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Executive summary

The Working Group on the Application of Genetics in Fisheries and Mariculture (WGAGFM) met in Bangor, UK, 4–6 May 2011. The meeting was very well attended; with a total of 24 representatives present from 11 countries. In addition a number of master and PhD students were attending parts of the meeting.

WGAGFM have established a three-year period for the Chair person, and this meant that this year we had an election of a new Chair. There were two candidates and Dorte Bekkevold (Denmark) was elected the new Chair.

Time was allocated for members to present projects that are ongoing or have just ended, and this year the preliminary results from the EU project SALSEA-MERGE was presented, The SALSEA-MERGE has been discussed and presented at an earlier WGAGFM meeting (2009), and the results are very encouraging using genetic markers for identifying the region or even river of origin for any salmon caught in the sea.

Increasing evidence shows that the marine environment is highly variable in space and time. The effects of physical features such as currents, fronts and eddies on the transport of material can fluctuate on a range of scales. Understanding their interaction with biological variation in life history, development and behaviour remains a central goal for effective integration of population ecology, conservation and management. Information about the exchange of individuals among geographically separated subpopulations – encompassing the dispersal phase, is relevant to fisheries management for several reasons. For example the extent to which populations self-recruit or receive migrants from other populations impacts significantly on processes that influence population regulation and persistence, together with the potential for local adaptation. We examined recent advances in the coupling of genetic and oceanographic approaches in elucidating population connectivity in marine fish, and importantly, we examined the utility of combining such interdisciplinary approaches into a predictive framework. Incorporating oceanographic realism like currents, eddies and turbulence, into genetic studies, while presenting a challenge and requiring modified model assumptions, can yield increased accuracy in population identification and, possibly, valuable insights into drivers of genetic population structure. To date, the main approach has been to use a land- or seascape genetic framework, combining genetic information with information about seascape features like basins, trenches or main currents, and has been successful in linking strong population genetic breaks with major oceanographic boundaries.

The comparison of genetic data with oceanographic models is relatively recent, and although specific approaches have been developed in the landscape genetics field, e.g. isolation by resistance distance theory, there remains a lack of genetic modules in existing modelling packages. Moreover the number of studies integrating the modelling of oceanographic variables to investigate the population genetics of a marine organism is still scarce. Seascape genetics has mainly looked at oceanographic features to influence distributions of larvae; yet this by no means can be a fully exhaustive predictor of genetic structure and demographic independence. The question is: is it possible to employ a so-called "resistance surface" approach without them becoming too complex and cumbersome to be effectively employed in the management arena?

The second ToR is closely connected to the first looking at networks of Marine Protected Areas – dispersal connectivity and seascape genetics. As marine populations

tend to be large, allelic diversity changes largely in response to gene flow and adaptation. Here, population genetics, in combination with other disciplines, has much to contribute, especially in view of connectivity, which is a determining factor in affecting the function of MPAs. Population connectivity refers to the exchange of individuals among geographically separated subpopulations – encompassing the dispersal phase from reproduction to the completion of the settlement process (including habitat choice and metamorphosis). MPAs aim at preserving the marine biodiversity and/or to guarantee the sustainable exploitation of natural resources. Their design and implementation depends on informed decisions and consent between a broad range of stakeholders, including fishers, scientists and the public. Scientific information from the biology of organisms and communities, and in this case more specifically genetic information, contributes to the organization at a broad scale, the validation of the design and follow-up (monitoring). Four aspects are crucial to the design of MPAs from a genetic perspective, size, size structure, spacing and coverage. Size and size structure are only effective if the link between the habitats is guaranteed for the taxa using them. An important ecological determinant to delineate MPAs is the dispersal of larval and adult organisms in time and space of now and hence the connectivity between populations. The structure and functioning of MPAs depends on the habitat, ecosystem interactions and biological characteristics of key species. Here we discuss the biological characteristics, especially dispersal, connectivity and gene flow from a genetic perspective.

Over the past two decades, exceptional advances in molecular analytical methodologies have resulted in a myriad of new types of genetic markers. Single Nucleotide Polymorphisms (SNPs) have been one of the latest additions to the molecular toolbox. The rate of SNP development and genotyping, particularly its potential for non-model organisms, has been greatly accelerated by the advent of Next Generation Sequencing (NGS) techniques. Because of this rate of SNP development and genotyping the WGAGFM recommends that issues pertaining to ascertainment bias, cost, SNP choice, ease of analyses, screening platform, technical aspects related to genotyping, data management, and broader technological and statistical approaches should be further considered by members of this working group on an ongoing basis.

In its user guide on the Common Fisheries Policy (CFP) {European, 2009 #296} the European Commission underlines that fisheries management in the EU relies on scientific advice, and is therefore dependent on accurate, relevant and up-to-date data. Since 2001, the CFP has set aside funding to help national authorities collect both economic and biological data related to fisheries management. The "Data Collection Framework Regulation" – DCF covers a broad array of biological data that can be integrated in fisheries modelling and stock assessment and feed into fisheries management, but there is currently no reference to genetic data. We believe this absence of genetic data coverage to be unfortunate and counterproductive as genetic data can and has been applied to address questions of immediate relevance to fisheries management. WGAGFM is convinced of the benefits incorporation of genetic data into the DCF can bring. In order to achieve this outcome it would be useful if at a political level ICES initiated an informative mutual dialogue on doing so with relevant stakeholders such as DGMARE, ICES Stock Assessment Working Groups, and national and local fishery managers.

Genomics of marine organisms can contribute to better understand how they can adapt to variation of environmental factors in the wild or under aquaculture conditions. In the wild, environmental variation can result from climate change, acidification of oceans, increasing levels of pollutants or fisheries. In aquaculture, adaptation

can result from changes in rearing practices or to the extension of new pathogens. Adaptive responses can have phenotypic and genetic components that must be disentangled to model the evolutionary response of species. Monitoring of the genetic components of local adaptation in fisheries and aquaculture is required in view of changing selective pressures such as global change and fisheries induced evolution affecting productivity. Understanding of the dynamics of fitness, an important determinant of local adaptation in populations, requires the integration of the various levels linking genotypic to phenotypic variation.

1 Opening of the meeting

The Working Group on the Application of Genetics in Fisheries and Mariculture (WGAGFM) met in Bangor, Wales from 4–6 May 2011. The Terms of Reference (ToR) were decided by ICES Science Committee in Nantes, France, in 2010. Dr Geir Dahle (Norway) chaired the meeting, which opened at 09:00 on Wednesday, 4 May and closed at 12.30, Friday, 6 May 2011.

1.1 Attendance

Twenty four persons from eleven countries (Belgium, Denmark, France, Iceland, Ireland, Italy, Germany, Norway, Poland, Spain, and UK) attended the meeting (Annex 2). The meeting was also attended by master and PhD students from Bangor University at different times during the meeting.

1.2 Venue

The meeting was held at the Environment Centre Wales in Bangor, and was hosted by Bangor University. The WG wishes to express their appreciation to the local host Dr Gary Carvalho and the rest of his staff at the University and School of Biological Sciences for their kind hospitality and assistance. The meeting venue was ideal with hotel available in walking distance from the accommodation for the meeting. The venue had a big room with projector and also small meeting room for group meetings.

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 each 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.

2 Adoption of the agenda

2.1 ToR a) Oceanographic–genetic coupling in elucidating population genetic structure in exploited marine fish

Gary Carvalho and Dorte Bekkevold

2.1.1 The dynamics of marine systems:

Despite the long tradition of fisheries oceanography, which has its origins in the work of Johan Hjort (1914, 1928) with emphasis on the link between the dynamics of fish populations and the dynamics of their environment, it remains a formidable challenge to characterize and predict the recruitment and population dynamics of most exploited marine fish. General mechanisms of environmental control have focused mainly on the abundance, growth and survival of egg and larvae (Hjort, 1914; Cushing, 1975), while ocean physics have been assumed traditionally to influence fish by regulation of the availability of larval food, i.e. the plankton production (Leggett and Frank, 2008). However, increasing evidence shows that the marine environment is highly variable in space and time. Associated with this, the effects of physical features such as currents, fronts and eddies on the transport of material can fluctuate on a range of scales. Understanding their interaction with biological variation in life history, development and behaviour remains a central goal for effective integration of population ecology, conservation and management. While some data show clearly the predictive links between various biological and physical factors and dispersal (Bradbury and Snelgrove, 2001, Selkoe *et al.*, 2006, Bradbury *et al.*, 2008, White *et al.*, 2010), others demonstrate that larval connectivity is inherently an intermittent and heterogeneous process on annual time-scales (Bay *et al.*, 2006, Siegel *et al.*, 2008, Galarza *et al.*, 2009), driven especially by the advection of planktonic larvae by chaotic oceanic circulations.

Population connectivity refers to the exchange of individuals among geographically separated subpopulations – encompassing the dispersal phase from reproduction to the completion of the settlement process (including habitat choice and metamorphosis). It is becoming increasingly clear that establishing trends in patterns of population connectivity and genetic differentiation will require a sound understanding of detailed case studies (e.g. Selkoe *et al.*, 2008), in which multiple factors and their interactions can be explored.

A combination of difficult to measure factors, often acting in concert, will influence distribution and abundance, including historical events, life history variation (e.g. timing and distribution of eggs, larval behaviour), the location of feeding, spawning and settlement sites, adult movements, the nature and extent of population connectivity, a plethora of mortality factors (natural and anthropogenic), and physical processes affecting dispersal.

2.1.2 How can we assess population connectivity?

In an effort to understand these processes and their effects on dispersal, a wide variety of methods to directly measure dispersal have been applied, including; artificial and natural markers in the calcified structures, satellite tagging, and genetic assignment.

Fluorescent compounds (e.g. tetracycline or calcein), elemental markers (e.g. rare earth elements), and radioactive isotopes (Jones *et al.*, 1999; Moran and Marko, 2005;

Thorrold *et al.*, 2006) have all been used to artificially tag the calcified structures of marine species (e.g. shells, otoliths, and statoliths reviewed by Thorrold *et al.*, 2002). The marked larvae are released at their natal locations to allow natural dispersal, with the recapture of individuals in the target populations. However, because of high larval mortality rates significant portions of the total larval population must be tagged. A recent development that may overcome this is the TRAnsgenerational Isotope Labeling (TRAIL) technique, based on maternal transmission of an enriched stable Barium isotope incorporated into the embryonic otoliths of larval fish, (Thorrold *et al.*, 2006), this allows the tagging of a much larger proportion of the total larval production (Almany *et al.*, 2007; Pecl *et al.*, 2010), and is particularly useful for species that form large spawning aggregations. Natural variations in environmental conditions, including temperature, salinity, and seawater chemistry can also be exploited as these generate natural tags by determining the elemental or isotopic composition of the calcified structures of marine organisms. As structures such as otoliths are chemically inert, once laid down the chemical characteristics of the otolith records changes in the seawater composition or temperature, with the innermost core of the otoliths reflecting the origins of the fish as an egg/larvae (Swearer *et al.*, 1999; Thorrold *et al.*, 2001). The ability of these natural tags to track larval movement depends upon the existence of substantial variation in the elemental composition of the seawater among locations of interest (Thorrold *et al.*, 2002). Additionally all of these otolith based methods are lethal, and so are not practical for small or endangered populations.

Technological advances in satellite tracked tags, such as Archival and Pop-up tags have demonstrated the nature of the spatial connections across oceans for a growing range of species with highly mobile adults, such as tuna, salmon, whales and sharks (e.g. Eiler 1995; Eckert and Stewart, 2001; Boustany *et al.*, 2002; Block *et al.*, 2005: Cartamil *et al.*, 2011). However, these methods are extremely expensive, with tags costing between $3,500 and $5,000, hence the restriction of their use to these larger and/or commercially important species.

Genetic estimates of population connectivity can be made with assignment via variable molecular genetic markers to calculate the probability of assigning an individual either to a source population, or to a set of parents (e.g. Jones *et al.*, 2005; Rios-Cardenas and Webster 2008). However many of the analytical programs require that all potential source populations, or potential parents are sampled. Additionally, population assignment methods are most effective when the effective migration rate (Nm) < 5 (Waples and Gaggiotti, 2006) and level of genetic structuring is high (Cornuet *et al.*, 1999), suggesting they may be most useful in determining patterns only when connectivity is low. Population assignment and parentage tests are conceptually similar to studies using environmental signatures (see above) however, very few studies have combined genetic markers and otolith microchemistry to specifically address population connectivity (Miller *et al.*, 2005; Higgins *et al.*, 2010).

The oceanographic modelling of movement of larvae and juveniles is composed of two main aspects, the integration which is a major challenge; the *physical* aspect is determined by the oceanic processes which transport and disperse the larvae, and the *biological* aspect determined by the timing of spawning, larval behaviour, and mortality. While the processes affecting larval transport are known, these processes are complex, and small differences in their starting location can result in large differences in the destination of larvae. These processes include buoyancy-driven flows, tidal currents, wind-driven transport, internal waves and tides, surface waves, and turbulence and are particularly complex in coastal regions (Ridderinkhof and Zimmerman,

1992). Additionally although population connectivity in marine populations is often dominated by the dispersal of non-swimming or weakly swimming early life stages (e.g. eggs, spores, larvae, juveniles), even simple larval behaviour such as selective tidal stream transport (e.g. vertical swimming phased with tidal motions, Forward and Tankersley, 2001) can lead to the organisms having trajectories that are drastically different from those of neutrally buoyant particles (see, for example, Simons *et al.*, 2007). While there is still a need to resolve oceanographic transport and dispersal with Lagrangian measurements and for this to be done in an appropriate manner to accurately simulate larval dispersal, it is crucial that studies of dispersal based on physical oceanographic observations are compared with results from demographic, microchemical tagging, and population genetic studies (e.g. Palumbi and Sotka, 2006). In general these methods of estimating dispersal rates are good at estimating connectivity or retention over short time-scales, i.e. a single or a few generations, but these snapshots are unlikely to document stochastic events (e.g. hurricanes) or recurrent environmental patterns (e.g. El Niño/La Niña-Southern Oscillation) on connectivity and demography.

