistical and analytical methods (such as the newly developed Bayesian paradigm) are likely to improve potential applications and precision of MSA even further in the near future.

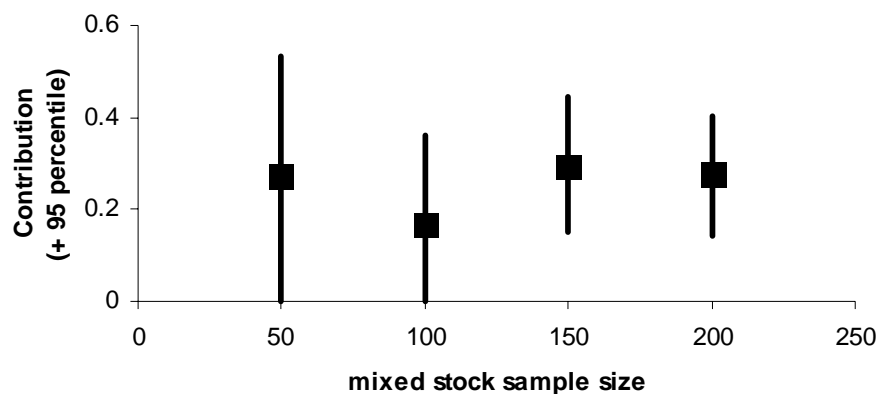


Figure 2.2.4.1. Example from Atlantic herring MSA showing the effect of mixed stock sample size on point estimates of stock contribution, with bars indicating 95 percentiles of estimate.

### 2.2.5 Recommendations

Genetic mixed stock analysis is a powerful tool for establishing differential individual population contributions to many mixed-stock fisheries. For these cases, it is likely to present the only way to address questions about specific stock contributions to fisheries. These techniques can be applied to both adult and juvenile aggregations yielding useful information even where

levels of population structure among contributing populations is low. This information can be used to define exploitation rates of different populations in the mixed groups as well as helping to elucidate adult movement and juvenile dispersal patterns in numerous important fisheries species. With the likelihood of increased usage and application of MSA to marine fisheries questions and problems, a number of specific recommendations can be made with reference to the implementation and analysis of such studies.

- 1) Given the large potential of the MSA approach to fisheries management, the application should be extended to all exploited species, if at all appropriate and possible.
- 2) The MSA approach should be used to evaluate currently applied stock separation methods based on morphological traits.
- 3) Prior to undertaking MSA analyses, elucidate the statistical power associated with the required level of resolution of stock proportions by applying simulation studies based on standard analyses of genetic population structure.
- 4) Include all potential contributors to the mixed stocks in baseline samples, if possible. Although some techniques allow for missing baselines, precision and accuracy can be reduced in these cases.
- 5) Baseline samples should represent spawning aggregations. Sample sizes should inversely reflect levels of differentiation and should in most cases constitute a random sample of ca. 100 individuals. Different baseline samples should contain equivalent numbers of individuals. The need for directed, rather than opportunistic, sampling strategies is emphasized.
- 6) Include temporal data as part of the core-research in MSA applications. As population characteristics might change to a greater or lesser extent over time (as a result of within-population dynamics in response to, e.g., environmental changes, random genetic drift and fisheries) it is important to test for temporal stability of allele frequencies within and among baseline samples. Tests for temporal stability should be conducted among cohorts and over generations.
- 7) Mixed-stock sample sizes should reflect the number of potential baseline contributors. In general, an increased number of mixed-stock individuals are required as the number of populations contributing to the stock increases. A minimum sample size of 100–200 is recommended for most applications but considerably more (or in some cases less) may be required in certain situations.
- 8) The use of highly polymorphic markers such as microsatellites is recommended for species with limited *a priori* information about genetic structure. Where low variability markers, such as allozymes and SNPs, are being used, precision will in most cases be increased by including many loci.
- 9) Determining mixed stock proportions, with the highest statistical precision, is best achieved using a Bayesian approach (e.g., Pella and Masuda 2001). This is due to its superior statistical properties along with its capability for handling, e.g., missing baseline information, rare alleles and novel alleles in mixture samples.
- 10) We recommend that ICES take the lead in developing initiatives to establish central repositories for archiving baseline samples. These samples can be used in temporal stability investigations and also be of use in monitoring temporal changes in population contributions to mixed-stocks. Furthermore, it is unknown which species will be of interest in future applications and the collection of samples now will facilitate elucidation of existing structure in these species for later comparison.
- 11) Include, where possible, information from non-genetic data (e.g., morphometric, meristic, otolith morphology and microchemistry, parasite loading data; oceanographic and physical habitat information, and the results of tagging experiments are also important). These can be of utility to help define and interpret the results of MSA.
- 12) We recommend increased cooperation by strengthening networking between laboratories examining fisheries questions; especially those spanning international boundaries. Calibration of marker sizes, alleles and the use of the same or at least overlapping suites of loci will greatly increase the amount of information available.

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### **2.3 Synthesize the evidence and methods for detecting local (genetic) adaptation in marine fishes (ToRc)**

This text was based on a working paper prepared by G. Carvalho, M. Møller Hansen, E. Eg Nielsen, E. Gosling and T. Cross and adopted by WGAGFM at Silkeborg, Denmark in 2005.

This ToR was suggested for the 2005 WG meeting, and prior to the meeting an outline for a position paper was produced. The WGAGFM discussed the outline in detail and concluded that local adaptation in marine fish populations is a crucial topic, of utmost relevance to fisheries management and conservation biology. At the same time, the topic is very complicated, as it encompasses theoretical and empirical information from a number of different disciplines, including general fish biology, ecology, evolutionary biology, physiology, population genetics, quantitative genetics, molecular biology and genomics. We are at a point in time where novel conceptual, statistical and methodological developments have the potential to provide numerous ways to target the issue of local adaptation. Therefore, addressing this ToR in depth requires a very thorough literature review, and the WG recommends putting this ToR on the agenda for the 2006 meeting. We also recommend that we modify the justification to include shellfish.

The WG discussed and developed an extended outline for discussing and reviewing the topic at the 2006 meeting.

### 2.3.1 Annotated outline for ToRc

#### **Local adaptation in marine fish populations: a review of methods and evidence**

##### *What is local adaptation?*

Adaptation is a broad term, which encompasses both genetic and non-genetic factors by which an individual adjusts to specific environmental conditions. Here, we focus exclusively on adaptations that have a genetic basis. **Local adaptation** is present when an individual exhibits higher fitness (in the Darwinian sense) in its indigenous environment compared to a foreign environment due to different selection pressures in the different environments. For example, in a “reciprocal transplant” experiment Nissling and Westin (1997) found that egg buoyancy was an inherited trait, with values differing between individuals sampled in the Belt Sea and in the Baltic proper. Sea (neutral egg buoyancy was obtained at  $14.5 \pm 1.2$  psu and 20–22 psu, respectively).

Obviously, local adaptation requires genetic variability. Genetically based differences in a given trait are due to different alleles at one or more loci that affects the trait. It also follows that in order for a population to respond to future environmental changes, genetic variation must be present at ecologically important genes. This is referred to as **evolutionary potential**, and in order not to reduce a population’s evolutionary potential it is important not to deplete genetic variability within the population.

- A short introduction to quantitative genetics will be included in the 2006 ToR.
- All phenotypic traits have an environmental and a genetic component. Methods exist that can partition these components.

##### *Which factors affect local adaptation?*

- Local adaptation is essentially a result of the relative magnitude of three evolutionary forces; selection, migration (gene flow) and genetic drift. Different local selection pressure promotes local adaptation. Genetic drift counteracts local adaptation, because random genetic changes can become a more powerful evolutionary force than directional selection. Gene flow among populations experiencing different selection regimes decreases local adaptation, depending on the rate of local selection relative to the rate at which non-adaptive alleles are being brought into the population by gene flow.
- Populations must experience different selection regimes. In the case of marine fishes this could encompass a variety of factors, such as different salinities, temperature, food availability, predation pressure, and pathogens and parasite fauna.
- Heritability of traits and strength of selection. The higher the heritability, the greater the response to selection for a particular trait if differential selection is operating.

##### *Which types of traits are involved in local adaptation?*

- Morphological traits
- Life history traits
- Physiological traits
- Behavioural traits
- Traits important in sexual selection



### ***Relevance of local adaptation to fisheries management***

- Local adaptation is one of the most significant components of intraspecific biodiversity.
- Knowledge on local adaptation in marine fish populations is crucial in order to predict if depleted or extinct populations can be effectively replaced by recolonisation from other populations. Are local population so locally adapted that it is unlikely that they can be replaced on a historic time-scale by individuals from other, neighbouring populations of the same species. This includes both natural recolonisation and artificial restocking.
- Knowledge of local adaptation can be used to predict response to harvesting and environmental change.
- Adaptation to local ecosystems (abundance of prey and predators) could lead to negative effects if ecosystems are altered due to human exploitation.
- Local adaptation could be important for deciding which populations should be used for founding new aquaculture strains.

### ***Detecting local adaptation in the marine environment is a challenge***

- Marine environments cover vast areas and often no obvious boundaries are detectable between environments.
- Identifying genetic population structure in marine fishes remains difficult. Population sizes of many commercially important species are commonly very large, and if that translates into high effective population sizes ( $N_e$ ), this is expected to lead to very little genetic drift and thereby low genetic differentiation at neutral molecular markers (as supported by numerous empirical studies). The lack of clear physical boundaries in the ocean also facilitates the possibilities for gene flow. Consequently, it is not known whether low genetic differentiation reflects high effective population sizes and low gene flow, high effective population sizes and high rates of gene flow, or low effective population sizes and high rates of gene flow. The only thing that is certain is that the low genetic differentiation observed among most populations of marine fishes cannot at the same time reflect low effective population size and low levels of gene flow. If effective population sizes are high and gene flow low then there is a high potential for local adaptation, despite low genetic differentiation at neutral markers. In contrast, if migration rate is high then the likelihood of local adaptation is low.
- There is very little knowledge about rates of gene flow among marine fish populations. The magnitude of effective population size and its relationship to census population size remains controversial. Some studies suggest surprisingly low effective population sizes in marine fishes despite high census population sizes, whereas other studies suggest high effective population sizes and temporal stability.

### ***Methods for detecting local adaptation in marine fish populations***

- Analysis of local adaptation can be done in both an indirect way, where the potential for local adaptation is assessed, and in a direct way, where local adaptation is demonstrated.
- **Indirect approaches:** Assessing the potential for local adaptation involves estimating the magnitude of gene flow and effective population size using neutral molecular markers and assuming arbitrary selection coefficients (e.g., representing “weak” and “strong” selection). Based on the relative magnitude of these parameters it can then be determined whether local adaptation is likely to occur. For instance, Adkison (1995) developed and applied such an approach to predict the likelihood of local adaptation in Pacific salmon, and this method has also been used to assess the possibility of local adaptation in anadromous brown trout (Hansen *et al.* 2002). Another possibility is to use the approach of Hendry *et al.* (2001) which focuses on quantitative traits rather than single loci. Based on the magnitude of differences at a quantitative trait between two populations, knowledge or assumptions about heritability of the trait, assumptions about selection coefficients and estimates of gene flow between populations it can be assessed if gene flow from one population to the other constrains local adaptation for the specific trait.
- A classical way to assess (but not prove) local adaptation is to investigate the relationship between allele frequency clines and environmental variation.
- A further possibility is to analyse relationships between genetic population structure and elements of marine landscapes (e.g., temperature and salinity). A published example from Baltic Sea herring is expected to be available soon.

**Direct approaches:**

**Common-garden experiments** denote set-ups where individuals from different populations are reared in a common environment. This should eliminate all environmental variation and leave only genetically based differences in quantitative traits between populations. In practise, however, maternal effects pose a significant problem which must be accounted for.

- The simplest common garden experiments involve just keeping individuals from different populations in the same environment and measuring differences among populations at quantitative traits.
- Common garden experiments can also be used to measure relative fitness of individuals from different populations in an identical environment. A variation of this is to transplant individuals between different environments and measure fitness in indigenous versus foreign environments.
- Finally, common garden experiments can be used to estimate additive genetic variation ( $V_A$ ) at quantitative traits. As different populations are reared in the same environment the variance components are directly comparable and the differentiation among populations at quantitative traits,  $Q_{ST}$ , can be estimated.  $Q_{ST}$  can be directly compared to differentiation at neutral loci,  $F_{ST}$ , and if  $Q_{ST} > F_{ST}$  then this implies that differences among populations at the trait is maintained by local selection, i.e., evidence for local adaptation.
- **Candidate genes** are coding genes assumed to have a known function. If genetic variation is studied at candidate genes that are supposed to be ecologically important, then this can provide evidence for local selection and thereby local adaptation. This can be achieved using a number of different statistical tests, such as outlier tests comparing genetic differentiation at the candidate loci to differentiation at neutral loci. If differentiation is significantly higher at candidate loci than at neutral loci then this would imply that local selection is acting at the candidate loci.
- Quantitative traits are affected by both inheritance and the environment and are typically polygenic. **Quantitative trait loci (QTL)** denote loci that affect a quantitative trait. In reality, the specific loci are often not identified, but it is possible to identify molecular markers (for instance microsatellite loci) linked to the coding loci. This is done by constructing a linkage map of molecular markers and then analysing the specific trait of interest among individuals in a fullsib family cross. If there are alleles at a locus that segregate along with a specific variant of the trait, then this is assumed to be a QTL. Accordingly, QTLs can be used for detecting local adaptation.
- **Genomic scan** denotes analyses of a large number of genetic markers ( $>>50$ ) randomly distributed throughout the genome. The genetic markers applied are usually AFLPs, RAPDs (the quality and reproducibility of this technique is questionable) and microsatellites. If genomic scans are conducted for different populations, then the degree of genetic differentiation ( $F_{ST}$ ) can be estimated for each individual marker, and it can be assessed if some of the markers are “outliers” and thereby potentially subject to local selection. The method does not in itself provide evidence for local adaptation, but it provides important information on questions such as how much of the genome that is actually subject to local selection. Moreover, genomic scans and QTL analysis can be combined, thereby providing information about the function of markers suggested to be subject to local selection.
- **Microarray analysis.** Global gene expression can be analysed using microarray technology. This can provide important information on which genes are expressed under certain environmental conditions. What would be really interesting to know in the context of local adaptation is whether or not fish from different populations exhibit similar gene expression under common garden conditions.

***Evidence for local adaptation in marine fishes***

There are very few examples that illustrate local adaptation in marine fish populations. Examples can be found in Conover *et al.* (2002)

### *Future priorities*

- Evaluate environmental gradients
- Investigate candidate genes and genomics
- Undertake long-term studies and integrate approaches
- Obtain quantitative genetics information from selective breeding programmes for marine fish species.

### **2.3.2 Recommendations**

- 1) Continue work on this ToR for the next WG meeting and provide a review based on the outline presented here.

### **2.3.3 References**

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## **2.4 Evaluate the usefulness of probabilistic maturation reaction norms as ecological quality objectives (EcoQOs) as an early warning signal for the negative impact of fishing and other anthropogenic activities (ToRd)**

This text was based on a working paper prepared by P. McGinnity, B. Ernande and E. Kenchington and adopted by WGAGFM at Silkeborg, Denmark in 2005.

ICES, through its various expert groups, is developing a framework for an ecosystem approach to fisheries management. This framework is being advanced in three areas. First, by broadening techniques used to model fish populations so that they consider not just single stocks but also their interactions with the wider ecosystem. Second, by developing an improved understanding of how the marine ecosystem works, including the effects of climate, oceanography, etc., and third, through an understanding of the effect of fishing and mariculture on the marine ecosystem (Frid, 2003).

The framework includes the development of tools to measure and monitor the state of the ecosystem, or “ecological quality”. According to the Working Group on the Ecosystem Effects of fishing pertinent definitions are as follows (WGECO, 2001):

*Ecological Quality (EcoQ)*: Ecological quality of the surface water is an overall expression of the structure and function of the aquatic systems, taking into account the biological community and natural physiographic, geographic and climate factors as well as physical and chemical conditions including those resulting from human activities.

*Ecological Quality Objective (EcoQO)*: EcoQO is the desired level of EcoQ relative to the reference level.

*Reference points:* In ICES advice regarding fisheries, reference points are specific values of measurable properties of systems (biological, social or economic) used as benchmarks for management and scientific advice. They function in management systems as guides to decisions or actions that will either maintain the probability of violating a pre-determined risk tolerance, or keep the probability of achieving a reference point above a pre-identified risk tolerance. There will be multiple reference points for any single property of a system, each serving a specific purpose.

*Reference levels:* In OSPAR usage, reference level began as a level of EcoQ where the anthropogenic influence on the ecological system is minimal. It became clear that it could be very difficult or impossible to determine such reference levels, when systematic monitoring of properties related to the EcoQ began well after pristine conditions were perturbed.

*EcoQO reference level* has been defined as the level of EcoQO where the anthropogenic influence on the ecological system is minimal.

The same working group has established a set of EcoQs metrics, which can be used for monitoring (WGECO, 2001):

- a) Spawning stock biomass in the North Sea;
- b) Local availability of North Sea sand eels for black legged kittiwakes;
- c) Proportion of large fish and hence the average weight and average maximum length of the fish community, based on input from WGFE and Assessment Working Groups;
- d) Density of sensitive (e.g., fragile) species;
- e) Density of opportunistic species;
- f) Presence and extent of threatened and declining species in the North Sea.

However, to date no metrics have been proposed to directly monitor aspects of genetic diversity. WGAGFM's ToR d from 2004 considered the use of reaction norms to evaluate the genetic impact of selective fishing on the maturation process of target species. At that time the WG considered that probabilistic reaction norms might serve as suitable EcoQOs as an early warning sign of the negative impact of fishing and other anthropogenic activities.