It is no surprise therefore that our understanding of population dynamics and spatial distribution in marine fish is especially obscure when compared to other biological systems (Selkoe *et al.*, 2008), though certain approaches and the use of long-term datasets do yield informative insights (Hauser and Carvalho, 2008). Here, we examine recent advances in the coupling of genetic and oceanographic approaches in elucidating population connectivity in marine fish, and importantly, we examine the utility of combining such interdisciplinary approaches into a predictive framework.

2.1.3 Why is knowledge of population structure important?

The genetic population structure of fish, in common with all taxa, describes the temporal and spatial distribution of genetic diversity; whether for example, populations from different geographic areas exhibit low levels of among-population genetic differentiation, or whether analogous groupings are genetically distinct.

Based on fundamental assumptions relating to population size and response to environmental pressures, the former case would suggest regular interbreeding throughout the sampled range, whereas in the latter case, infrequent interbreeding would allow the accumulation of biological differences, some of which may enhance survival and reproduction in local habitats. Crucially, we refer to "populations" as assemblages that are genetically distinct, and usually with some restriction to gene flow from proximate populations, allowing the detection of genetic differences. If such detectable differentiation is shown to be temporally stable, the assumption made is that such units will exhibit some level of demographic independence. However, the converse is not necessarily true: that assemblage showing no detectable population differentiation will be demographically open. Thus, here we focus on the utility of oceanographic and genetic data to explain the primary drivers of *genetically discrete* assemblages. Linked to population genetic structure is the concept of population connectivity: the exchange of individuals among geographically separated subpopulations – encompassing the dispersal phase from reproduction to the completion of the settlement process (including habitat choice and metamorphosis).

Such information is relevant to the management of exploited fish resources for several key reasons. For example, the extent to which populations self-recruit or receive migrants from other populations impacts significantly on processes that influence population regulation and persistence, together with the potential for local adaptation.

2.1.4 Defining Connectivity

Distinguishing between genetic and demographic connectivity is pertinent here: genetic connectivity depends mainly on the absolute numbers of effective migrants (those that contribute reproductively to the next generation), whereas demographic connectivity is driven by the relative contributions to population growth of rates of dispersal vs. local recruitment (that is survival and reproduction of residents (Lowe and Allendorf, 2010). Furthermore, genetic differentiation among populations integrates dispersal patterns over many generations, while demographic connectivity may be variable between seasons, years and climate regimes (Hauser and Carvalho 2008). Studies that incorporate a time-series across spatial scales combined with simultaneous genetic and oceanographic estimates of connectivity, allow a shift from descriptive (levels and patterns of structuring) to mechaniztic (drivers of patterns) consideration. This integrative approach enhances the prospects for generating predictive estimators of population structure.

2.1.5 Genetic markers

Adequate delimitation of genetic structure is crucial if the impact of oceanographic currents on the dynamic and evolutionary processes of marine organisms is to be understood. Molecular Ecologists now employ a wide range of genetic markers, analytical procedures and statistical indices, among which the choice techniques employed in oceanographic-genetic coupling exercises will depend on the questions to be answered (Manel *et al.* 2010).

Highly polymorphic microsatellites offer the advantages of high levels of genetic variability arising from high mutation rates combined with many allelic states, which are invaluable when evaluating recently emerged genetic structures (Payseur and Jing 2009), or those of species with large population sizes (because of slow drift), characteristics typical of many marine European organisms. The traditional constraints of slow and expensive microsatellite development (Zane *et al.,* 2002) can now be overcome through next-generation sequencing (Santana *et al.,* 2009). Cross-calibration among laboratories and studies, and the impact of technical scoring errors may undermine their employability in larger projects (LaHood *et al.,* 2002; DeWoody *et al.,* 2006), but standardized quality controls and checks can be undertaken (Ellis *et al.,* 2011). Novel and corrected estimators of differentiation are available (Jost 2008; Meirmans and Hedrick 2011) to cope with the problems of classical estimators of differentiation (i.e. F_{st}) in conveying adequate notions of differentiation and connectivity when employing highly polymorphic markers (Hedrick 2005; Jost 2008). This shortcoming has contributed to the apparent low levels of structuring recorded in many marine organisms (O'Reilly *et al.,* 2004; Carreras-Carbonell *et al.,* 2006; Heller and Siegismund 2009). When employing highly polymorphic markers or when comparing different types of markers (Hemmer-Hansen *et al.,* 2007), these novel estimators of differentiation provide a more intuitive statistic of connectivity, and being standardized, would be better suited to comparisons with oceanographic models (Selkoe *et al.* 2010; White *et al.* 2010).

Recently there has been a shift from anonymous markers such as microsatellites to direct analyses of sequence variation including single nucleotide polymorphisms (SNPs). This shift has evolved from the initial uptake of such markers in humans and other commercially important species, to their application in a wide range of non-model species. SNPs are attractive markers for many reasons (for reviews see Brumfield *et al.,* 2003; Morin *et al.,* 2004; Helyar *et al.,* 2011), including the availability of numerous annotated markers, low-scoring error rates, relative ease of calibration

among laboratories compared to length-based markers and the associated ability to assemble combined temporal and spatial datasets from multiple laboratories. Additionally, the potential for high-throughput genotyping improved genotyping results for poor quality samples [such as historical, non-invasive or degraded samples (Morin and McCarthy 2007; Smith *et al.,* 2011)], a simple mutation model, and the ability to examine both neutral variation and regions under selection offers unparalleled scope for expansive screening of genomes and large sample sizes from natural populations. However, identifying the most appropriate genetic marker for empirical estimates of differentiation is an issue that is unlikely to be settled easily, especially considering temporal scaling and influence of other factors, including selection (Galindo *et al.,* 2010).

2.1.6 Adaptive vs. Neutral molecular markers

Detected population genetic structure can be the product of several processes, and differentiating (1) the mechanical effects of oceanographic currents, from (2) random genetic drift, and (3) local selective pressures and adaptation, will require careful examination. One way to differentiate genetic structure due to local adaptation from that resulting from drift or oceanographic currents is to follow an adaptive marker approach where neutral and putatively adaptive genetic diversity are analysed independently (Manel *et al.* 2010). Marine habitat variables like local temperature, salinity regimes, and even anthropogenic impacts are expected to leave stronger signature of differentiation (due to selection) on actual genes involved in the adaptive processes of populations to their local environment (Hemmer-Hansen *et al.,* 2007, Narum *et al .,* 2010; Narum and Hess 2011). Therefore, patterns of significant correlation between given environmental variables and adaptive genetic variation, as opposed to neutral variation, will thus indicate a substantial role of the surrounding environment compared to what can be inferred from purely neutral genetic variation. Adaptive markers with strong allelic differences among locations may be useful to detect demographic connectivity (first generation migrants); but being under selection they may be ineffective and underestimate detection of long-term genetic connectivity among locations.

Many studies have demonstrated how standing neutral genetic variation reflects historical geographical separation, including, Atlantic wolffish (McCusker and Bentzen 2010) and European sprat (Debes *et al .,* 2008). And indeed, genetic drift differentiating populations in allopatry during, and after the last glacial maxima (LGM; ~10-20,000 YA) have left strong signatures of population differentiation that still dominate current genetic patterns in many Northeast Atlantic species (Chevolot *et al.* 2006; Hoarau *et al.* 2007; Pampoulie *et al.* 2008; Maggs *et al.* 2008).

Once differentiation due to adaptive and/or allopatric drift processes is removed from the studied system, the importance of oceanographic features (i.e. ocean currents, local eddies, stable fronts, and storms) in explaining patterns of differentiation can be evaluated. Oceanographic features can either act as migration barriers reducing gene flow and leading to genome wide genetic differentiation due to drift(Galarza *et al.* 2009); or catapulting otherwise sessile individuals among populations and homogenizing genetic diversity. These effects on population connectivity can be modelled/simulated and the resulting simulated genetic patterns compared to empirical observations (Galindo *et al.,* 2006; Galindo *et al.,* 2010), allowing the testing of ecological hypothesis.

2.1.7 Oceanographic modelling

For many decades, there has been an interest in determining the oceanographic processes that delineate the distributions of individuals, populations and species in the sea. Specifically, it is of interest to describe the oceanographic processes that respectively mediate transport and retention in a spatio-temporal setting. In relation to climate change, the field has become even more important in attempts to predict future fish distributions, based of changes ranging from destabilization of entire global circulatory systems to de- or acceleration of local currents, discharge, buoyancy and temperature regimes (Lenoir *et al.*, 2011). In many marine fish and shellfish, dispersal is dominant during a pelagic larval phase that is followed by settlement and less migratory life stages, and a main focus has been the study of oceanographic vectors for transport of eggs, larvae and juveniles from spawning sites. Here, the recruitment and productivity of a species in a particular area will depend on the oceanographic vectors for movement from spawning to nursery habitat, and oceanographic changes may thus lead to passive advection of eggs and larvae into suboptimal or unsuitable habitat, and may thus conversely lead to spatial changes in spawning habitats.

Galindo *et al.*, (2006) coined the term '*seascape genetics*' in their use of population genetic methods - typically employed in the field of 'landscape genetics' - applied to the marine environment. This landmark study used a coupled oceanographic-genetic modelling approach to understand how 'seascape' (landscape) features impacted on population connectivity. Coupled biological and physical oceanographic models provide powerful tools for understanding marine population connectivity. Such approaches can be used to simulate the dispersal of marine larvae, based on oceanographic features (e.g. currents/gyres/eddies) and informed by the biological characteristics of the organism in question (e.g. pelagic larval duration/salinity tolerance, etc.), often derived from laboratory studies (Pfeiffer-Herbert *et al.*, 2007). Typical biophysical modelling outputs include a series of connectivity matrices, predicting larval dispersal over relatively short geographic and temporal (i.e. several years) scales.

2.1.8 Oceanographic–genetic coupling – the approach

Population genetic models examining meta-population connectivity commonly assume that migration and dispersal fit either an island or a stepping stone model using Euclidian distances to predict the spatial distributions of dispersing life stages.

At broad scales (>500 km), such assumptions may be largely valid, as corroborated by the multitude of empirical studies demonstrating that genetic isolation increases with distance. However, at small to intermediate scales (10–500 km), mere linear distance is unlikely to present a good model predictor, as oceanographic features like currents and fronts are likely to have a substantial effect on rates of dispersal. Even passive transport along a relatively straight coastline is typically stochastic and unpredictable (Siegel *et al.*, 2003, 2008). Passive transport of eggs and larvae in the pelagic zone can, for example, respectively be either facilitated (in one direction), or halted (in the other direction) by currents, and eddies and turbulence may act as barriers across even relatively small spatial scales. However, if such oceanographic processes can be incorporated as model parameters, increased accuracy in population genetic models can be expected. Thus, incorporating oceanographic realism into genetic studies, while presenting a challenge and requiring modified model assumptions, can yield increased accuracy in population identification and, possibly, valuable insights into drivers of genetic population structure. Variance in the magnitude of gene flow and effective population size (broadly, the reproductive contributors) may lead to a corre-

sponding array of population structures (Figure 2.1.1). Populations may be entirely closed (all recruits from within), which will endow them with full demographic independence, or completely open (all recruits from other populations), where population fluctuations depend entirely on patterns of emigration and immigration. More likely, natural populations of marine fish will fall somewhere between these two extremes, where samples may exhibit progressively reduced genetic similarity with increasing geographic distance (stepping stone gene flow).

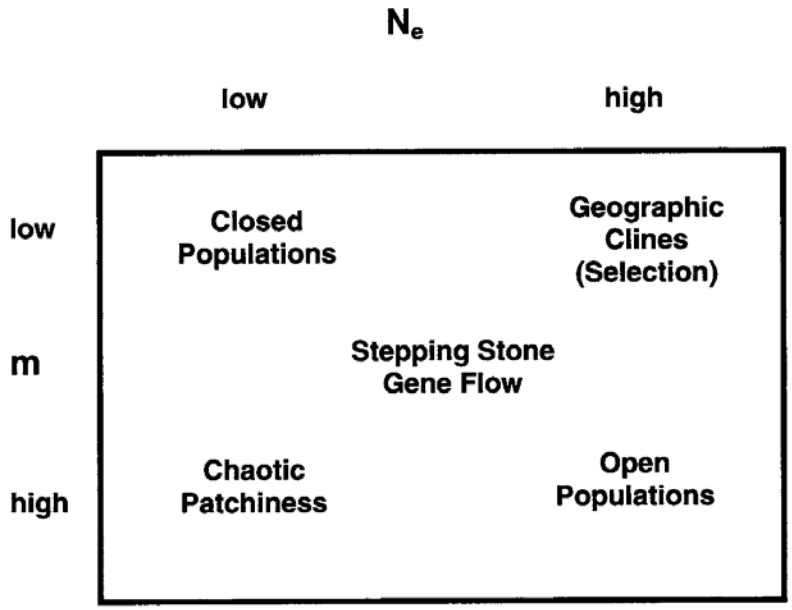

Figure 2.1.1. Combinations of gene flow (m) and effective population size (N_e) associated with different patterns of population structuring. Historical effects must also be considered, especially for species with low levels of gene flow. After Hellberg *et al.*, (2002).