## **2.4.1 Genetic impact of human activities on living marine resources**

### **2.4.1.1 Overview of human activities impacting the genetic composition of living marine resources and general consequences**

Identified causes of human mediated potential genetic change in fish populations are: (i) introgression; (ii) human-mediated disease spread; (iii) genetic effects of culture (selective breeding); (iv) loss or changes of inter- and intra-specific variation as a consequence of human impact on the environment (climate change, habitat destruction); (v) loss or changes of inter- and intra-specific variation by selective fishing.

Genetic diversity is the product of thousands of years of evolution, yet irreplaceable losses can occur very quickly (c.f. Nielsen and Kenchington, 2001). This diversity is important for long-term ability of a species to adapt to extrinsic factors such as pollution or climate change, and loss of populations (extirpation) most likely equates to loss of adaptive variation. Initially, conservation focus was on the protection of species, but with the growing body of evidence of within species differences, there has been an increasing awareness of the need to protect intra-specific variation (cf. Nielsen and Kenchington, 2001). Yet fisheries management units are often discordant with population structure, making one of the priorities, and common objectives of genetic research being to elucidate population structure. A parallel awareness appears to have evolved in the thinking of fisheries managers. Initially there was a focus on the impact of fishing on stock numbers and stock biomass, but with a growing body of evidence, such as application of probabilistic maturation reaction norms (PMRNs etc.), there has been growing

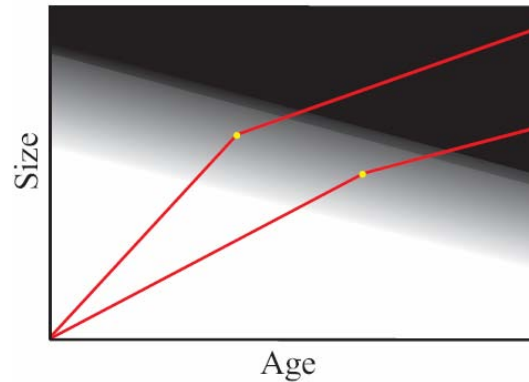
awareness of the need to address the evolutionary effect of fishing on target and by-catch species.

#### **2.4.1.2 Fisheries-induced evolution and probabilistic maturation reaction norms (PMRNs)**

In commercially exploited fish stocks, fishing is the major cause of mortality. Since all fish species were genetically adapted to the environmental conditions experienced prior to intensive exploitation, the current, drastically altered conditions cannot possibly leave their life-history patterns unaffected. In other words, fishing not only decreases the abundance of fish in exploited fish stocks, but also changes their genetic composition (Law and Grey, 1989; Stokes *et al.*, 1993; Palumbi, 2001; Conover, 2002; Ashley *et al.*, 2003).

However, although selective pressures imposed by fishing has been recognized (Stokes *et al.*, 1993; Law, 2000; Heino and Godo, 2002; Stokes and Law, 2002), no substantive basis that fishing actually induced life history evolution that could affect yield of the resource was available until very recently. One major breakthrough in this area was made possible by the development of probabilistic maturation reaction norm (PMRN) analysis (Heino *et al.*, 2002a,b; Barot *et al.*, 2004a), which allowed demonstrating that most of the documented changes in the maturation properties of exploited fish populations are indeed evolutionary responses, and not mere effects of phenotypic plasticity.

The principle of PMRN analysis is rather simple. When observing changes in life history traits, the challenge is to be able to disentangle variation due to phenotypic plasticity (the capacity of a genotype to express different phenotypes according to the environment experienced) and variation due to modifications in the genetic basis of the life history trait considered. Reaction norms allow disentangling these two components in the sense that they describe variation in the trait considered as a function of the environment, the genotype being fixed. A life history trait's reaction norm is thus a genotype's property and temporal trends in reaction norms are evidences of genetic evolution for the traits considered. This methodology is theoretically applicable to any life history trait as soon as one can access the related reaction norm. However, in practice, accessing the reaction norm requires being able to measure environmental variation affecting the life history trait considered, which is far from easy in the field. One exception is maturation, because growth (or size-at-age) is (supposedly) a *proxy* accounting for environmental variation affecting the maturation process (Stearns and Crandall, 1984; Stearns and Koella, 1986). Reaction norms for age and size at maturation describe the age and size dependence of an organism's maturation process and were first introduced by Stearns and Koella (1986). Maturation is not, however, fully determined by age and size alone. The residual effects not captured by age and size introduce an unavoidable probabilistic element to the description of the maturation process. Taking this probabilistic nature of maturation into account is crucial if maturation reaction norms are to be estimated from data. The probabilistic reaction norm for age and size at maturation (Heino *et al.*, 2002b) is defined as the probability that an immature individual, depending on its age and size, matures during a given time interval. A probabilistic reaction norm is thus specified by determining these probabilities for all relevant ages and sizes (see Figure 2.4.1.2.1).



**Figure 2.4.1.2.1. Probabilistic reaction norms for age and size at maturation describe how the probability of an organism to mature during a given time interval depends on its age and size. Shades of grey illustrate how this probability may vary with age and size. Two growth trajectories are shown in red, one for a slow-growing fish and one for a fast-growing fish. Yellow dots indicate the age and size at which these fish mature.**

The traditional way of describing maturation in fisheries science is based on so-called maturity ogives. These depict the proportions of mature individuals in a population as functions of age and/or size. However, it is crucial to realize that maturity ogives characterize only the maturity status of a stock, and not the maturation process itself. This is because the maturity status of a population is determined not only by the maturation process itself but also by growth and survival. When analyzing trends in maturity ogives, changes in the maturation process are thus not distinguishable from changes in the rates of growth and/or mortality. All three factors are affected by fishing, and it is therefore very difficult, if not impossible to use maturity ogives for building an understanding of how specifically exploitation impacts a stock. Maturation reaction norms, by contrast, largely overcome these difficulties: by describing the maturation process itself (in terms of the effects of age and size) they strip away the confounding effects of varying growth and survival. This property of maturation reaction norms facilitates addressing important research problems, including disentangling phenotypically plastic and genetic changes in maturation.

### **2.4.1.3 The impact of fisheries-induced evolution in maturation**

Evolutionary changes due to fishing are expected to have adverse effects on exploited stocks. Specifically, evolutionary changes in maturation have consequences both at the individual and population level. At the individual level, maturation incurs a reduction in body growth (Roff, 1992; Stearns, 1992; Roff, 2000; Ernande *et al.*, 2004; Lester *et al.*, 2004) and evolutionary changes toward earlier maturation occur at a cost of reduced fertility at later ages because of the allometric relationship between fecundity and body weight (Roff, 1992; McCann and Shuter, 1997; Trippel, 1998, 1999; King and McFarlane, 2003). Also, it is often observed that eggs produced by small/young females have lower quality than those produced by large/old ones (Trippel, 1998, 1999). In species that undertake long spawning migrations, small body size may compromise their ability to reach spawning grounds. In addition, the market price of fish tends to increase with size. At the population level, evolutionary changes in maturation have a potential for strongly influencing recruitment of young fish to a stock through their effect on body size and fecundity. Fisheries-induced earlier maturation is expected to lead to a decrease in population biomass and population size of the same order of magnitude as the direct demographical effect of fishing on the same quantities (Ernande *et al.*, 2004), and thus to entail a decrease in yield (Law and Grey, 1989; Heino, 1998, Conover and Munch, 2002; Ernande *et al.*, 2004). It is also expected to shift the age and size distribution of the population towards younger ages and smaller sizes, the order of magnitude being again the same as the direct demographical effect of size selective fishing (Ernande *et al.*, unpublished results). Such

shift in the size distribution of exploited populations may strengthen the fishing down food web process (Pauly *et al.*, 1998), presumably younger and smaller animals consuming smaller prey items and thus having lower trophic level. Finally the combination of the decrease in fecundity potential and population size/biomass due to the evolutionary decrease in age and size at maturation might ultimately lead to population extinction depending on other life history characteristics of the population considered and the management strategy in use (Ernande *et al.*, unpublished results).

#### **2.4.1.4 On the lack of assessment of genetic impacts of fishing**

Traditionally, the management community does not assess the risks incumbent in genetic changes. Given the potential detrimental effects of genetic changes for fisheries, EcoQOs cannot be achieved if genetic /evolutionary components are ignored. As recommended in the latest issue of the ICES Journal of Marine Sciences, specifically focusing on “Quantitative ecosystem indicators for fisheries management” (eds. Daan, Christensen and Cury, 2005), a whole series of ecosystem status indicators or EcoQOs should be used, each of them addressing a specific property of the ecosystem. More specifically, there is a clear need for accounting for the genetic impact of fishing. In this context, we now evaluate the potential for probabilistic maturation reaction norms as an EcoQ metric assessing the genetic impact of fishing on exploited stock.