To date, the main approach has been to use a land- or seascape genetic framework, combining genetic information with information about seascape features like basins, trenches or main currents, and has been successful in linking strong population genetic breaks with major oceanographic boundaries (Barber *et al.*, 2002; Gilg and Hilbish, 2003; Bekkevold *et al.*, 2005, Baums *et al.*, 2006; Galindo *et al.*, 2006; Kenchington *et al.*, 2006; Dupont *et al.*, 2007; Fontaine *et al.*, 2007; Schultz *et al.*, 2008; Galarza *et al.*, 2009; Knutsen *et al.*, 2009; Pelc *et al.*, 2009; Yasuda *et al.*, 2009, Galindo *et al.*, 2006; Selkoe *et al.*, 2008). To date, however, few studies have attempted to link seascape factors to patterns of genetic differentiation at finer spatial scales (<500 km) relevant to management (Banks *et al.*, 2007; Fievet *et al.*, 2007; Selkoe *et al.*, 2010, White *et al.*, 2010).

For those marine species and populations where dispersal is not (predominantly) passive, instead taking place during adult life-stages in response to environmental and biological (incl. reproductive and behavioural) cues, a useful approach may be to apply 'landscape matrix' or 'landscape resistance surface' modelling to assess the distribution and movements of individuals. The principle behind these approaches is to estimate the 'effective distance' as some measure of separation between sampling sites or individuals that incorporates multiple effects of environmental and biological variables that affect the permeability across the matrix. Such matrix is thus assumed

to represent the functional connectivity or the ability of individuals to move between geo-referenced locations. However, in contrast to recent developments in terrestrial landscape genetics (e.g. Spear and Storfer, 2010), knowledge of individuals' physiological habitat requirements during dispersal and corresponding probability of moving through environments that differ in terms of 'habitat resistance' or 'landscape permeability' is generally too limited to be parameterized in seascape analyses. Schultz *et al.,* (2008) found a positive relationship between genetic differentiation and what they termed 'oceanographic distance' which incorporated minimal distances traversed at specific depths and temperatures known to be physiologically constraining in two species of lemon shark. In contrast, no relationship was detected between genetic differentiation and either geographical distance or maximum depth, showing the value of incorporating this type of information in attempts to elucidate which factors determine genetic structure for specific species and populations. Developing these types of analyses, where knowledge of (population specific) physiological tolerance and behaviour is incorporated is expected to yield high power for understanding population connectivity, also at sea. However, it is also expected that there will be limits to the scales of functional connectivity that can be resolved, especially at high environmental complexity and when the contrast between the permeability of land (or sea-) scape elements is low (Jaquiery *et al.,* 2011), which may often be the case for marine organisms. In some cases, it would also be of interest to combine hydrodynamic drift models with the resistance matrix based models, for example in cases where main dispersive life stages differ among populations (e.g. in Atlantic herring, see Gaggiotti *et al.,* 2009).

2.1.9 Temporal mismatch between oceanographic and genetic data

A key issue when coupling oceanographic and molecular data are how to manage the temporal mismatch between them. Molecular data are likely to reflect long-term 'averaged' evolutionary processes, while the physical data reflect the very recent short term. Climatic shifts over the longer term are difficult to model, as past variability may have impacted significantly on global oceanic circulation patterns. Nevertheless, global oceanographic models, implemented within platforms such as NEMO (Nucleus for European Modelling of the Ocean), help to circumnavigate this problem, by predicting future, and retrodicting historical, oceanic variability. These models may be particularly useful for formulating hypotheses regarding past or future genetic connectivity in some regions that are more 'climatically homogeneous' (e.g. the North Atlantic), but the models are recognized to perform poorly in others (e.g. the Southern Ocean), where climatic warming trends are inconsistent over short geographic scales. More climatic data are therefore required, particularly from regions such as the Southern Ocean, to better inform the physical models.

Within the shorter term, major climatic influences can drastically affect connectivity, and should be parameterized within the model. These events include periodic widespread (inter-basin) oscillations, such as El Niño/La Niña, and more regionally, the Southern- or North Atlantic Oscillation (SO), for example. These climatic drivers will influence wind-driven currents, fronts, tides, and surface- and bottom-boundary layers and mixing, for example, which in turn will have large effects on both biological and physical connectivity (matrices). Oceanic response to these climatic forcing events is today routinely hindcast successfully, attesting to the quality of the data and ability of the models to capture this variability (Werner *et al .,* 2007). At smaller geographical scales, such as within shelf or coastal regions, other factors come into play, and have been modelled with varying degrees of success (Werner *et al .,* 2007). Public

domain models, such as the Regional Ocean Model System (ROMS) and the Princeton Ocean Model (POM) provide the tailoring of site-specific applications to regional forecasting. Further, established protocols for the use of these models exists, alongside recognized model limitations. The importance of data quality and validation for these models has been recognized and reviewed (Bellocchi *et al.,* 2010, and references therein).

Most of these models also allow for incorporating temporal variation in hydrodynamics into predictions of fish distributions, yielding estimates of dispersal patterns both within specific years and for averages across time-scales of higher relevance for genetic processes. Some models further allow for analyses simulating rare stochastic events (such as cyclones and El Niños) that could have repercussions for large-scale patterns of genetic connectivity. This type of modelling approach and developments hereof hold great promise for insights into the effects of hydrodynamics on passive transport of eggs and larvae from spawning sites.

2.1.10 Basic principles of seascape genetics

Over the past decade, marine population genetics has seen a dramatic shift from the traditional approaches to investigate genetic differentiation on the basis of geographic distance, to an increasingly preponderant use of oceanographic models. Palumbi (2003) was perhaps the first to raise the standard from this point of view, by integrating dispersal potential in the Gen/Geo relationship. Knutsen *et al.,* (2004) and Bekkevold *et al.,* (2005) represent examples based on hypothesis testing (expectations from water flow in the former, and from salinity gradient in the latter). Manel *et al.,* (2003) more or less "coined" the term "landscape genetics" (to date the most highly cited on the subject, with nearly 500 citations): the marine world followed suit and went for "seascape" (Galindo *et al .,* 2006), but this term is still used somewhat inconsistently: Fontaine *et al.,* (2007) largely referred to Geneland-type clusters, while Selkoe *et al.,* (2008) specifically intended the use of physical and biologically modelled scenarios to contrast with empirical population genetic data. This effectively prepared the ground for the two recent papers: White *et al.,* (2010) and Galindo *et al.,* (2010).

Several studies have examined the concurrence of genetic breaks and large-scale oceanographic features whereas few studies address the effect of oceanographic processes on population structures on smaller scales. Two of the main reasons for the paucity of the latter, have been 1) the relatively low levels of population differentiation that are observed in marine species, resulting in weak resolution for distinguishing among local population components, and 2) the difficulty with parameterizing the 'perceived' dispersal distance, incorporating major oceanographic parameters across space and time. A fairly recent, and potentially very useful, approach for addressing the effects of oceanographic processes on small-scale population structure and connectivity is to combine inference from population genetic data with a 'particle advection simulation approach' (Mitarai *et al.,* 2009) to estimate dispersal probabilities between population pairs. The simulations are typically based on a high-resolution three-dimensional hydrodynamic model of the study area, where passive particles (simulating fish larva) are 'released' at species-specific spawning sites, -depths and -times, and tracked over a time-span reflecting the duration of the pelagic larval phase. Dispersal probabilities can then be estimated among patches (also incorporating interannual variation) and compared with genetic marker-based estimators of dispersal rates.

2.1.11 Case studies to illustrate utility and applications

2.1.11.1 White *et al.* (2010) case study

White *et al.,* (2010) showed that the frequency of larval exchange introduced by ocean currents could explain nearly 50 per cent of the variance in empirical genetic differences. Such detail can change the interpretation of empirical population genetic structuring. They prepared a sophisticated "derived oceanographic distance" based on a variety of physical data obtained from particle modelling across a grid, which explained empirical genetic data much more exhaustively than simple Euclidean distance. The approach of combining genetic and oceanographic data were achieved in five steps. First, he calculated single annual matrices which were given information about the frequency with which the larvae released from nearshore grid cell *j* dispersed with ocean currents to grid cell *i* (given the spawning season and larval settlement competency window). In a second step he focused on combining data from whole experiment periods and he standardized the values in the all-years matrix. Next, he incorporated the effects of multi-generational gene flow on the long-term probability of dispersal between locations, followed by averaging uni-directional dispersal probabilities to estimate mean probability of dispersal between pairwise locations. Finally he performed the isolation-by-distance analysis tests requiring conversion of the matrix of mean dispersal probability into a distance matrix.

2.1.11.2 Treml *et al.* (2008) case study

Treml *et al.,* (2008), building on earlier theoretical work (e.g. Roughgarden *et al.,* 1988, Possingham and Roughgarden 1990, Gaylord and Gaines 2000), were the first to apply a 'graph-theoretic framework' (West, 2001) to understand the influence of pelagic larval duration (PLD), and interannual sea-surface current variability, on population connectivity of coral larvae in the tropical Pacific. This study simulated coral larval dispersal over three years, including strong El Niño and La Niña years, and a third 'neutral' year. Such climatic events are known to impact substantially on circulation patterns in the Pacific (Glynn and Ault, 2000) and elsewhere, and could thus potentially affect dispersal pathways. Model parameter estimates included: initial concentration of larvae, time of coral spawning, larval mortality and pelagic larval duration, and included the inclusion of a mortality component. Results suggested that coral dispersal in the Pacific was on average some 50–150 km, and that major ocean currents and islands provided pathways and 'stepping stones', respectively, for larval coral dispersal.

2.1.11.3 Kool *et al.* (2009) case study

Kool *et al.* (2009) developed a 'matrix-based projection model', used in conjunction with a coupled biological-physical larval dispersal model, to understand dispersal dynamics within coral reef patches of the Caribbean. In this case, the contribution of spatially-explicit migration to the development of population genetic structuring was taken into account. Transition matrices of the probability of dispersal between populations were modelled using 'individual-based Lagrangian particle tracking'. This method allows biologically-informed 'particles' to advect and diffuse based on documented oceanic current data. Settlement and retention was then parameterized into the model based on established biological information. To project expected genetic structure forward in time, the authors used a modified version of the matrix-based approach of Bodmer and Cavalli-Sforza (1968; see Kool *et al.,* 2009 for specific details). Results identified a strong genetic break between eastern and western coral

reef patches, and a gradient along the Bahamian archipelago, consistent with empirical data on corals (Baums *et al.,* 2005) and coral-reef fish (Taylor and Hellberg, 2003). The modelling also indicated various islands (e.g. Jamaica, Caymans) were potentially important stepping-stones facilitating connectivity. The method thus generated novel hypotheses, which could be tested with additional empirical datasets from coral and coral-reliant taxa.

2.1.11.4 Galindo *et al.* (2010) case study

Galindo *et al.* (2010) used an elaborate modelling approach in the attempt to explain a long-established genetic cline in populations of the barnacle *Balanus glandula*, along the Monterey Bay coast. First, the environmental and biological backdrop was built through a coupled biophysical dispersal model. This model integrated, on one hand, oceanographic and physico-chemical parameters recorded both remotely and in-situ, and on the other hand, productivity, plankton and 3D habitat distribution of *B. glandula* larvae during ontogeny. Second, a 'connectivity matrix' among the studied locations was devised using a particle tracking approach. Third, simulated genetic structure patterns were produced, using as 'yardsticks' the most northern and the most southern populations, and allowing allelic frequencies to vary among locations, depending on a range of settings of the connectivity matrix (including three additional settings that assumed, respectively, i- increased larval retention, ii- increased larval output from the south, iii- increased selection coefficients for the southern alleles in the southern location). Finally, the simulated 'expected' genetic structure patterns were compared with the empirically observed genetic data using a simple sum-of-squares approach. Interestingly, in this case, predicted genetic patterns did not match empirical results, failing to identify the genetic cline existing at both mitochondrial and nuclear DNA markers. However, the three scenarios that included differentials in larval output, larval retention and selection for local alleles – and a combination of these – yielded a refined picture by explaining over 90% of the empirically observed pattern.

The study is rather exemplary in incorporating a wealth of information on the environmental and biological context that can explain spatial genetic structure. Even when initial models seem to fail to predict empirical data, the introduction of additional testable hypotheses can allow the incorporation of 'adjustments' to improve the efficacy of the model. The authors used their wisdom to advance what mechanisms could be introduced to improve the model, and both increased larval retention and local selection are plausible factors, but it remains to be seen how many additional drivers – or variations of these – could have also helped improving the model. The risk here is to 'cherry-pick' solution to force the model to work fine. How robust is it to assume a certain selection coefficient in one specific area? What could the specific selective agents be (also considering the markers employed)? The fitting of the model does not necessarily implies that the environmental and biological drivers of a given genetic structure pattern have been identified.

Future studies should look into the criteria used to choose predictive variables. Further work will be required to match the nature of the built predictive model with *a-priori* choices of genetic markers that are expected to respond to the environmental background developed.

See synthetic diagram below:

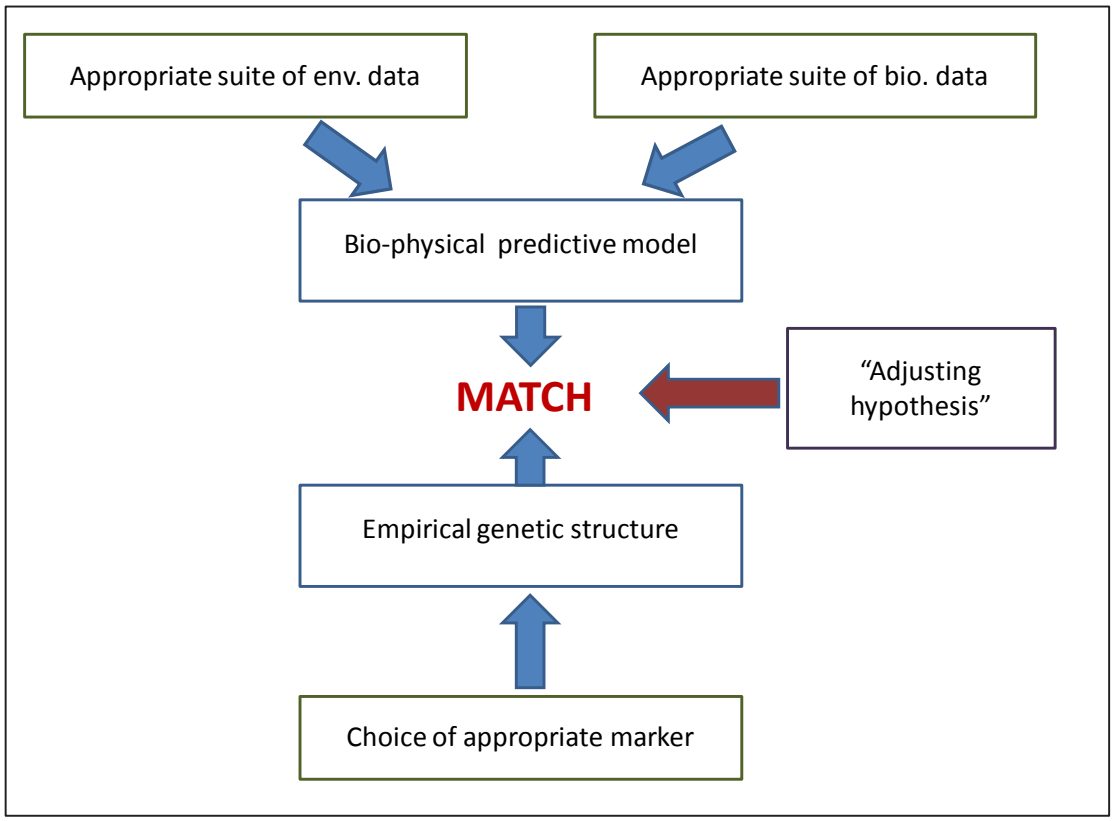

Figure 2.1.2. Schematic model of best practice for examining match/mismatches between empirical population genetic patterns and possible biological and environmental predictors.

2.1.11.5 Selkoe *et al.* (2010) case study

The work by Selkoe *et al.*, (2010) introduces two key novelties: a) a multispecies approach, and b) an additional step towards habitat mapping, by including 'kelp coverage' as a predictive variable in the biophysical model. This work identifies four main environmental variables (geographic distance, current flow, and temperature and kelp coverage) to be used as predictors of spatial genetic structure in three sympatric species (a teleost, a gastropod and a decapod crustacean). The analysis is conducted in a multiple regression fashion, with a generalized linear mixed model, and partial Mantel test (both techniques allow – with some limitations – to correct for multi-co linearity, respectively for genetic diversity and genetic differentiation). By analysing data from different species and including the four predictor variables, the authors manage, literally, to put some 'order in the chaos', arguing that even subtle differences at the limits of statistical significance and analytical power (Waples, 1998) can be interpreted by leaning on realistic environmental scenarios and looking at cross-species consistencies.

The approach attempts to address the issue of weak genetic differentiation, which in the past had been deemed as "chaotic patchiness" that could not be interpreted biologically. Although the approach suggested is perhaps susceptible to spurious correlations, it does effectively contribute to the debate on statistical vs. biological

significance, and also provides a first attempt to incorporate benthic habitat features, providing a mechaniztic prediction for adult organismal habitat suitability, whereby earlier oceanographic approaches had put most emphasis on earlier life-stages.

Caveats and pitfalls in oceanographic genetic coupling

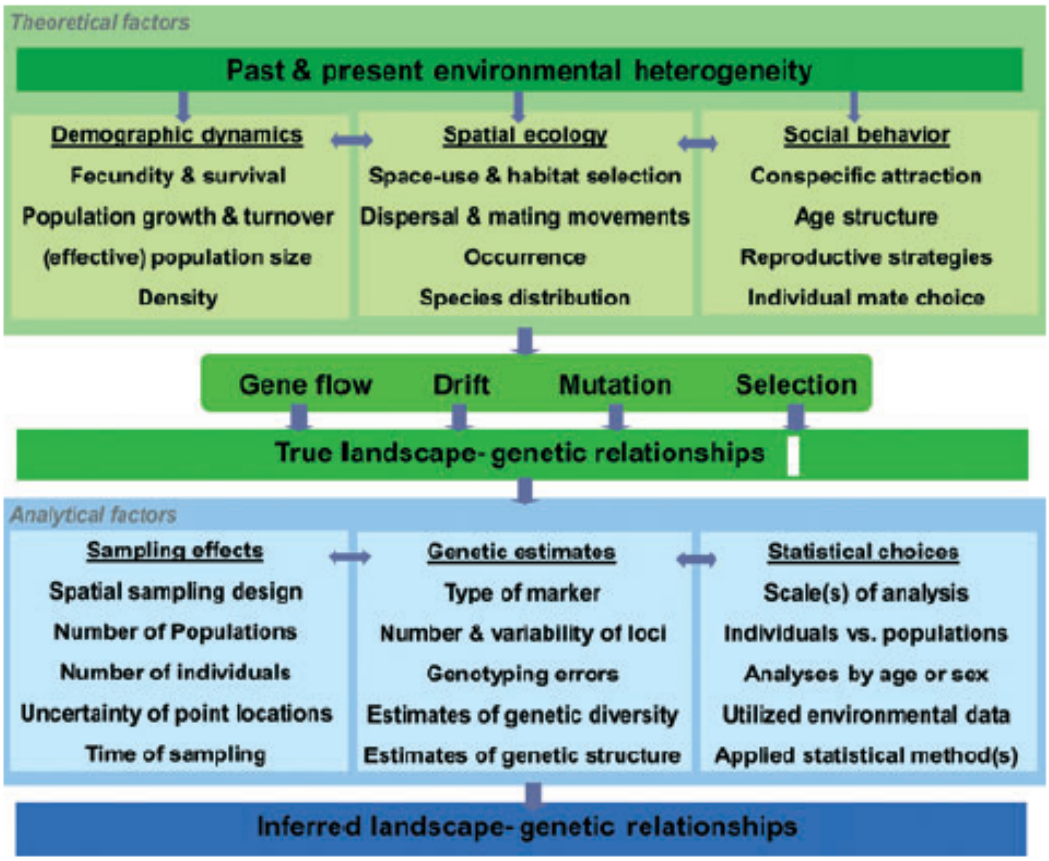

Figure 2.1.3. Theoretical and analytical factors that combine to infer landscape genetic relationships. Theoretical factors include the influence of past and present environmental heterogeneity (e.g. landscape composition and configuration, amount and quality of habitat and matrix, and disturbances) on demographic dynamics, spatial ecology and social behaviour. These combine with the four sources of genetic variation (gene flow, genetic drift, mutation and natural selection) to produce the true landscape-genetic relationships. Analytical questions revolving around sampling effects, genetic estimates and statistical choices then influence the correct inferences of the true landscape-genetic relationships.

The complexity of the factors to be considered when modelling the effect of environmental variables on genetic structure is shown in Figure 2.1.3 (Balkenhol and Landguth, 2011), and have been reviewed extensively (McRae and Beier 2007, Selkoe *et al.*, 2008 and 2010, Guillot *et al.*, 2009, Anderson *et al.*, 2010, Epperson *et al.*, 2010, Francois and Durand 2010, Storfer *et al.*, 2011, Thomassen *et al.*, 2010, Jaquiery *et al.*, 2011).

While some of these reviews included the marine environment, most were restricted to terrestrial ecosystems, and hence, the intrinsic differences between those two realms have to be considered. Balkenhol and Landguth (2011) review a list of questions/issues to be considered when coupling environmental and genetic models. We suggest adapting the following points (in italics) to the specific features of the marine environment to yield a concise list of caveats and pitfalls

2.1.11.6Theoretical questions (from Balkenhol and Landguth, 2011)

- What kind of scale dependencies in genetic diversity and structure can we expect to find for species showing different distributional patterns and behavioural traits (e.g. fecundity, dispersal, survival of offspring and dispersers)? (Focus on among-species level; comparative landscape genetics.)
- What influence does environmental heterogeneity have on within-population factors (e.g. local growth rates, density) and among-population factors (e.g. effective dispersal rates and distances) that determine spatial genetic patterns? (Linking landscape genetics with spatial population ecology.)
- How does individual, temporally explicit space-use behaviour (e.g. seasonal habitat selection, territoriality, mating and dispersal movements) impact gene flow and resulting genetic patterns in continuous populations? (Linking landscape genetics with individual-based spatial ecology.)
- How do individual, spatially explicit mate-choice and resulting fitness consequences affect the distribution of neutral and adaptive genetic variation within and between populations? (Focus on selection and evolutionary consequences; adaptive landscape genetics.)

Oceanographic models have now been developed to a high extent (even including scientific journal devoted to the development of them: e.g. Ecosystem Modelling). However, the comparison of genetic data with such models is relatively recent, and although specific approaches have been developed in the landscape genetics field, e.g. isolation by resistance distance theory (McRae and Beier, 2007), there remains a lack of genetic modules in existing modelling packages, such as Ecopath with Ecosim.

Moreover the number of studies integrating the modelling of oceanographic variables to investigate the population genetics of a marine organism is still scarce (e.g. Galindo *et al.,* 2010). There is a need to catalogue existing modelling packages including a module for genetic variation and/or including genetic measurements (F_{st}) as a variable. In this sense, individual based Bayesian clustering analysis, such as Geneland and STRUCTURE, perform a mere visual representation of spatial genetic data but no oceanographic variables are included apart from the geographical position of sampling hauls. ***So is there any available software to couple oceanographic and genetic data?***

Although PCA analysis does combine genetic and oceanographic variables, they are not suited to model trends in those. More recently, Bayesian models (e.g. GAM) may be better suited for landscape genetics approaches but still lack the adaptation of a powerful modelling software as the Ecopath with Ecosim, currently used in many marine institutes to model ecosystems, to integrate genetic variables within them. Therefore, most studies in seascape genetics are limited to the spatial analysis of gene frequencies, typically without including geographic information. These data within oceanographic models, including a range of variables covering from temperature and salinity to food requirements and mortality losses, and are not ideal to be used as proxies of the genetic response to future changes (climatic change). When modelling gene frequencies, factors that have to be taken into account, include among others: The fact that different life stages (eggs, larvae, juvenile, and adults) in marine animals are subjected in a different degree to the diverse range of oceanographic structures/factors.

Different time-scales are relevant to different oceanographic variables (e.g. river plumes extension vs. tropical fronts), how can we merge them in the same model? Moreover, how can we model the effect in gene frequencies of this different time-scales? In this sense, the fact that different molecular markers reflect processes taking place at different temporal scales (e.g.mtDNAvs.nDNA) could be of use. The use of other tools as e.g. otolith microchemistry in combination with molecular markers could help to address those questions.

Analytical questions

- What influence does the spatial distribution of samples (individuals or populations) have on the quantification of genetic patterns and on the inference of landscape–genetic relationships?
- Can we accurately quantify individual-based genetic structure and landscape–genetic relationships in animals with different home range behaviours when we only use a single point to represent the location of each animal?

Adequate sampling design, especially in marine environments, will play a crucial role in tackling these two issues. Whenever possible, grid-like sampling designs with even coverage of an area should be encouraged. However, fishery surveys are rarely designed to suit genetic analyses. Conventional sources of marine samples, such as uneven distributed fishing hauls, may not be optimal in spatially explicit analyses such as Geneland. How could we get the maximum benefit from those sampling designs? An additional problem arises when using trawling as sampling technique, where the sampling haul can be covering several nautical miles area, potentially sampling together different subpopulations. How can we reduce noise when analysing data?

- How should we best quantify environmental complexity for different datasets and different landscape genetic research questions? (E.g., least-cost paths vs. effective resistances; continuous vs. categorical data.)

How to measure spatial distances within marine ecosystems as to perform isolation by distance analysis? Calculate distances following coastal lines? How can we accommodate marine frontal structures / barriers in isolation by resistance distance approach as the one of McRaer and Beier 2007?

- How comparable and accurate are different analytical approaches for inferring the relative effects of different landscape variables on (individual-based) genetic structure?

2.1.12 The challenges ahead – in a management perspective

Seascape genetics has thus far employed ideas similar to the field of "landscape genetics". Currently the "resistance surface" approach – or "friction map" – has revived the field (McRae and Beier 2007, Spear *et al.,* 2010), with multivariate GIS-based landscape reconstructions which indicate areas of greater "resistance"/friction for dispersing organisms. Seascape genetics has mainly looked at oceanographic features to influence distributions of larvae; yet this by no means can be a fully exhaustive predictor of genetic structure and demographic independence. Can we produce **exhaustive multivariate resistance surfaces at sea**? Is it possible to employ such approaches **without them becoming too complex and cumbersome** to be effectively employed in the management arena?