### **2.4.2 Evaluating PMRNs as an EcoQ Metric**

#### **2.4.2.1 Do PMRNs fulfil criteria for a good EcoQ metric?**

*Relatively easy to understand by non-scientists and those who will decide their use*

Although *estimating* the PMRNs is a rather complex task (see above), the principle for using them to detect ongoing evolutionary changes in the maturation process is rather simple as shown in Figure 2.4.2.1.1.

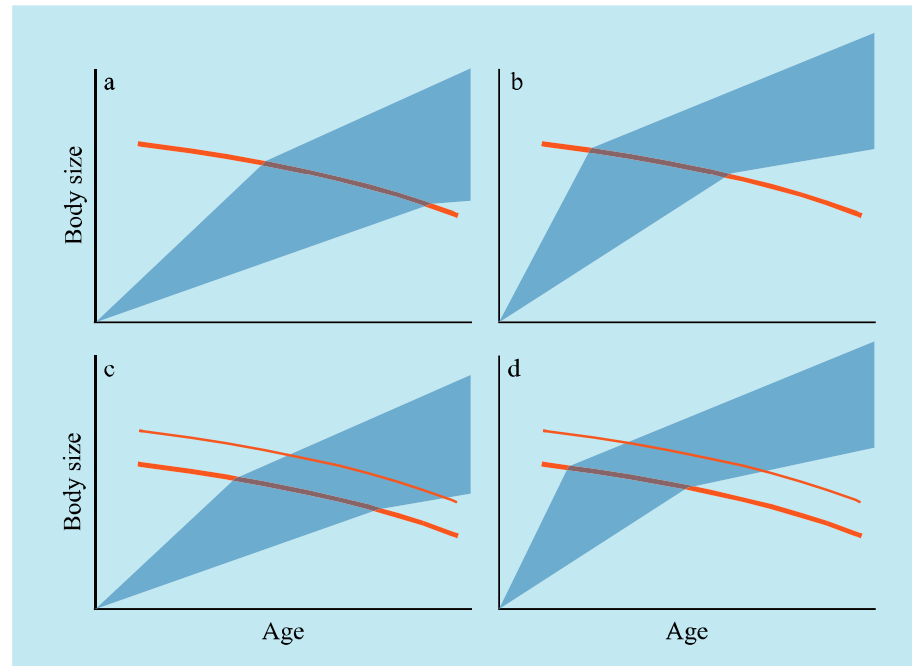
Basically, any constant temporal trend in PMRNs is a signal for ongoing evolutionary/genetic changes affecting the maturation process in the considered population.

*Sensitive to a manageable human activity*

As already extensively described above, PMRNs are very sensitive to fishing, although there is an asymmetry in the involved selective pressures (see below for more details). This means that fisheries-induced evolutionary changes are manageable through fisheries management.

*Relatively tightly linked in time to that activity*

Contrary to the common belief, significant evolutionary changes can actually take place on contemporary time scales. Several experimental and field studies (Conover and Munch, 2002; Reznick *et al.*, 1990; Reznick *et al.*, 1997; Thompson, 1998) have shown that substantial evolutionary changes in life history traits can occur within a few generations. Dealing specifically with a model parameterised for North East Arctic cod, Dieckmann and Heino (in press) showed that, with a rather conservative estimate of heritability for age and size at maturation ( $h^2=0.2$ ), the selective pressure imposed by the fishing history of this stock was sufficient to lead to evolutionary rates consistent with the significant change in age and size at maturation observed over a few decades in empirical data. In addition, Law (2000), reviewing fish breeding experiments, showed that mean heritability for age at maturation was rather high ( $h^2=0.31$ ), allowing for fast evolutionary rates given sufficiently strong selective pressures. Based on these studies, the time scale on which PMRNs should prove being useful is of the order of a decade, which is still relevant from a fisheries management point of view.



**Figure 2.4.2.1.1. Probabilistic reaction norms for age and size at maturation. Thick orange curves shows reaction norm midpoints, that is, combinations of age and size at which the probability of maturing is 50%. In each of the four scenarios shown, maturation is likely to occur in the vicinity of this curve. Growth trajectories (spread across the dark blue area) determine which part of the reaction norm will be observed (a-d). An increase in growth rates (from a to b) leads to earlier maturation along a different part of the reaction norm, but will not change the observed position of the reaction norm itself (b). By contrast, a genetic change (from a to c or d) toward maturation at younger ages and smaller sizes results in a shift of the reaction norm: the observed midpoints (thick orange curves) therefore differ from the initial ones (thin orange curves). Importantly, the corresponding shift in the position of the reaction norm can be detected both in the absence (c) and in the presence (d) of concomitant environmental change in growth rates. Adopted from Olsen *et al.* (2004).**

#### *Easily and accurately measured with a low error rate*

Measuring or estimating PMRNs is a rather complex statistical methodology and this might look like a drawback as an EcoQ metric (see Heino *et al.*, 2002a; Baort *et al.*, 2004a; Van Dooren *et al.*, 2005 for the estimation methods). Yet, one cannot expect very much from simple and straightforward statistics in such a complex issue as evaluating the ecosystem status. In addition, relative to other indicators of the genetic impacts of fishing one could envisage (genetic variation in life history traits for instance), PMRNs prove to be much easier to measure since it involves only phenotypic data that are routinely collected by most institutions responsible for fish stock assessment.

With regard to accuracy and error rate, Heino *et al.* (2002a) and Barot *et al.* (2004a) did a study about the robustness of probabilistic maturation reaction norm estimates against the violation of the simplifying assumptions underlying the computation of the probability of maturing and developed a bootstrapping method to evaluate confidence intervals for PRNs estimates. According to these studies, accuracy and error rate both proved to be rather satisfying.

Besides the accuracy of the PMRN estimation, the quality of the data is also important. For instance, age determination is especially prone to random and/or systematic bias due to the methodology used (otolith or scale reading) and the human factor. A problem could arise when comparing PMRNs based on data that have been gathered by different people or with different methods.



*Responsive primarily to human activity with low responsiveness to other causes of change*

Temporal trends in PMRNs can theoretically be linked to 3 other causes than selective fishing causes (Olsen et. al., 2004; Barot et al., 1994):

- 1 ) Plasticity not mediated only by growth, but also by some other environmental factors: social suppression of maturation, body condition, temperature;
- 2 ) Changes in the genetic composition of the stock due to migration processes/gene flow from a stock with a different life history;
- 3 ) Evolutionary changes due natural changes in mortality regimes instead of fishing.

Case 1 and 3 are expected to be rather unlikely in the sense that the likelihood for directional trends over several decades in environmental factors affecting maturation non-channelled through growth or in natural mortality is very low. In contrast, gene flow/migration processes (case 2) seem rather difficult to control for at the moment. Still, the universality of the trends observed in PMRNs for exploited stocks (over 12 case studies, 11 displayed a temporal trend of PMRNs towards younger ages and lower sizes; see below) suggests fishing as the main cause since it is the main constant factor over all case studies.

*Measurable over a large proportion of the area to which the Eco Q metric is to apply*

PMRNs are limited to stock units and therefore concerns the geographical area matching the spatial distribution of the stock considered.

*Based on an existing body or time series of data to allow a realistic setting of objectives*

The computation of PMRNs is based on time series of data that are routinely collected by most fisheries Institutes all around the world, at least for commercial species: maturity ogives according to size and age, cohort abundances, size at age curves and survival estimates. More specifically, three kinds of dataset can be used to estimate PMRNs:

A sample of individuals, measured for age and size and classified as juvenile, first-time spawners or repeat spawners; the last class is not used in the analysis. For estimation of the whole reaction norm for a cohort, samples tracking that cohort in time are needed. In the case of sampling with replacement, no individual identification is required.

Two consecutive samples of individuals, measured for age and size and classified as either juveniles or adults (or as immature or mature). In the case of sampling with replacement, no individual identification is required. As above, several consecutive samples are needed for the characterisation of maturation reaction of a cohort.

Data on individual growth and maturation histories, originating from a controlled experiment, a mark-recapture study, or other study where individually identified animals are followed. At minimum, one snapshot after the initiation of the study is necessary, assuming that the individuals were aged at the beginning of the experiment. For estimating the maturation reaction norm of a cohort, individuals have to be marked before the cohort starts to mature and must then be followed until all individuals mature.

See Heino et al. (2002a), Barot et al. (2004a), and Van Dooren et al. (2005) for more details on the methodology related to each kind of dataset.

### **2.4.3 Other Advantages of PMRN**

To date, probabilistic maturation reaction norms have been estimated for eleven marine and one freshwater stocks of exploited fish (see Table 2.4.3.1).

**Table 2.4.3.1. Empirical case studies of fisheries-induced evolution in maturation reaction norms.**

STOCK	PERIOD WITH DATA	REFERENCE
Northeast Arctic cod	1932–1998	Heino <i>et al.</i> , 2002b
Georges Bank cod	1970–1998	Barot <i>et al.</i> , 2004b
Gulf of Maine cod	1970–1998	Barot <i>et al.</i> , 2004b
Northern cod	(1977)-1981–2002	Olsen <i>et al.</i> , 2004, 2005
Grand Bank cod	1971–2002	Olsen <i>et al.</i> , 2004, 2005
St. Pierre Bank cod	1972–2002	Olsen <i>et al.</i> , 2004, 2005
North Sea plaice	1955–1995	Grift <i>et al.</i> , 2003
Newfoundland plaice	1973–1999	Barot <i>et al.</i> , 2005
Grand Bank plaice	1969–2000	Barot <i>et al.</i> , 2005
St. Pierre Bank plaice	1972–1999	Barot <i>et al.</i> , 2005
Atlantic herring	1930–1992	Engelhard and Heino, 2004
Norwegian grayling	20 <sup>th</sup> century	Haugen and Vøllestad, in press

All but one of the investigated stocks exhibited clear temporal trends in their maturation reaction norms. These always occurred towards increased maturation probabilities at younger ages and smaller sizes, in accordance with predictions from life-history theory. In the Canadian cod stocks, there are tentative signs for a reversal of this trend, resulting from the moratorium declared on directed offshore cod fishing in 1992. The one exception in an otherwise overwhelmingly clear pattern of evolutionary changes is the Atlantic herring stock, where maturity changes have been predominantly plastic.

Although applications of the PMRNs methodology have only utilized data from commercially exploited fish stocks so far, the approach is rather general in the sense that there is no theoretical limitation in terms of species to which the PMRN methodology can be applied. As soon as the life cycle of the species include both immature and mature stages, the method can be applied although some adjustments might be needed for depending on some life history characteristics: indeterminate vs. determinate growth, iteroparous vs. semelparous life cycle, dioecous vs. hermaphrodite species. However, the interest of the methodology from a management point of view might differ between the species according to the impact of age and size at maturation on population dynamics: depending on the life cycle of the species and their other life history characteristics, changes in age and size at maturation might be more or less detrimental.

PMRNs can also be applied effectively to other life history transitions than maturation, like hatching and metamorphosis, although the time series data needed for such analyses are generally not available for commercially exploited marine living species.

Olsen *et al.* (2004, 2005) argued that trends in PMRNs towards younger ages and lower sizes could be used as an early warning signal of serious impacts of fishing on the life history characteristics of the exploited stock under consideration, among which the recruitment potential which determines population viability. Quoting the forthcoming paper by Olsen *et al.* (2005) in Canadian Journal of Fisheries and Aquatic Sciences: “information on trends in the maturation process may serve as a helpful warning signal with regard to changes in population size and recruitment potential. With the collapse of the cod populations off Labrador and Newfoundland in mind, Hutchings and Myers (1995) argued that the sustainability of any fishery clearly depends on quantifying a wide range of biological indicators of population health. Specifically, Trippel (1995) suggested that the age  $A_{50}$  at which 50% of fish are mature holds promise as one such “stress” indicator. We build on this argument and put forward maturation reaction norms as a biological indicator with important advantages over  $A_{50}$ . A reduction in  $A_{50}$  is ambiguous in that it may reflect either fisheries-induced selection favouring early maturation, or maturation facilitated by faster individual growth in response to declining stock size. Both of these possibilities imply that fishing heavily impacts the population, which hence

may be considered as being “stressed”. However,  $A_{50}$  may also decline if maturation is merely facilitated by a temperature increase or when the survival of mature fish increases. Neither of these scenarios represents a cause of concern for the management of a stock. By contrast, estimation of maturation reaction norms reveals changes in the maturation tendency itself, as shown here for the cod populations off Labrador and Newfoundland in the 1980s. A more robust indicator of population health may therefore be the length  $LP_{50}$  (Grift *et al.*, 2003) at which the probability of maturing reaches 50% for a given age. The methodology described and utilized here enables estimation of  $LP_{50}$ .”

#### **2.4.4 Defining Reference Points and Objectives for PMRN as EcoQOs and Potential for Recovery/Restoration**

As a diagnostic tool or EcoQO/metric, identifying trends in the PMRN might be insufficient. It is important that the degree or size of deviation some reference condition or point be measured or articulated, thus allowing some kind of assessment of the amount of damage that has been done to the stock. The theoretical basis for this approach has been well worked out within the context of the European Unions Water Framework Directive. Two types of reference point for applying PMRNs as EcoQ metrics can be identified. The first one would establish base line targets for restoration of the genetic composition of the stock. For this case, the reference point might be assessed on the basis of the historical PMRNs, if data are available (temporal studies), or on the basis of the condition of stocks in un-exploited or least-impacted areas, if such exist (spatial studies). The second type of reference point would allow for sustainable harvesting at current exploitation regimes while reducing the impact as far as possible by determining the PMRN leading to sustainable population dynamics given a certain fishing effort or yield. Which of these types of reference point should be ultimately chosen as an EcoQO is not only a scientific matter and is still to be debated.

When defining reference points or levels, the question of the potential for rehabilitation and restoration of populations has also to be addressed otherwise reference points might happen to be eventually unattainable. Adverse genetic changes may actually not be easily reversed. Indeed, with regard to age and size at maturation, there is an asymmetry in the selective pressures, i.e., halting fishing or turning back to historical fishing regimes is expected to lead to a recovery but the rate of evolution would be much lower than the rate of fisheries-induced evolution, future generations thus incurring a “Darwinian debt” (Law and Grey, 1989; Rowell, 1993; the evolutionary rate after turning back to the historical fishing regime was found to be 5 times slower in a model parameterised for North-East Arctic cod, Dieckmann and Heino, in press). The rate of recovery (i.e., returning to the historical reference point) might be enhanced by imposing a selective pressure in the other direction, presumably by fishing only adult fish (on spawning grounds for instance) but unselectively relative to size (Ernande *et al.*, 2004). With regard to restoring quantitative genetic variation, everything depends on the part of the evolutionary process under consideration. At the beginning of the evolutionary process, there is directional selection ongoing, which leads to an increase of genetic variation for the traits under selection. At the end of the process, selection becomes stabilizing thus reducing genetic variation (Dieckmann and Heino, in press). This means that during the directional selection phase there is no loss of genetic variation. It is only when the stabilizing phase is reached that some management rules would be needed to restore genetic variation. For age and size at maturation, restoring genetic variation might be achieved by conserving both old and big maturing fish and young and small maturing ones. This could be achieved by imposing both a minimum and maximum size limit for landing (Ernande *et al.*, 2004).

#### **2.4.5 Recommendations**

- 1) Along with other genetic indicators, probabilistic maturation reaction norms for a number of species (commercially-exploited and discarded species when data are available) should be considered together in determining ecological quality in terms of

genetic effects of fishing in a given ecosystem, e.g., Grand Banks, North Sea, Baltic Sea, Irish Sea, English Channel.

Two types of reference point are needed to apply this EcoQ metric: the first establishes base line targets for restoration of the genetic composition of the stock; the second allows for sustainable harvesting at current exploitation regimes while reducing the impact as far as possible.

- 2 ) In order to establish the first kind of reference point, unexploited, historical or least impacted population maturation state should be determined. This will help to quantify the level of genetic impact caused by historical and contemporary fishing and to assess the required management measures to restore this state. The second type of reference point would be determined by identifying the maturation parameters required to maintain long term sustainable fisheries for a given yield (or fishing mortality).
- 3 ) PMRNs allow the assessment of changes in the mean breeding value of the population for maturation. However, the genetic variance is also an indicator of population health since it determines the evolutionary potential of the population for the maturation process and this could also have potential as ecological quality indicator for genetic impact of fishing. In addition to experimental approaches, we recommend that changes in genetic variance for maturation in exploited populations are assessed through the use of “quantitative genetics in the wild” when feasible (coefficient of relatedness between individuals measured for phenotypic traits using neutral markers).
- 4 ) The most recent application of probabilistic reaction norm has been to the genetic impact of fishing on maturation. However, we recommend that other important life history transitions, which can be genetically impacted by fishing, e.g., timing of migration, are investigated using this methodology.
- 5 ) In order to maximize the potential of the PMRN approach, we recommend inter-calibration between the different collectors of data to achieve standardization and, where possible, samples representing reproductively distinct stocks should be targeted.

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## **2.5 Evaluate the evidence for genetic erosion and changes in life history characteristics of local stocks due to mariculture activity (ToRe)**

This text was based on a working paper prepared by G. Dahle and P. Boudry and adopted by WGAGFM at Silkeborg, Denmark in 2005.

### **2.5.1 Introduction**

In recent years there has been increasing interest and concern for the consequences of the translocation of organisms within their natural geographic range. The potential risk associated with translocations arises principally from (1) the introduction of pathogens and parasites to new areas, and (2) genetic shifts in natural populations through hybridisation with reared and/or translocated individuals.

The importance of recognising populations (= breeding stocks) has long been part of fisheries management, and fisheries biologists have been quick to utilise new techniques to identify such structure. However, most studies are based on presumed neutral markers, that are first needed to estimate genetic structure of populations, and little is known about genetically determined adaptive traits. With increasing threats to natural populations more focus is put on the possible importance of genetic differences among populations, especially differentiation between reared and wild populations.