The integration of Approximate Bayesian Computation (see Review by Bertorelle *et al.*, 2010) into the generation and testing of alternate models of mechanisms driving population genetic structuring in marine organisms would appear to hold great promise for this rapidly developing field.

Recommendations

We recommend that;

- multidisciplinary methods- e.g. genetic, direct tagging, demographic, behavioural, and oceanographic are integrated to address population connectivity
- spatio-temporal sampling schemes are carefully planned (micro-, local, regional scales) and should incorporate empirical knowledge or predictions from oceanographic models, e.g. distributions/habitat requirements of different life stages.
- analytical approaches (e.g. Approximate Bayesian Computation) are integrated into the generation and testing of alternate models of mechanisms driving population genetic structuring in marine organisms
- long-term empirical studies of genetic and environmental data are instigated to evaluate rare extreme events (such as ENSO, hurricanes etc.).

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2.2 ToR b) Networks of Marine Protected Areas – Dispersal, connectivity and seascape genetics

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2.2.1 Introduction

The human use of ocean resources is accelerating faster than our ability to manage them (FAO, 2010). To control, reduce and eliminate the discrepancy between available resource and the exploitation rate, management of resource and users is required. Historically the first management measures date back several centuries, but broad international agreements are less than a century old. Traditionally measures focused on effort (e.g. quota system of catches, number of fishing vessels and type of fishing gear), while spatial and temporal measures were considered less. Overall the efficiency of the effort-based management has been poor, given the overfished state of the majority of the global fish stocks (Worm *et al*. 2009; FAO, 2010). Two major developments are directing resource management into a more multi-disciplinary and multispecies based context. First spatial and temporal measures are increasingly gaining acceptance as a management tool of fish populations (e.g. FSBI 2001) and for the conservation of biodiversity (Agardy, 1997). Under the name of 'nature reserve', 'sanctuary', 'refuge', 'park', 'no fishing zone' and 'small-scale management units' (CCAMLR - Commission on the Conservation of Antarctic Marine Living Resources) small or large areas of the shelf and deep-sea area are restricted for human interference. This has lead to a global agreement to establish and manage 10% of the global marine space as Marine Protected Areas (MPA) by 2012 (CBD-UNESCO 2010). A second aspect is the growing awareness that the exploitation of the natural environment is set in an ecosystem context (Rice, 2011). The ecosystem-based management approach takes a holistic angle towards the ecosystem (Halpern *et al*., 2010). Although in temperate, deep-water and cold water fisheries typically single species are targeted, they do live in an ecosystem characteristic for and in equilibrium with the local environment. Hence, removing a top predator affects the dynamics of other top predators, their prey and through cascading effects nutrient regeneration, pH dynamics etc. (Scheffer *et al*., 2005). Fishing almost always leaves a signature on the ecosystem, varying from almost unnoticeable (exploratory fishery) to major effects (overfishing). The ecosystem based approach to fishing fits in a wider perspective of ecosystem based goods and services originating from the ocean (EcolEcon).

Spatial management of marine natural resources has the advantage to control and ultimately reduce conflicts between users and to preserve the integrity of the system. The - in principle - reduced open access (usually targeted to fishing, but also to other

uses such as mineral extraction, tourism, shipping, scientific research and navy activities) is regulated within a legal framework. To install and maintain a MPA, a decision cycle is used to set goals (Airamé *et al*., 2003). Once the goals have been set, agreement has to be reached on the spatial context and access between users. It is at this level that scientists can make a valuable contribution (Sutherland, 2006); scientific information may facilitate, guide and influence the decision process.

The definition of MPAs varies greatly from almost full access to exclusive no interference zones. Several categorizations have been proposed. A helpful classification is provided by IUCN.

MPAs may serve **different purposes** (FSBI, 2001). They may have conservation goals to preserve biodiversity in the context of the Convention of Biological Diversity (CBD-UNESCO, 2010), which includes biodiversity at the level of genes, species and ecosystems. Here any threat from overexploitation, habitat loss, pollution, climate change or exotic species should be mitigated as much as possible. A second goal may be the sustainable exploitation of marine resources by the fishery. Fisheries change at the generation level population characteristics such as age distribution, reproduction, stock structure, diversity and effective population size. Either way, both perspectives do not mutually exclude each other and share the aim to maximize the natural resource (Worm *et al*., 2009).

The **design of MPAs** includes questions related to size, size structure, spacing and coverage. What is the size of a viable MPA? Does it make a difference whether it affects sedentary or highly mobile organisms? Do all MPAs have to have the same size or is a patchwork of sizes more effective? What is the distance between the large and small MPAs? How much coverage is needed before a MPA system makes a measurable and effective impact? Does one design one single large MPA or a patchwork of small and large sized MPAs?

MPAs are largely set in an **ecological context**. Demography and ecophysiological traits, foodweb dynamics, habitat and landscape characteristics, and the biodiversity portfolio differentiated by life stage (life cycle triangle) set the stage. However, in the long-term evolution is an important motor of adaptation to changing conditions. This may happen over just a few generations (fisheries induced evolution, Jørgensen *et al*., 2007), but usually acts over geological time periods (evolutionary significant units, Avise, 2000). In the current context of fast global change, the adaptive potential harboured in genetic biodiversity is an important asset. Major progress in access to highly sophisticated genetic tools, makes it feasible to reveal patterns and processes which otherwise would have escaped attention. The aim of this paper is to highlight the role of the genetic blueprint of life in the characteristics and design of MPAs.

2.2.2 The characteristics of MPAs through the eyes of a geneticist

Mutation, drift, gene flow and adaptation are the evolutionary forces creating, maintaining or losing allelic frequency changes and hence genetic variation. Given a sufficiently long time and in the absence of environmental change, the genetic composition of populations will reach equilibrium. Gene flow will tend to homogenize populations while adaptation and drift to diverge. The relative importance of each process depends on a number of factors, such as time and the effective population size. As marine populations tend to be large, allelic diversity changes largely in response to gene flow and adaptation. Here, population genetics, in combination with other disciplines, has much to contribute (Cressey, 2011), especially in view of connectivity, which is a determining factor in affecting the function of MPAs.

MPAs are characterized by spatial dimensions such as size, size structure, spacing and coverage without including factors such as shape and persistence (time of existence).

Size Important characteristics of MPAs are minimum viable population sizes for broadcast spawners, spillover capacities and seeding capacities of unprotected sites (larvae and juveniles; Christie *et al*., 2010). Below a threshold, populations may be too small and inbreeding may start to erode genetic diversity (Frankham, 2002). Eroding genetic diversity may lead to extinction in the long term after passing through a period with an extinction deficit. Surface integrates the habitats suitable to have populations spawn, grow-up, feed and migrate. Smaller sedentary species with no planktonic stage (typically micro- and meiobenthos, and to a lesser extent macrobenthos) require less space, while planktonic stages (most macrobenthic species and all planktonic species) and larger mobile species (typically fish and mammals) require large areas. Sanctuaries for feeding or breeding populations of marine mammals require sizes of 10^4 km^2. If MPAs are too small, age-specific population dynamics may be out of equilibrium. For example species may suffer from boosting of the larval population to the detriment of the adult population (De Roos *et al*., 2006). It is also crucial that access to sufficiently large areas is guaranteed across the full life-cycle, as population crashes may lead to genetic bottlenecks. Allelic diversity and future adaptability is compromised by the limited number of survivors.

Size structure: The diversity of species, life-histories and reproduction strategies makes that one size won't fit for all taxa and ecosystems. Smaller sedentary species with no planktonic stage require a single habitat with less diversity in structure as the full life-cycle may be covered in a small patch of ocean bottom. Many micro- and meiobenthic taxa respond to such characteristics. However, most organisms have very different requirements throughout their life-cycle. For example fish start as minute plankton which drifts in the ocean, putatively over long distances. Larvae of demersal fish settle on specific substrates in a habitat suitable to find small prey, and to escape prey and infections. As they grow, food requirements and mobility scale up several orders of magnitude (body mass may differ by 10^9 orders of magnitude). Adults return to the spawning grounds which may have very specific characteristics. For example many fish spawn at determinate hydrodynamical zones in the ocean, named larval retention zones (bluefin tuna: Block *et al*. 2005; herring: (Sætre *et al*. 2002); cod: Knutsen *et al*. 2004).

Spacing: Size and size structure are only effective if the link between the habitats is guaranteed for the taxa using them. An important ecological determinant to delineate MPAs is the dispersal of larval and adult organisms in time and space of now and hence the connectivity between populations. The seemingly well connected ocean offers a range of natural and anthropogenic impediments to connectivity. Frontal systems, changing currents and abiotic factors, lack of suitable prey, high densities of predators, changing communities and seascapes, all may obstruct connectivity and hence gene flow. In the long term, the evolutionary potential to move latitudinally or else, will determine the potential for gene flow; populations will have to adapt or else they will go extinct.

Coverage: the size of naturally functioning ecosystems and hence the area accessible to breed, grow up and mature is determined by the cumulative requirements of individual taxa and the communities they harbour. They have to buffer the current re-

quirements of maintaining viable populations but also the long-term requirements of offering opportunities for evolution.

A **common delineator** among the features characterizing MPAs is connectivity, the exchange of individuals among geographically separated subpopulations (Cowen and Sponaugle, 2009).

2.2.3 Concepts and models of dispersal and connectivity

The structure and functioning of MPAs depends on the habitat, ecosystem interactions and biological characteristics of key species. We will focus on the biological characteristics, especially dispersal, connectivity and gene flow from a genetic perspective.

2.2.3.1 Larval dispersal

Population connectivity plays a critical role in local and metapopulation dynamics, community structure, genetic diversity and resilience of populations to human impact (Kinlan and Gaines, 2003). In the context of MPAs, proper connectivity is necessary to ensure both the persistence of local populations and the export of adults/larvae outside the boundaries of the MPAs (Gaines *et al*., 2010). However, despite a growing body of research, empirical data on population connectivity in the marine environment, in particular data related to larval dispersal remain scarce (Cowen *et al*., 2006).

Many marine species (invertebrate, coastal fish, algae) have a bi-partite life history; while adults are associated with the benthos, they produce planktonic propagules. These propagules remain in the plankton and develop for an amount of time before settling into an adult or a nursery benthic habitat (Shanks *et al*., 2003). For species with limited adult movement, the pelagic larval phase is the main dispersal stage.

During the pelagic phase, the propagules will be transported or dispersed ocean currents. Therefore, patterns of connectivity among subpopulations of marine species result from the interaction between physical processes (advection, diffusion, retention) and biological phenomena (life history characteristics, larval behavior, survival; Cowen *et al*., 2006; 2007; 2009). The duration of the pelagic larval phase has been widely used as an indicator of the dispersal potential of a species (Shanks *et al*., 2003; Shanks, 2009). Both the duration of the pelagic larval phase and dispersal distance show extreme heterogeneity among marine species, ranging over orders of magnitudes. Time in plankton ranges from minutes to months and dispersal distance from meters to 100s of km (Shanks *et al*. 2003; Shanks, 2009). Looking at 67 marine species, Shanks (2009) found that pelagic larval duration and dispersal distance are correlated, and larval duration can be considered as a crude proxy for dispersal potential: the more time the propagules spend in the water column the more they tend to disperse. However they are many exceptions and most species show shorter dispersal than expected under passive dispersion model (Shanks, 2009). Indeed, the shape of the dispersal kernel is not only determined by advection and diffusion (passive transport) but larval behavior (vertical migration); along trajectory mortality; and temporal and/or spatial variation can lead to significant reduction in effective dispersal.

The problem of population connectivity is inherently a coupled biophysical problem. Resolving the mechanisms controlling larval dispersal requires a coherent understanding of the relevant physical processes and how organisms mediate the physical outcome

Box 1. Glossary

Biological dispersal: refers to those processes by which a species maintains or expands the distribution of a population. Dispersal implies movement - movement away from an existing population (population expansion) or away from the parent organisms (population maintenance). In the latter case, dispersal may simply involve replacement of the parent generation by the new generation, with only minor changes in geographic area occupied (ref).

Connectivity: the extent to which populations in different parts of a species range are linked by exchange of larvae, recruits, juveniles or adults (Palumbi, 2003); the demographic linking of populations through the dispersal among them of individuals as larvae, juveniles or adults. Successful dispersal requires that individuals move between populations, and become successfully incorporated into the recipient population (Sale, *et al*., 2005)

Connectivity: the exchange of individuals among geographically separated subpopulations, (larval dispersal, post-larval survival) (Pineda *et al*. 2007 – Oceanography)

Demographic connectivity: the degree to which population growth and vital rates are affected by dispersal (Lowe and Allendorf, 2010)

Dispersal kernel: the distribution of dispersal distance based on repeated event that theoretically captures the temporal variability in dispersal process (Cowen and Sponaugle, 2009)

Ecological connectivity: connectness of ecological processes across multiple scales (Lindemayer and Fisher, 2006)

Effective dispersal: realized modal dispersal, typically quantified with its standard deviation around the arithmetic mean.

Fully protected marine reserves: Lubchenco *et al*., 2003

Genetic connectivity: the degree to which gene flow affects evolutionary processes within subpopulations (Lowe and Allendorf, 2010)

Larval dispersal, the spread of larvae from a spawning source to a settlement site (Pineda *et al*. 2006)

Larval transport: is the horizontal translocation of a larva between points x1y1 and x2y2 where x and y are horizontal axes, (physical transport, larval behavior) (Pineda *et al*. 2006 – Oceanography)

Marine protected Area: areas of the ocean designated to enhance conservation of marine resources (NRC, IUCN in Lubchenco *et al*. 2003); fits in the ecosystem approach; benefits within reserve (size, density, biomass, diversity – Lester *et al*. 2009)

Metapopulation: a group of spatially separated populations which interact at some level, a "population of populations" (Levin, 1995; Kritzer and Sale, 2006)

2.2.3.2 Ecological models of dispersal

Knowledge of the dynamics of local subpopulations requires the inclusion of different life stages because migration or dispersal of individuals might occur at different levels: adults at spawning grounds, larval stages, and juveniles in nursery areas, (sub) adults at the feeding grounds or a combination of these. Classically, the migration triangle is used as a conceptual model in ecology linking ontogenetic life stages with specific habitats and demonstrating the role of migrations in connecting these habitats (Harden Jones, 1968). Many fish produce pelagic larvae which drift in the prevailing currents to suitable nursery grounds. To complete their life-cycle, adults need to migrate towards suitable spawning grounds. The original model of Harden Jones (1968) describes a closed circuit of migration with individuals always returning to the place where they were spawned (philopatry). The member-vagrant theory of Sinclair (1988) expands on this theory and emphasizes the importance of life-cycle closure (i.e. 'members') as a requirement for reproductive isolation. Individuals that deviate from the population's trajectory (i.e. 'vagrants') are lost to the population.

According to Secor (1999) the migration circuit is a path that can expand or contract according to the energetic demands of a population. Individuals might deviate from the mean trajectory in order to find more favourable habitats, but if they deviate too much they cannot rejoin the migration circuit. Groups with different seasonal migration behaviours between feeding and spawning areas but sharing the same spawning ground might exist, resulting in multiple patterns within one population. Such groups are defined as 'contingents', as described by Clark (1968).

Since its original development and use in terrestrial ecology, the metapopulation concept (Levins, 1969) has been increasingly integrated in marine systems and many of the assumptions of the classical definition have been relaxed to some degree (Wright *et al*., 2006). The number of patches may be finite, they can differ in size and extinction is not required (Kritzer and Sale, 2004). A metapopulation refers to a system of discrete local subpopulations with their own local dynamics but with a large degree of connectivity and demographic influences from other local populations through dispersal of individuals (McQuinn, 1997). Metapopulations differ from patch populations, where individuals are also distributed among discrete groups but share one common larval pool with interpopulation exchange so large that all populations equally affect each other (Kritzer and Sale, 2004).

2.2.3.3 Demographic connectivity

Demographic connectivity is key to basic population biology and to resilience of species to human impact (Lowe and Allendorf, 2010). Populations are demographically connected when their growth rates and/or specific vital rates (survival and birth rates) are affected by inter dispersal (immigration or emigration). Thus, the level of exchange, when referring to population connectivity, must be sufficient to significantly impact the demographic rates of the local populations. What is significant can be seen as context dependant as demographic connectivity is a function of the relative contribution of net immigration to total recruitment (Lowe and Allendorf, 2010).

Demographic connectivity is considered to enhance population stability both at the individual populations scale by providing an immigrant subsidy that compensates for low local recruitment and at the meta-population scale by increasing colonization of unoccupied patches (Hanski, 1998). Proper demographic connectivity will ensure both the persistence of local populations and the export of adults/larvae outside the

boundaries of the MPAs, thus determining the success of MPAs for both conservation and fisheries management goals (Gaines *et al.*, 2010).

2.2.3.4 Genetic connectivity

Over sufficiently long periods of time, the genetic composition of a population arrives at an equilibrium determined by a balance between opposing forces (genetic drift, selection, migration; Hedegecock *et al.*, 2007). Genetic connectivity acts to homogenize populations and to maintain the genetic cohesion of a biological species (Mayr, 1963). The concepts of genetic and demographic connectivity are fundamentally different; demographic connectivity depends on the relative contribution to population growth rates, whereas genetic connectivity depends the absolute numbers of dispersers (Lowe and Allendorf, 2010). The level of demographically relevant exchange is several orders of magnitude larger than the level of connectivity required for the maintenance of genetic homogeneity among subpopulations (only a few individuals per generation; Slatkin, 1993).

A meta-analysis on the range of variation in dispersal in marine communities based on genetic data also shows extreme heterogeneity with scale of dispersal ranging over five orders of magnitude with distinct patterns within taxonomic and functional groups (Kinlan and Gaines, 2003). This study also reveal for most species a discrepancy between direct dispersal estimates and genetic estimates with direct estimates down to three orders of magnitude lower compared to genetic dispersal (Kinlan and Gaines, 2003). A likely explanation is that genetic estimates integrate secondary (by adults) and/or the occasional "lucky" long distance dispersers.

These discrepancies highlight the difference in the relevant time-scale between direct and genetics approaches. Indeed these approaches lie at the opposite ends of a temporal spectrum (Hedgecock *et al.*, 2007). Direct estimates of connectivity are a snapshot over a single or a few generations but are unlikely to document stochastic or recurrent events. On the other hand genetic methods estimate connectivity over evolutionary time frame. The relevant demographic/ecological time frame for the populations is lying in between.

2.2.3.5 Structure of marine (meta) populations

In contrast to terrestrial species, marine organisms with pelagic larval in general do show higher dispersal potential. Together with the lack of obvious barriers for dispersal in the marine environment, this has led to the paradigm that marine populations are demographically open, potentially over hundreds to thousands of kilometers. This paradigm was supported by studies that found little genetic structure over large spatial scales.

However, a growing body of research has shown evidence of restricted dispersal, pointing to the existence of fine-scale structure in dispersal patterns among locations and thus challenging the paradigm that marine populations are demographically open at large spatial scales (Jones *et al.*, 2005; Almany *et al.*, 2007; Cowen and Sponaugle, 2009). Recent syntheses argue against broad generalization of the relative open or 'closedness' of marine populations. Connectivity in marine population is not uniformly polarized towards long or short distances, but instead distributed over a wide continuum of scales (Bradbury *et al.*, 2009; Mora and Sale, 2002; Kinlan and Gaines, 2003; Shanks *et al.* 2003; Shanks, 2009). Furthermore, evidence from hydrodynamic models and genetic structure data indicates that the average scale of connectivity can vary widely even within a given species, at different locations in space and

time (e.g. Cowen *et al*. 2003; Sotka *et al*., 2004) and the degree to which a population is 'open' or 'closed' depends on the scale on which population dynamics are being studied. The wide variation in scales of connectivity argues that the best answer to the oft-debated question 'How open are marine populations?' is, 'It depends.' (Mora and Sale, 2002).

Many marine species are characterized by high fecundity, creating the potential for sweepstakes reproductive success, in which a relatively small proportion of adults contributes to reproduction and recruitment, owing to chance matching of reproductive activity with temporally and spatially variable environmental conditions conducive to fertilization, larval development, and settlement (Hedgecock, 1986, 1994; Li and Hedgecock, 1998; Planes and Lenfant, 2002; Turner *et al*., 2002). One consequence of sweepstake recruitment is that only the winners of the sweepstakes reproductive lottery contributed to the effective size of a natural marine population (*Ne*) leading to *Ne*/*N* in marine populations several orders of magnitude smaller than ratios measured for terrestrial organisms (Frankham, 1995; Paalstra *et al*., 2008). With respect to connectivity sweepstake recruitment can lead to chaotic genetic patchiness (Hedgecock, 1994). The spatial distribution of reproductive success, moreover, is critical information for location-dependent management

2.2.3.6 Seascape genetics

The marine landscape shapes the population dynamical and evolutionary processes taking place in the ocean. When population genetics takes into account the impact of the landscape an alternative approach is available to understand populations. In a marine context with less obvious barriers to dispersal and a 3D environment, the description, modelling and understanding of the marine landscape (seascape) from a genetic perspective has proven helpful to grasp dispersal, connectivity and population structure (Hohenlohe, 2004; Galindo *et al*., 2006). The two major approaches taken are multidisciplinary and require strong collaboration between disciplines with very different goals and conceptual frameworks. In one approach empirical environmental, ecological and genetic data are evaluated statistically in a spatial (GIS) context (Jørgensen *et al*., 2005; Selkoe *et al*., 2010). Correlations between these factors allow to isolate variables of any importance in shaping the patterns. They visualize the underlying factors of structuring. Good access to spatially structured data has increasing helped to test hypotheses. A second approach is heavily based on modelling, starting from individual based models linked to particle dispersal models, which include hydrodynamical and ecological submodels. Connectivity matrices plot the chances that an egg/larva at a point of release will end up elsewhere. Hydrodynamical and biological (e.g. behavior, life history, ecophysiology) features provide statistical estimates where the growing individuals end up (Heath *et al.* 2001, Fox *et al*., 2006; Fogarty and Botsford, 2007; Bolle *et al*., 2009; PNAS, 2010). The dispersal kernels are evaluated statistically over a set time range and summarized in connectivity matrices. Each matrix provides a proportional distribution of dispersing particles between source and endpoint. These matrices form the basis for the testing of hypotheses through genetic modelling. So far relatively simple single locus neutral genotypes characterize individuals during their dispersal over a preset number of generations. The outcomes are then tested against empirical data (Hohenlohe, 2004; Galindo *et al*., 2006; 2010). This is very important for the interpretation of empirical data (White *et al*., 2010).

Outstanding challenges include two prominent aspects. Although connectivity matrices are used to model gene flow over generations, this should be complemented by

multi-generational modelling in order to include interannual differences. From the particle models temporal variation is known to be very important (match–mismatch dynamics of Hjort, 1914). With the ongoing climate change (increased variability in windiness and increased temperature) dispersal patterns are likely to be affected. Secondly, the landscapes modelled so far include neutral markers without including adaptive features. As balancing and directional selection shape marine populations (Larmuseau *et al*., 2010) their inclusion in the IBMs should learn about the dynamics and causes of selection in shaping patterns.

2.2.4 Genetic tools

Genetic tools have become an essential component to detect and monitor genetic diversity. Genetic markers come in a broad range of information content and technicality. For an overview on the characteristics of molecular markers as they are often named see Sunnucks (2000) TREE. From a perspective of MPAs one has to make a distinction between markers used as within generational tracers of dispersal and markers used over evolutionary times (between generations). In a third paragraph we pay attention to the latest developments in genomic markers, a field which is evolving very fast and offers many new opportunities.

2.2.4.1 Direct markers:

Direct markers are conceptually similar to tagging, elemental analysis, isotope analysis and parasite markers. They provide information within a generation, within the period from hatch to death. As physical marking is often impossible, DNA markers provide a privileged perspective on dispersal. In combination with other markers such as elemental analysis of otoliths (Thorrold *et al*., 2002; Cuveliers *et al*., 2010), isotope analysis of tissues (Guelinckx *et al*., 2009) and modelling the approach can be very powerful. They allow to calculate relatedness (Pouyaud *et al*., 1999) and parentage and, usually in a restricted spatial context. But recently several fish larvae have been assigned to their parents over distances from 15 to 184 km thanks to new statistical developments (Christie *et al*., 2010).

2.2.4.2 Indirect markers:

If dynamics are to be understood over a longer time period (generations), hence in an evolutionary context, population based information such as genotype and allele frequencies will be sued. The causes of frequency changes relate to gene flow, genetic drift and selection. From F_{ST} , genetic distances, variance analysis (AMOVA) for a range of markers (sequence, microsatellites, SNPs and allozymes), each carrying its own history.

2.2.4.3 Markers for the future: Genomics

Most research published on connectivity, dispersal and population structure is based on limited sets of genetic markers. Poor genomic sampling may lead to unresolved patterns and hence underestimate structure. As gene flow is high and sampling noise may be high too, patterns are often not recognized. The fast shift towards full sequence information has changed the landscape of population genetics considerably. The reason is driven by developments in Next Generation Sequencing (NGS) and bioinformatics.

2.2.5 Implementation of MPAs – cases

The proof of concepts comes with the presentation of cases. We present here four cases where MPAs are discussed from a genetic perspective. The first three are linked to a specific geographical area in the North Atlantic Ocean while a fourth case deals with Highly Migratory Species which by the nature of their biology require access to a large area and many MPAs.

2.2.5.1 Coral Conservation on the Scotian Shelf and Slope

Canada has established 83 federal MPAs and 705 provincial or territorial MPAs (the marine portions of protected areas) accounting for 1% of its oceans (Government of Canada 2010). In addition there are numerous fisheries closures and other such spatially defined conservation measures which offer protection to specific habitats and/or species. Together, these areas provide the foundation for building a future national network of MPAs, guidelines for the establishment of which have recently been drafted (http://www.isdm-gdsi.gc.ca/oceans/publications/dmpaf-eczpm/framework-cadre-eng.asp, accessed on 3 May 2011). Because each of these existing MPAs and fisheries closures were designed to meet site-specific conservation objectives, their inclusion in a network must be considered in light of their interrelationship. Canada envisions a network concept that "corresponds to the highly interrelated quality of marine ecosystems and allows species, habitats and biophysical processes to stay connected, even when they are not in proximity." (http://www.isdm-gdsi.gc.ca/oceans/publications/dmpaf-eczpm/framework-cadre-eng.asp, accessed on 3 May 2011). Further, MPA networks should achieve conservation objectives which are broader than that of any single component MPA. Here we explore the placement of three areas closed to fishing activities to protect large gorgonian corals on the Scotian Shelf. Two of the areas were closed by variation order, while the third is a federal MPA. We consider whether the placement of these closed areas allows for connectivity among them by modelling larval trajectories using a three-dimensional model of the currents in the area. We then consider what is known about the reproductive biology and genetics of one of the key species to assess the potential for a MPA network to enhance its conservation.