Genetic subdivision of a species indicates potential for local adaptation, and the genetic differences observed among populations are a key component of genetic diversity. Genetic markers used to measure structure might indicate where there is opportunity for local adaptation, i.e., to estimate the relative impact of gene flow, drift and mutation on populations, but they may not be directly related to adaptation, that is the ability of the individual to cope with the local environment. This local environment can be different at different scales: geographically (across the natural range of a species) or spatially (related to human activity, e.g., mariculture). Many marine species show relatively low levels of structuring even over large distances. Some markers are capable of showing higher levels of differentiation than others, for example non-neutral markers or adaptive traits can show higher differentiation, indicating local adaptation.

Today, most of mariculture production is based on stocks that have not been subject to selection, as broodstock is regularly wild-caught. Despite the recommendations made by WGAGFM in 2002, confinement systems do not seem to be a feasible option in cod farming as well as other marine species. Thus, genetic consequences of escapes must be considered. Selection and management of broodstock is an important component for the outcome of this activity. For example, in cod it has been shown that larval and juvenile growth differs between north east Arctic cod and Norwegian coastal cod, when reared under similar environmental and feeding conditions (van der Meer and Joerstad, 2001). For species with a longer domestication and breeding history, more information about life history traits is available. For example, studies of sea-ranched salmon have shown that selective factors during rearing can have a genetic influence on life history traits, e.g., growth rate and sea-age at first maturity (Kallio-Nyberg and Koljonen, 1997). Their conclusion is that hatchery rearing might change the genetic composition of a salmon stock.

One other possible impact of maricultured species is the genetic shifts in natural populations through inter-population hybridisation. When this results in a loss of genetic diversity, it is referred to as genetic erosion. More specifically, genetic erosion could be defined as loss of genetic diversity between and within populations of the same species over time; or reduction of genetic variability of a species due to human intervention, environmental changes, etc. Genetic erosion in a population may result in a permanent reduction in richness or evenness of common localized alleles or the loss of combination of alleles over time in a defined area.

This suggests that it is specifically loss of locally coadapted gene complexes that is most significant. Indicators of genetic erosion have been previously reviewed by WGAGFM (2004 report of WGAGFM ToR a: “Provide recommendations on the applications for the estimation of effective population size in wild populations of marine fish and shellfish”). Even in the absence of genetic erosion fitness reduction can result from hybridisation.

The “review and report on genetic issues related to escapes of farmed marine fish and shellfish” was presented in the 2002 annual report from the WGAGFM (ToR b). The present report aims to update this topic and further develop possible outcomes and alternative issues. However, since the topic was last addressed (2003) there has been very little new data to evaluate. However, a new EU Concerted Action project has just been announced which should provide information about genetic impact of mariculture activities on wild populations, specifically on their genetic interaction. This project, entitled GENIMPACT, includes many WG members, and will deal with important marine species such as Atlantic cod, European sea bass, gilthead sea bream, turbot, halibut, scallops, mussels, oysters and European lobster. This project should be completed by 2008 and their report could be evaluated by WGAGFM in 2009.

## **2.5.2 Case Studies**

### **2.5.2.1 Cod**

Survival of different cod stocks seems to be more related to environmental effects derived from specific rearing conditions, quality of the egg or larval batches, rather than stock origin. However, population differences are apparent in survival dependent on light regime, e.g. different light spectra with higher intensity enhanced survival, particularly for the coastal cod larvae (Puvanendran and Brown, 2002.). It is not known to what extent the geographic differences in maturation reflect genetic variation or phenotypic plasticity. Since genetic analysis suggests that Atlantic cod from along the Norwegian Skagerrak coast are structured into several local populations, differences in size at age and maturation patterns might have a genetic component. Life-history traits may vary on a small geographical scale even within a marine habitat with no obvious barriers to migration (Olsen *et al.*, 2004).

Fishes generally have highly plastic life histories, but there is evidence for genetically based variation in Atlantic cod life-history traits (Purchase and Brown, 2000; Jonsdottir *et al.*, 2002).

Age and size at maturity among Canadian Atlantic cod have declined significantly in conjunction with historically, unprecedented 92–99% reductions in abundance (Hutchings and Reynolds, 2004). These changes in the two life-history traits most critical to population growth and population recovery are most parsimoniously explained as genetic responses to fisheries that preferentially target individuals genetically predisposed to mature at older ages and larger sizes. The new life-history characteristics selected for by the fisheries thus imply smaller size and younger age at maturation, which, in turn, can lead to lower post-reproductive survival, reduced life span, slower post-reproductive growth, fewer eggs, and smaller eggs. All of these effects can negatively affect reproductive output and, thus, recovery from collapse.

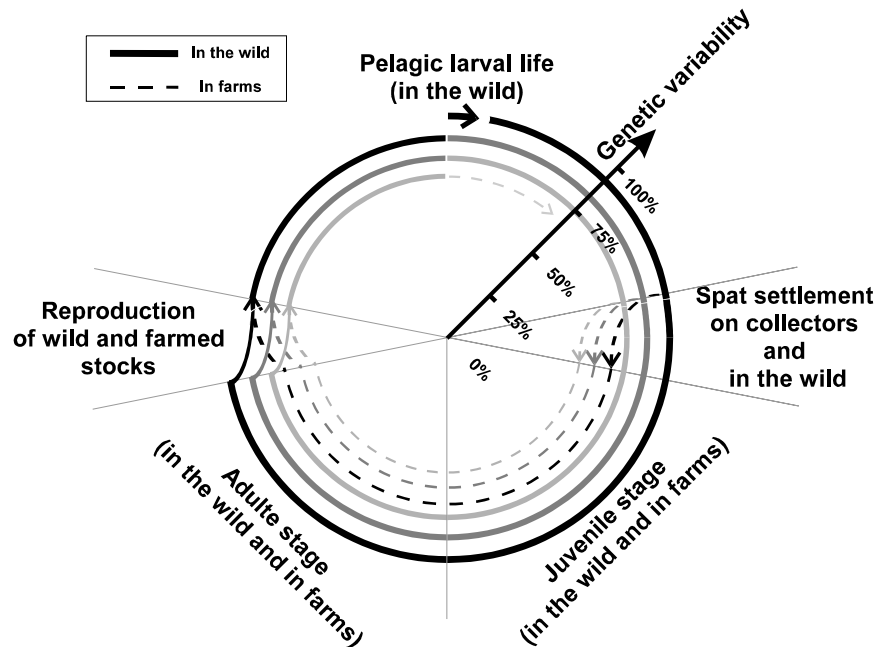
As a consequence of this drastic reduction in abundance followed by changes in life-history traits, mariculture is now expanding as an alternative and more sustainable source of cod. However, mariculture of cod must be developed in such a way that the impact of escapes will be minimized. This implies reducing changes in life-history traits related to the domestication process and minimizing the changes in genetic composition relative to wild populations. This might bring additional constraints on broodstock management and possible selective breeding.

### **2.5.2.2 Marine Bivalves**

Relative to fish mariculture, most bivalves are reared under environmental conditions that are the same, or very similar, to the wild (i.e., they are not fed, no disease treatments are available



and they are often not confined). Consequently, life-history traits are less likely to be differentially selected in farmed versus wild conditions. Aside from selective breeding programmes, any domestication of bivalves in mariculture is more likely to occur at the early life stages, i.e., hatchery and nursery where intensive rearing conditions are clearly different from those encountered in the wild, however, this remains to be documented. However, genetic erosion and possible local adaptation should be monitored because hatchery-based propagation and transport of juveniles over long distances are common in bivalve mariculture.



**Figure 2.5.2.2.1.** Evolution of the genetic variability available in wild and farmed stocks, is dependant on the efficiency of the spat collection used to constitute farmed stocks (from Arnaud-Haond *et al.*, 2003).

Despite many well documented cases of genetic drift in closed hatchery stocks (review in ToR d in the 2001 annual report of WGAGFM, section “Oysters and other shellfish”), relatively little is known about the impact of this practice on wild populations. Large population sizes and the long dispersal distance of larvae might buffer the possible genetic impacts of hatchery propagation. However, the impacts could be significant in highly depleted stocks (due to overfishing or disease issues). For example, stock enhancement using disease resistant strains with low genetic variability, is considered as a possible way to restore depleted *Crassostrea virginica* populations, but the genetic impact of such a practice is still debated. In the pearl oyster, *Pinctada margaritifera*, the recent development of this production has led to massive translocation of juveniles between atolls in French Polynesia. As a result, genetic differentiation between atolls was strongly reduced (Arnaud-Haond *et al.*, 2004). Additionally, the current practice of spat collection (Figure 2.5.2.2.1) might lead to a progressive loss of genetic variability (Arnaud-Haond *et al.*, 2003).