Paragorgia spp. are among the largest sessile benthic corals commonly observed on continental slopes and seamounts of the Northwest Atlantic (Kenchington *et al*., 2010). *Paragorgia arborea*, is a large fan-shaped ahermatypic gorgonian coral and is the dominant species in the area. Individual colonies can attain heights of 3 m and they are long-lived and slow growing with ages on the order of 70 to 80 years (Sherwood and Edinger, 2009). The species is globally distributed and eurybathic, found at depths ranging from 18 to 3000 m (Strychar *et al*., 2011).

The conservation importance of cold water corals has been widely recognized. They are highlighted as "vulnerable marine ecosystem" components in the FAO Deep Sea Fisheries Guidelines (2009), as examples of ecosystems that are highly sensitive and vulnerable to impacts of fisheries using bottom-contacting gear. In Canada, the locations of significant concentrations of gorgonian corals to depths of 1500 m have been mapped from Davis Strait in the north, to the Scotian Shelf (Cogswell *et al*., 2009; Kenchington *et al*., 2010). Some of the highest densities of this species are found on the Scotian Slope in the Northeast Channel, separating Georges Bank from Brown's Bank (Cogswell *et al*., 2009).

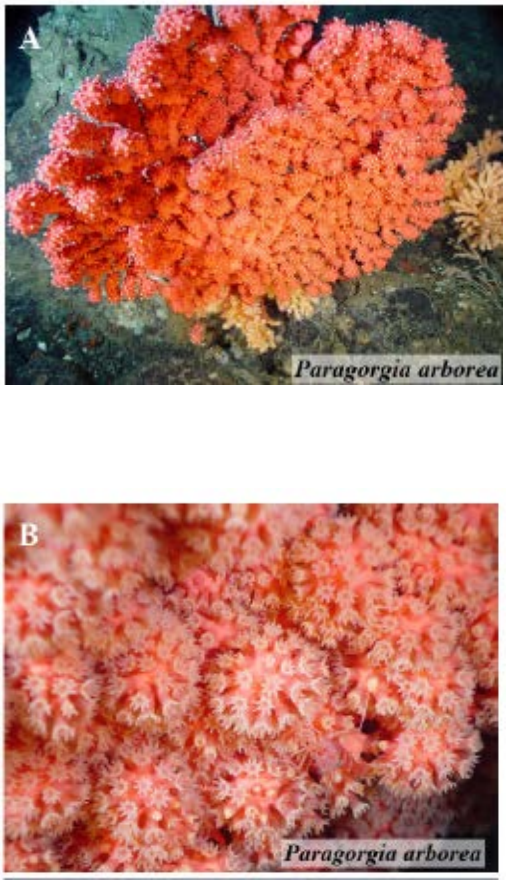
Canada has three spatial closures on the Scotian Shelf in place to protect *Paragorgia arborea* and similar coral species. In June 2002 the Northeast Channel Coral Conservation Area (NEC CCA) was established through a variation order (fisheries closure) by the Department of Fisheries and Oceans (DFO). The area of the protected site is 424 km^2 and consists of a restricted bottom fishing zone (90% of total area) and a limited bottom fishing zone (10% of total area). The conservation area was primarily selected on the basis of having the highest density of large branching octocorals, *Paragorgia arborea* and *Primnoa resedaeformis* (another long-lived slow growing gorgonian coral), in the Maritimes. In addition, there was visual evidence of recent disturbance such as broken live coral, tilted corals and skeletal fragments, indicating that the large gorgonians were subject to bottom fishing damage. From the NEC CCA, the nearest known large concentration of *Paragorgia arborea* along the Scotian Slope occurs some 500 km away (along the slope) southeast of Sable Island in the Gully canyon (Figure 2.2.1). In 2004 the DFO designated the Gully as a Marine Protected Area with the objective of protecting both the endangered bottlenose whale and the great diversity of coral species observed there. Activities that disturb, damage, or remove organisms or their habitat are not permitted within the MPA. The Gully MPA is 2364 km^2 and has been divided into 3 zones, with varying levels of management for each zone. Lastly the *Lophelia* Conservation Area (LCA) is in an offshore region known to fishers and others as the Stone Fence. It is located at the mouth of the Laurentian Channel, about 260 km southeast of Louisbourg, N.S. The reef is comprised of both living and dead coral, and has been damaged by fishing activity over the past few decades. In June of 2004 the 15 km^2 LCA was created through variation order (fisheries closure) in consultation with representatives of active fisheries in the area. The boundaries were set at a 1 nautical mile buffer closed to all bottom fisheries around the known extent of the reef. *Paragorgia arborea* is also known from the LCA and from some of the canyon heads between the Gully MPA and the LCA (Figure 2.2.1).

Potential for Connectivity Among Coral Conservation Areas based on Larval Drift Trajectories: The Gully MPA and the LCA are in proximity (~160 km) and are connected by a strong southwesterly flow of cool and relatively freshwater originating from the Gulf of St. Lawrence and Newfoundland Shelf along the shelf break (Han *et al*., 1997). Web Drogue (http://www2.mar.dfo-mpo.gc.ca/science/ocean/coastal_hydrodynamics/WebDrogue/webdrogue.html, accessed on 3 May 2011) was used to predict the drift trajectory of particles (i.e. modelled *P. arborea* larvae) using circulation data derived from tides, seasonal mean circulation, wind-driven circulation, and surface-wind drift (Hannah *et al*., 2001). This mean flow is consistent through all seasons but is particularly intense during April and May, which coincides with spring phytoplankton bloom (Harrison *et al*., 2009). Spring shelf break flow does continue in a southwesterly direction from the Gully all the way to the NEC CCA but is highly variable depending on storms and the influence of warm-water eddies emerging from the Gulf Stream. However, the majority of the flow from the LCA and Gully between March and June ends up in a anticlockwise gyre south of both Sable and Western bank (Figure 2.2.2). When the spatial extent of the model is focused on the southwestern portion of the Scotian Shelf the theoretical particle placed in the Gully shows a similar trajectory following the southwesterly flow of the shelf break current then heading south then east when the particle reaches Western Bank (Figure 2.2.3). The NEC CCA particle is immediately forced southwest hugging the shelf break then begins a sharp turn bearing east then northeast. Figures 2.2.2 and 2.2.3 and the literature supporting these models, illustrates the connection between the LCA and the Gully and emphasizes the separation in circulation between these sites and the NEC CCA. According to Han *et al*. (1997), this separation

would be amplified when following the trajectory of particles in the deep waters at the base of the shelf break. In the deep water of the LCA and Gully, the southwesterly flow of the shelf break current is less intense than at the surface but also results in an anticlockwise rotation south of approximately Western or Emerald Bank. At depth this flow is less likely to be disrupted due to surface effects like storms and thus could result in a deep biological boundary between the Eastern and Western portions of the Scotian Slope.

Potential for Long Distance Dispersal Based on Known Reproductive Biology and Genetic Data: Of the ~2000 known species of coral, reproduction has been studied in only a few dozen largely tropical species. As for other cnidarians, reproduction may be asexual through budding of terminal polyps or fragmentation, or sexual. The species is gonochoristic, that is, with separate male and female colonies. Fertilization is external through broadcast spawning and colonies tend to be aggregated with a highly disjunctive distribution pattern. There is only one study of the population genetics of this species. Kenchington *et al*. (2007) developed the first set of microsatellite DNA markers for *P. arborea* and have confirmed that the 31 colonies sampled in the NEC CCA were sexually derived. Only one pair had identical genotypes (P=0.056) indicative of cloning although this could also be a rare chance occurrence. *P. arborea* showed a high level of inbreeding (F_{IS}= 0.250) which suggests that there is little gene-flow between the NEC CCA and other populations of this species on the Scotian Slope. Genetic characterization of populations from the Gully MPA and the LCA are in progress.

Conclusions: Modelling of larval trajectories suggests that *P. arborea* growing in the NEC CCA is likely to be isolated from the populations in the Gully MPA and the LCA which may be linked. The presence of the species in other canyon heads between the latter two provides stepping stones for genetic mixing. The limited population genetic data for this species supports this hypothesis in that the colonies in the NEC CCA are highly inbred. MPA network design should acknowledge the increased vulnerability of this population through aiming to protect as much of the population as possible (large spatial extent). Linkage between the Gully MPA and the LCA could be strengthened by providing new closed areas at the canyon heads where habitat is suitable between the two sites.



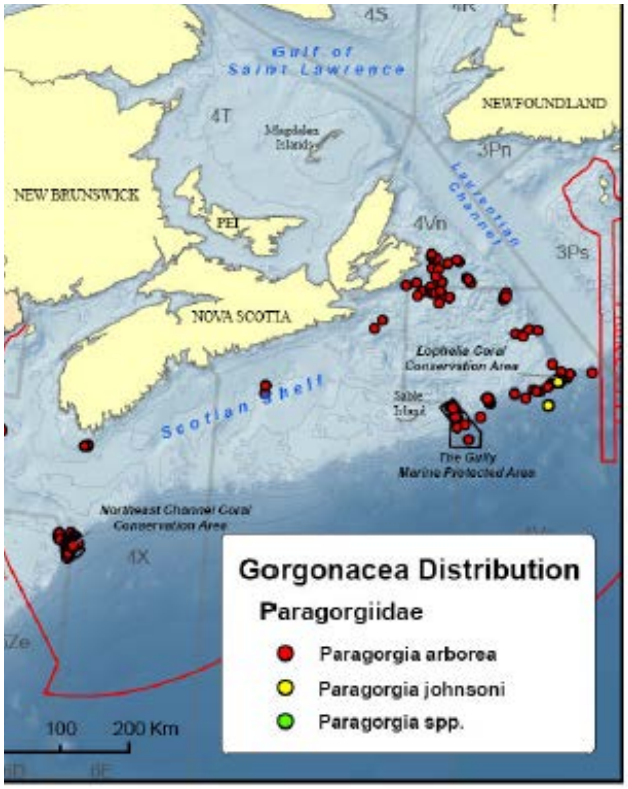


Figure 2.2.1. A. A colony of *Paragorgia arborea*. B. close up of polyps of *P. arborea*. Right: Known distribution of *Paragorgia* spp. on the Scotian shelf in relation to the three coral conservation areas.

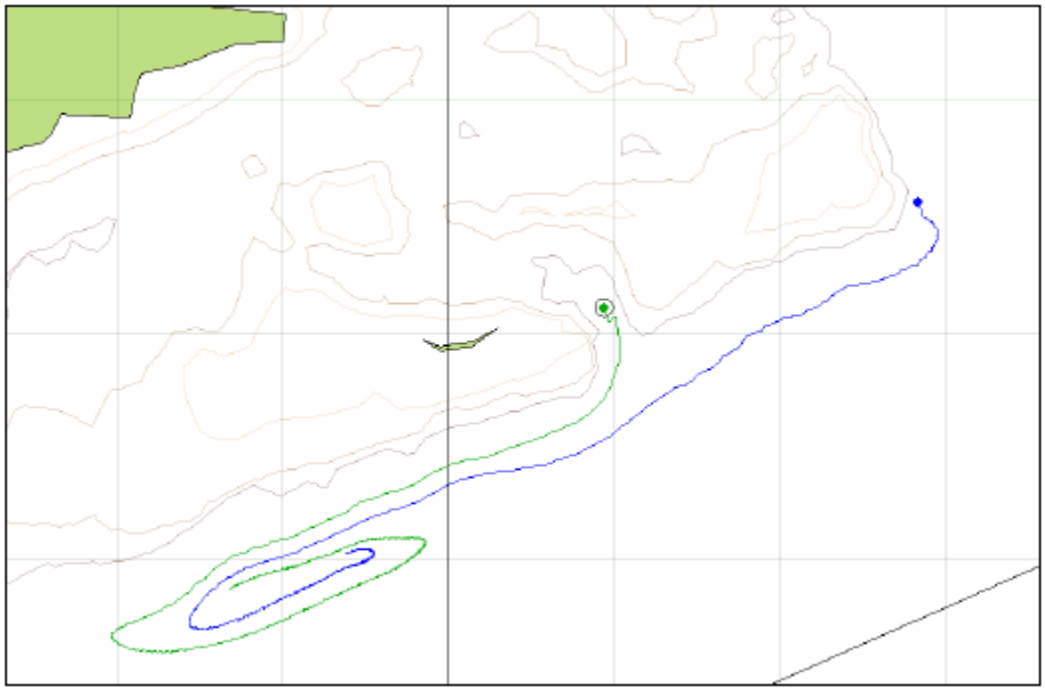


Figure 2.2.2. Webdrogue prediction of particle trajectory at 100 m water depth between March 1 and June 1. Particles "released" in the LCA are in blue, and in the Gully MPA in green.