### 2.5.3 Recommendations

- 1) Gather baseline genetic diversity data on wild populations in areas subject to farming or stocking as well as data from conspecific cultured individuals. These data would be used to quantify levels of risk and plan possible conservation interventions. This monitoring should be continued on a long-term basis.
- 2) Undertake common-garden experiments that will enable the study of genetic components (heritability, genetic correlations, candidate genes, etc.) of life-history traits in

mariculture species. These data will allow modelling of the cultured-wild interaction which can be used to assess the potential risk.

- 3) Monitor life-history traits such as age and size at maturation and reproductive effort in existing breeding programmes. The object of such monitoring would provide information that could be used to avoid detrimental correlated and other responses in life history traits.

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### 3 Group business

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#### 3.1 Draft Resolutions for 2006

The WG considered ToRs for the 2006 meeting and prepared a draft set for consideration by ICES (Annex 3). Four items were proposed, with one being a carry over from the 2004 ToRs.

#### 3.2 Meeting places in 2006 and 2007

In 2004 it was agreed that future meetings should plan for 3.5 days of business in order to allow for a full discussion of the ToRs. Over the past few years the ToRs are increasing in complexity and require more time for discussion in order to reach consensus on the report.

During discussions on meeting place in the year 2004, the WG responded positively to a generous invitation from Dr Philip McGinnity, The Marine Institute, Newport, Ireland, to host the 2006 WG meeting 25–28 April.

The WG finds it useful for planning purposes to determine meeting venues two years in advance. The 2007 meeting is provisionally planned for the European Commission Joint Research Centre at Ispra, Italy at the invitation of N. Kourti.

### **3.3 Other business**

#### **3.3.1 FishTrace**

The WG was given a presentation by Philippe Carreau and Naouma Kourti of the Monitoring, Mapping and Intelligence Group, Institute for Protection and Security of Citizen (IPSC), European Commission (EU) - Joint Research Centre (JRC) on the FishTrace database.

FishTrace is an EU project involving 10 geneticists and taxonomists, whose goal is to develop a database of the same name. FishTrace links in one system genetic, taxonomy and biology specimen data for the main European commercial species and can be considered as a reference database. For example taxonomists have formally identified the collected specimen so it is possible knowing a DNA sequence to know to what species it corresponds to without misidentification.

In order to ensure high data quality, strict procedures have been established. For each sequence, alignment and phylogeny are checked before loading in the database and the system keeps track of specimens stored in museums. Once described the museum specimens can be re-examined in case of doubt.

The WG proceeded to discuss:

- 1 ) The content of the database. Is the content proposed by the current FishTrace sufficient? Should we involve more species or genetic materials?
- 2 ) On the methodology for data entry in such a database. How can we have more labs entering new data, and maintain the high quality and organize quality controls with many partners?
- 3 ) How to define test cases for validation?
- 4 ) What's about creating an independent scientific board, which will monitor the development and the quality of the database so as to ensure it, being a reference?

How to adapt the system to work with stocks? It looks like for horse mackerel there is a proposal for a methodology that can help distinguishing among stocks. The methodology is based on variety of data from genetic, to morphological to parasites etc. Can we do this also for other species?

For the most part the working group felt that the database would not be useful in its present state for stock identification, however its utility as a tool for identifying unknown specimens or validating commercial products has greater application. However, the choice of genes (cytB and rhodopsine) may not separate some fish groups.

#### **3.3.2 SALMAN/SALGEN**

E. Verspoor followed with a presentation on SALMAN (Atlantic Salmon Microsatellite Analysis Network). The purpose of the network is to agree on standardised screening methods for data to develop an international database on microsatellite variation in Atlantic salmon for using in GSI work at local, regional and continental scales.

The available microsatellite markers for Atlantic salmon have been evaluated and a set of 15 tetra-nucleotide markers were optimized. Three multiplexes allow for 6, 5 and 4 simultaneous

amplifications which will greatly reduce the cost. Reference DNA samples are also being sought and the WG was canvassed for interest in participating in this initiative.

An update on the publication schedule and results of the SALGEN project was also presented at the conclusion of the meeting.

### **3.3.3 2006 Genetics in Aquaculture meeting**

The next IAGA meeting (“Genetics in Aquaculture”) will be held in Montpellier (France) from 24–30 June 2006. Similarly to previous meetings, the peer-review proceedings of this meeting will be published in the journal *Aquaculture*. The WG discussed this opportunity as a means of advertising our work, possibly through a poster. Further information on the meeting is available from Beatrice Chatain, Chair of the organizing committee ([Beatrice.Chatain@ifremer.fr](mailto:Beatrice.Chatain@ifremer.fr)).

## Annex 1: List of Participants

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## Annex 2: 2004 WGAGFM resolutions

2F01 The **Working Group on the Application of Genetics in Fisheries and Mariculture** [WGAGFM] (Chair: E. Kenchington, Canada) will meet in Silkeborg, Denmark, from 3–6 May 2005 to:

- a) document the evolutionary ability of fish stocks to respond to climate change by reviewing the information on the nature and rates of environmental change;
- b) evaluate methods and provide recommendations on the application of mixed-stock and assignment analysis to elucidate stock components, with an emphasis on marine fishes and fisheries;
- c) synthesize the evidence and methods for detecting local (genetic) adaptation in marine fishes;
- d) evaluate the usefulness of probabilistic maturation reaction norms as ecological quality objectives (EcoQOs) as an early warning signal for the negative impact of fishing and other anthropogenic activities;
- e) evaluate the evidence for genetic erosion and changes in life history characteristics of local stocks due to mariculture activity.

WGAGFM will report by 20 May 2005 for the attention of the Mariculture and Diadromous Fish Committees, ACME and ACE (WGECO).

### Supporting Information

Priority:	WGAGFM is of fundamental importance to the ICES advisory process and address a variety of questions raised in the ICES Strategic Plan.
Scientific Justification and Relation to Action Plan:	<p>Action Plan references: a)-1.3 b)-1.10, c)-1.10, d)-2.5,4.6 e)-2.6,3.11</p> <ol style="list-style-type: none"> <li>a) The Potential Impact of Climate Change on Fisheries. Significant progress has been made in modelling past environments and predicting likely future marine climate states. Fish stocks will respond in yet unpredictable ways to such changes. Consideration of such responses will include potential impacts on distribution and abundance, as well as evolutionary capacity. Part of these considerations will include reference to contemporary anthropogenic-induced direct and indirect genetic change as a result of selective fishing, introgression, habitat change, pollution, aquaculture activity. This exercise will yield information on the nature and rates of environmental change as well as key factors to determine the ability of fish stocks to respond to this change. Other expert working groups will find this information useful for broader ecosystem studies (lead: P. McGinnity (Ireland)).</li> <li>b) Fisheries management should maximize the sustainability of individual stock components. Many fisheries take place on mixed populations and this complicates management of individual population/stock components, and leads to risk of overexploiting smaller population components. Genetic mixed-stock analysis and assignment methods provide a means for disentangling complex stock structures and their temporal variability. Individual methods vary in their properties for identifying mixed stocks and estimating stock proportions in species exhibiting high gene flow, such as is characteristic of many marine fishes. We propose to provide a review of the available estimation methods, their application to date, and of advantages and disadvantages of applying different methods to different stock structures (lead: D. Bekkevold (Denmark)).</li> <li>c) Although it is widely accepted that fish stocks exhibit marked phenotypic variation in many traits, little is known of the genetic basis of such variability. The development of new markers and statistical theory has facilitated opportunities for estimating the nature and extent of the genetic component of this variation. This ToR will consider the range of options most appropriate for detecting local adaptation in marine fishes, including aspects of experimental design, applications of genomic technologies and quantitative genetic approaches. Such considerations will facilitate conservation of population diversity; more effective incorporation of population heterogeneity into stock assessment models and the translation of this information into management advice (lead: G. Carvalho (UK)).</li> </ol>

	<p>d) The successful application of the ecosystem approach to fisheries management will require empirical (defendable) diagnostic metrics that can detect changes in critical processes due to fishing that in turn affect key population characteristics, and that ultimately determine population demographics (population size, biomass, rates of extinction, (persistence) etc.), life history or quantitative variability and evolutionary (genetic) potential, particularly with regard to climate change and disease challenges. The development or identification of these metrics has to date proved problematic within WGECO, the ICES Working Group tasked with this objective. New research undertaken by Ulf Dieckmann, Bruno Ernande and co-workers working with probabilistic reaction norms and discussed within WGAGFM and in a Theme Session at the ICES ASC in 2002, provides a realistic opportunity for the application of this method as an EcoQO. It is recommended here that the WGAGFM summarize the current application and build on its 2004 ToR with a view to establishing reference limits for the react norms, and apply them to other factors causing selection variance such as disease, to evaluate their broader applicability as an EcoQO. We propose to take our results to the WGECO for their subsequent evaluation (lead: P. McGinnity (Ireland)) with support from U. Dieckmann (Austria) and B. Ernande (France).</p> <p>e) Increasing mariculture activity, including species such as cod, halibut and mussels, may impose genetic changes on local stocks which could translate to changes in time of spawning, spawning behaviour etc., with ecosystem-wide consequences. We propose to evaluate these interactions with two case studies, cod (Norway) and the pearl oyster (France) for which we believe sufficient information exists to assess this impact from a genetic perspective (lead: G. Dahle (Norway)).</p>
Resource Requirements:	None required other than those provided by the host institute.
Participants:	WGAGFM members, invited contributors and observers
Secretariat Facilities:	None required
Financial:	None required
Linkages to Advisory Committees:	ACME, ACE
Linkages to other Committees or Groups:	SIMWG (Delegates drew specific attention to the need to develop this link – the Chairs of these two Working Groups should correspond together to ensure that there is no unnecessary overlap in their work.)
Linkages to other Organisations:	None in the current year



### Annex 3: Draft 2005 Resolutions

The Working Group on the Application of Genetics in Fisheries and Mariculture [WGAGFM] (Chair: E. Eg Nielsen\*), Denmark) will meet in Newport, Ireland from 25–28 April 2006 to:

- a. Assess the current knowledge of the genetic basis of domestication processes in farmed fish and shellfish;
- b. Identify the technical and organisational requirements for establishing practical, functional and integrated international databases and supporting repositories for genetic stock identification;
- c. Synthesize the evidence and methods for detecting local (genetic) adaptation in marine fish and shellfish;
- d. Assess, through a case study of anadromous salmonids, the potential of genetic and spatial data analysis methods for resolving spatial boundaries of finfish and shellfish populations, and for gaining insight into the geographic and ecological factors controlling the development of population boundaries.

#### Supporting Information

Priority:	The current activities of this Group will lead ICES into issues related to the ecosystem affects of fisheries and mariculture, especially with regard to the application of the Precautionary Approach. Consequently these activities are considered to have a very high priority.
Scientific Justification and relation to Action Plan:	<p>Action Plan references: a)-2.5 b)-6.1, c)-1.10 d) 1.10</p> <p><b>Term of Reference a)</b></p> <p>Many farmed species are not subjected to selective breeding programs, but the genetic impact of the process associated with aquaculture at the successive steps of the rearing (hatchery reproduction, nursery, on-growing) can be significant. Aside from the well documented reduction of genetic variability due to genetic drift, genetic effects can be due to hidden selective pressures associated to the farming environment or, conversely, to the absence of selective pressures encountered in the wild. Domestication is a process that will favour the establishment of the aquaculture in species of interest, but can be detrimental in case of population enhancement and conservation programs.</p> <p>Domestication effects are difficult to disentangle from intentional selection effects in species for which selective breeding programs are already established. Consequently, new aquaculture species, or those where no intentional genetic improvement has been initiated, are more likely to provide insight on domestication processes. Alternatively, in selected strains, genetics changes of non-selected traits can also be due to domestication processes. We aim to review the present state of knowledge of genetic aspects related to domestication of aquaculture species by examining study cases. (lead: P. Boudry, France)</p> <p><b>Term of Reference b)</b></p> <p>Most, if not all, commercial fish and shellfish species are composed of multiple, genetically distinct, and more or less reproductively separated populations. Understanding the spatial distribution and abundance of these stocks, and their contribution to regional stocks and fisheries, is crucial to the development of effective management programmes. The potential of GSI for increasing understanding of population structure and improving fisheries management has long been recognised, and it is now technically possible and practical for an increasing number of species. However, a major impediment to the implementation of GSI is the development of the needed baseline databases. Doing so represents a considerable technical and organisational challenge, given the amount of data involved, the need to standardise genetic typing and nomenclature across diverse research groups and analysis methods for screening. In almost all cases, the development and exploitation of such data bases will involve international networking and cooperation. Given the potential benefits to be gained in the future, how such data bases should be developed needs to be carefully considered before they are set up. This will ensure that mistakes are minimised. This is important as some may prove costly or difficult to rectify once made and hinder progress in exploiting this important source of management information. This initiative is supported by the regular working group members as well as the EU Joint Research Centre. (lead: E. Verspoor, Scotland)</p>

	<p><b>Term of Reference c)</b></p> <p>Although it is widely accepted that fish and shellfish stocks exhibit marked phenotypic variation in many traits, little is known of the genetic basis of such variability. The development of new markers and statistical theory has facilitated opportunities for estimating the nature and extent of the genetic component of this variation. This ToR will consider the range of options most appropriate for detecting local adaptation in marine fishes, including aspects of experimental design, applications of genomic technologies and quantitative genetic approaches. Such considerations will facilitate conservation of population diversity; more effective incorporation of population heterogeneity into stock assessment models and the translation of this information into management advice (lead: G. Carvalho, UK).</p> <p><b>Term of Reference d)</b></p> <p>The existence of population structuring in most finfish and shellfish stocks is widespread, with established knowledge of the extensive levels of population differentiation among marine and freshwater species. However, the actual spatial boundaries of populations and the underlying geographic and ecological factors governing the spatial limits of population needed to support population centred management approaches remain poorly understood. Advances in two areas of methodological development, now offer the possibility of addressing these issues. The first is development of GSI (Genetic Stock Identification) methodology, based largely on microsatellite marker analysis, which gives a high power for assigning individuals to populations (see ToR 2005b). The second is the availability of advanced spatial analysis using GIS (Geographical Information Systems) methods which has considerable potential as a means of interpreting patterns and distribution of genetic variation. Integration of knowledge acquired from geographical and genetic studies will allow us to gain a greater understanding of the critical factors which determine the manner in which species become distributed as reproductively isolated populations in their natural habitat, and to identify the boundaries between them. This may, for example, allow us to predict and model how extirpated or depleted populations can become re-established. It may also allow for more targeted, population sensitive exploitation. Inferences regarding population boundaries drawn this insight using geographical and environmental data will also facilitate the targeting of regions for directed sampling of specimens (spawners/juveniles/larvae etc.) required for the development of baseline data sets for GSI. (lead: T. Cross, Ireland; E. Verspoor, Scotland).</p>
Resource Requirements:	None required other than those provided by the host institute.
Participants:	The Group is normally attended by some 20–25 members and guests
Secretariat Facilities:	None required
Financial:	None required
Linkages To Advisory Committees:	ACME, ACE
Linkages To other Committees or Groups:	SIMWG , WGECE, WGMAFC, WGMASC
Linkages to other Organisations:	Linkage with the EC Joint Research Centre at Ispra, Italy.
Secretariat Marginal Cost Share:	?

## Annex 4: Action Plan Progress Review 2005

Year	Committee Acronym	Committee name	Expert Group	Reference to other committees	Expert Group report (ICES Code)	Resolution No.		
Action Plan	Action Required	ToR's	ToR	Satisfactory Progress	No Progress	Unsatisfactory Progress	Output (link to relevant report)	Comments (e.g., delays, problems, other types of progress, needs, etc.)
No.	Text	Text	Ref. (a, b, c)	S	0	U	Report code and section	Text
2004/2005	MARC	Mariculture	WGAGFM		2004/F-01	2F01		
1.3	Please see below	Document the evolutionary ability of fish stocks to respond to climate change by reviewing the information on the nature and rates of environmental change;	a)	S				
1.10	Please see below	Evaluate methods and provide recommendations on the application of mixed-stock and assignment analysis to elucidate stock components, with an emphasis on marine fishes and fisheries;	b)	S				
1.10	Please see below	Synthesize the evidence and methods for detecting local (genetic) adaptation in marine fishes;	c)	S				The WG proposes to continue work on this ToR in 2006
2.5, 4.6	Please see below	Evaluate the usefulness of probabilistic maturation reaction norms as ecological quality objectives (EcoQOs) as an early warning signal for the negative impact of fishing and other anthropogenic activities;	d)	S				
2.6, 3.11	Please see below	Evaluate the evidence for genetic erosion and changes in life history characteristics of local stocks due to mariculture activity.	e)	S				

### Action Plan ITEMS

1.3	Increase knowledge of the effects of physical forcing, including climate variability, and biological interactions, on recruitment processes of important commercial species. [MHC/OCC/RMC/LRC/MARC/BCC/DFC]*
1.10	Develop better tools and training opportunities for monitoring and observation of physical, chemical and biological properties of marine ecosystems. [FTC]* [Other Science Committees]
2.5	Assess and evaluate the genetic consequences of human-induced selective factors, whether intentional (such as selective breeding for mariculture) or unintentional (such as selective effects of fishing). [MARC/LRC/RMC/DFC/ACE/ACME]
2.6	Evaluate and assess the intra- and interspecific interactions of wild and farm-reared stock as well as disease and genetic interactions. [MARC/LRC/DFC]
3.11	Evaluate information on technological change in mariculture, including the utilisation of new species, with particular emphasis on the consequences for production and the environment. [MARC/ACME]
4.6	Develop document guidelines for the preparation of Environmental Impact Assessments, and appropriate monitoring programmes. [MARC/MHC/ACME/ACE]