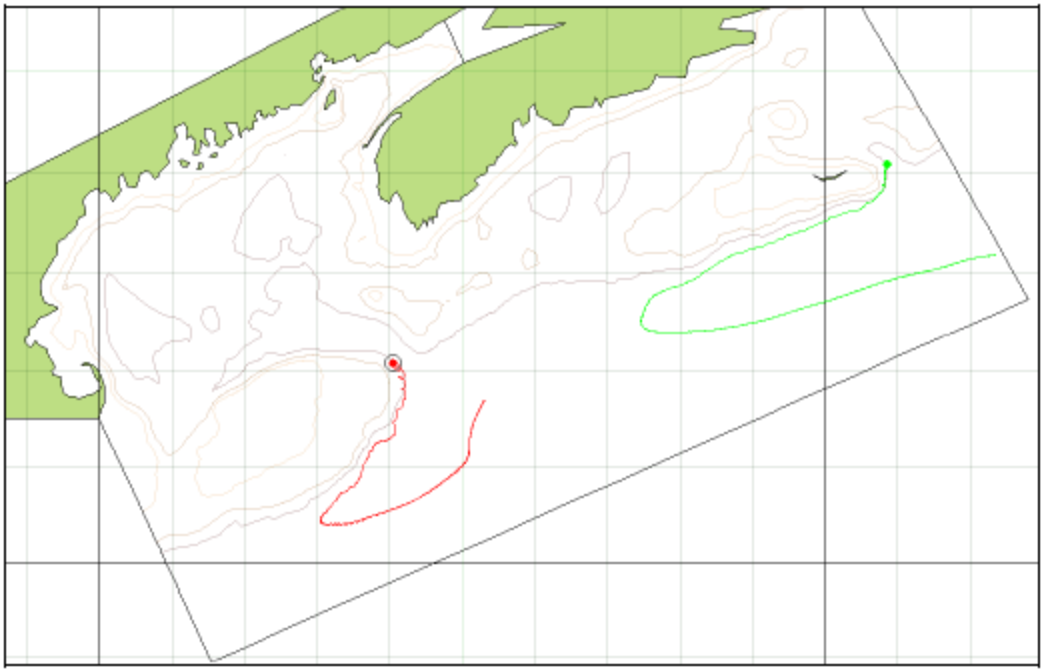


Figure 2.2.3. Webdrogue prediction of particle trajectory at 100 m water depth between 1 March and 1 June. Particles "released" in the NEC CCA are in red, and in the Gully MPA in green.

2.2.5.2 Norway: managing cod and lesser sandeel

In the beginning of the 21st century Norway initiated two processes aimed at managing the marine space. The first was the development of two regional plans, one for the Barents Sea and on for the Norwegian Sea. The second was a plan for establishing a network of representative MPAs along the Norwegian coast and waters. These processes have been interlinked, and the MPA networks are now integrated with the regional management plans.

In fisheries management one has come to see the use of area based measures like spatial and temporal closures of specific areas in order to reduce fishing pressure as possible MPAs where sustainable use is allowed. This type of area-based protection is seen both in management of Atlantic cod in the spawning areas, and sandeel in the North Sea.

2.2.5.3 Spatial management of Atlantic cod

In Norway the Atlantic cod (*Gadus morhua*) north of 62 °N is divided into two separate management units – Northeast Arctic Cod (NEAC) and Norwegian Coastal Cod (NCC). The NCC is managed as part of the Norwegian northeast Arctic cod fishery, but in contrast to the NEAC which is regarded a sustainable and therefore harvestable stock, the NCC stock complex is in a depleted condition. For the last years (2004–2009) the scientific advice (ICES) has been either a recovery plan (2004–2008) or a recovery plan in addition to zero catch (2009). The recovery plan should include monitoring the trajectory of the stock, stating specified reopening criteria, and monitoring the fishery when it is reopened. From the mid-1970s to 2003 an expected yield of 40 000 metric tons from the NCC was added annually to the quota for NEAC. From 2004 the additional catch expected from this stock has been set to 20 000 metric tons, e.g. catches from tourists and locals, and in order to avoid any commercial catch of the Norwegian coastal cod stock, strong restrictions should apply to all fisheries catching cod where it mixes with northeast Arctic cod.

The differentiation between the NEAC and the NCC have been demonstrated using a number of different methods from otoliths in the 1930s (Rollefsen, 1933), haemoglobin and mtDNA (Frydenberg *et al*., 1965; Dahle and Jørstad, 1993; Dahle, 1991), microsatellites and pantophysin (*Pan I*; Fevolden and Pogson, 1995; Wennevik *et al.*, 2008). Although the *Pan I* locus is under selection (Pogson and Mesa, 2004) and this would be the reason for the large differentiation between the NEAC and the NCC components, it serves as a good marker for identifying the different component in a mixed fishery.

The main spawning area for the NEAC is the Lofoten Islands, but it is also known to spawn in the Møre region further south on the Norwegian coast. Both these locations are also spawning sites for the local NCC, which spawn at the same time as the NEAC. Historically NEAC and NCC have been separated based on otolith reading, but in later years the PanI locus have been used for identification of NEAC in the spawning areas.

In an attempt to protect the vulnerable NCC populations, one area in the Lofoten islands is closed for commercial fishing (the use of Danish seine or gillnet is prohibited), during the spawning season in order to reduce catches of the threatened NCC. The commercial fisheries on both sides (east and west side) of this closed area are monitored on a regular basis during the spawning period. Samples from the fisheries are genotyped for PanI, and if the fraction of the NEAC component in the samples is higher than 70%, the fisheries managers will consider opening the closed area. Since

this monitoring started in 2007, the closed area has only been opened once, in 2011, when the fraction of NEAC increased from less than 20% to more than 90% in just 48 hours. The area was closed again after about two weeks when the fraction dropped below 70%.

The same approach is being used in the other major NEAC spawning area at Møre. Here the commercial fishing is prohibited inside a "line", and samples outside this limit will decide whether to keep the area closed or considered opened. However, the faction of NEAC in this area has never exceeded 45%.

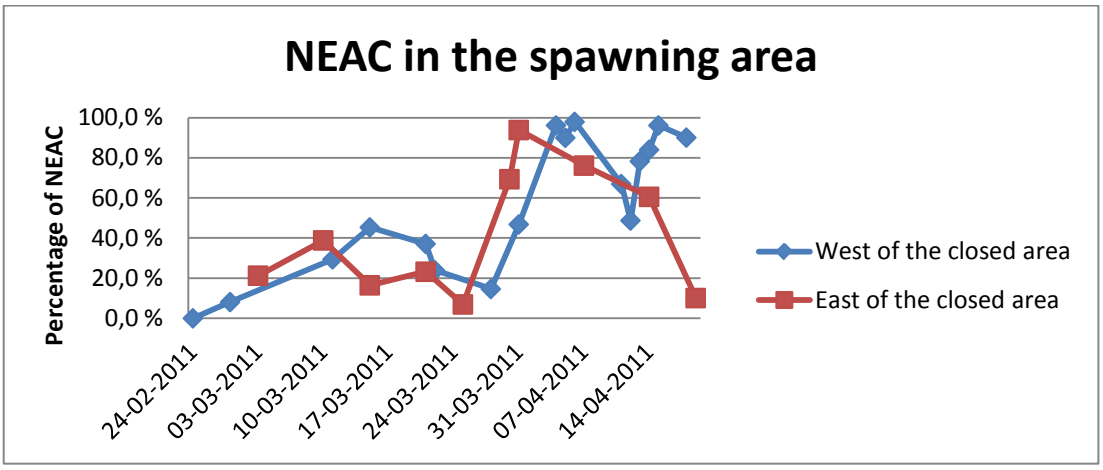


Figure 2.2.4. Example of observed fraction of NEAC in the sampling areas around the closed area (source: G. Dahle, IMR).

2.2.5.4 Spatial management of lesser sandeel

The lesser sandeel (*Ammodytes marinus*), a species that spends most of it life buried in sand, are fished by trawl during daytime when they emerge from the sand. Their dependence on a sandy habitat produces a patchwork of available fishing grounds in the North Sea. Tagging experiments indicate that once the sandeel has settled on one ground it does not migrate to another (Gauld, 1990), while a study of length distribution within and between fishing-ground indicated no mixing of sandeels between fishing-grounds, while within grounds the no difference in length distribution was found (Jensen *et al.*, 2011). A simulation tool for exploring the efficiency of Marine Protected Areas for sandeel stocks, the sandeel population analysis model (SPAM) has been presented (Christensen *et al.*, 2009)

A study to explore the genetic structure in the lesser sandeel stock in the North Sea using microsatellite markers, were initiated in 2010 at the Institute of Marine Research, Bergen, Norway (K. Glover, personal communication). For several years after 2001 almost all landings from the Norwegian Exclusive Economic Zone (EEZ) came from the Vestbank area. This area has "natural refuges" for sandeel between the fishing grounds in terms of areas that are too small for trawling. Such natural refuges are not present elsewhere in the Norwegian EEZ in connection with the sandeel fishing grounds. After having become commercially depleted these fishing grounds have suffered long-term recruitment failure, whereas the Vestbank area with its natural

refuges has never experienced long-term recruitment failure. This suggests that local spawners are important for the local recruitment; despite sandeel have a pelagic larval stage of ~4 months. Homing seems to be the most likely mechanism as bycatch of sandeel larvae appears suddenly and asynchronously on the various sandeel grounds (T. Johannessen, personal communication).

Evidence from the 2007 and 2008 fisheries in the Norwegian EEZ suggests that the fishing fleet might deplete the local sandeel grounds within a few weeks without significant changes in cpue, a known phenomenon for schooling species.

To mitigate the negative trend in the sandeel stock, Norway has initiated area-based management of sandeel. Individual sandeel fishing grounds are split in two subareas. One subarea is fished in one year and the second the following year. If the abundance on a fishing ground falls below a predefined level, the entire fishing ground will be closed. Sandeel becomes mature at the age of two. Hence, alternating closures of two subareas of each fishing ground is intended to provide sustainable local spawning stocks and to prevent local depletions to ensure sufficient prey for predators and to maximize fishing yield.

2.2.5.5 Belgium – The Netherlands: flatfish fishery on soft sediments in the Southern Bight of the North Sea

The shallow shelf of sandbanks and gravel beds of the southern part of the North Sea has been the focus of many exercises to coastal-zone planning and the assignment of MPAs (Maes *et al*. 2005). Between the UK and Belgian - northern French coasts the water column is well mixed by strong tidal currents and seasonal winds. Off the Dutch coast the water column tends to be stratified + Friesian front. It is highly productive and an important fishing ground for herring and flatfish. Trawling on the sandy or gravely bottom (otter and beam trawls) is among the most intensive in the North Atlantic Ocean (Jennings *et al.,* 1999) and has modified the habitat considerably. The area is intensively used by many users (e.g. shipping, energy production and mineral extraction) leading to spatial conflicts. Moreover pollution and eutrofication from atmospheric deposition and river run-off is considerable (OSPAR 2003 - North Sea quality status report). Management is multinational through the European Union (Habitat and Bird Directives; fisheries management of ICES zone IVc) and OSPAR.

5.46% of the greater North Sea is covered by MPAs under various schemes. NL has nominated five Natura2000 sites covering 8,400 km²), Belgium has officially not nominated any site but is in the process of proposing a site adjacent to the Dutch Vlakte van de Raan (east) and a large zone along the Belgian-French border (west; Degraer *et al*., 2008, in OSPAR 2008). The latter matches with a very rich and productive benthic community (Degraer *et al.,* 2009) including *Lanice conchilega* reefs (Rabaut *et al*., 2010) and important fishing grounds (ICES).

The weak genetic structure of thrash fish (*Pomatoschistus* gobies (Larmuseau *et al*., 2009), dragnonet *Callionymus lyra*), pipefish *Syngnathus acus* and *S. rostellatus*) and commercial fish alike (red mullet *Mullus surmuletus*, herring *Clupea harengus*, sea bass *Dicentrarchus labrax* (Lemaire *et al*., 2000), whiting, plaice *Pleuronectes platessa* (Hoarau *et al*., 2005), flounder *Platichthys flesus*, bril *Scophthalmus rhombus*, turbot *Scophthalmus maximus*, sole *Solea solea*) suggests a high connectivity of the area and a great similarity between populations of the Eastern English Channel, Thames Estuary, Belgian Coast, Friesian Front and German Bight. Spawning grounds for sole, plaice, herring and gobies occur in the region; some show evidence from hydrodynamic modelling for high levels of connectivity (sole: Erftemeijer *et al*., 2009; Savina *et al*., 2010; plaice:

Bolle *et al*., 2009; Erftemeijer *et al*., 2009) although evidence for retention (herring: Dickey-Collas *et al*. 2009) and restricted connectivity seems also the case (sole: Cuveliers *et al*. 2009). A remarkable local adaptation to light has been documented in sand goby (Larmuseau *et al*. 2009, 2010) suggesting that habitat choice is genotype dependent.

2.2.6 Conclusions

MPAs aim at preserving the marine biodiversity and/or to guarantee the sustainable exploitation of natural resources. Their design and implementation depends on informed decisions and consent between a broad range of stakeholders, including fishers, scientists and the public. Scientific information from the biology of organisms and communities, and in this case more specifically genetic information, contributes to the organization at a broad scale, the validation of the design and follow-up (monitoring).

Four aspects are crucial to the design of MPAs from a genetic perspective:

Size: MPA size is a critical factor in determining genetic diversity and effective population size. Sedentary species without planktonic stages seemingly require smaller areas, but in an evolutionary context (with the need for responding to habitat changes and regime shifts) they may require much larger areas to support minimum viable population sizes and avoid an evolutionary deficit. The latter has been well documented in terrestrial communities (Honnay *et al*., 2002). Size of MPA is also latitudinally determined by the longer development times in colder northern water (Laurel and Bradbury, 2006). Buffer (Lubchenco *et al*. 2003) and insurance function

Size structure: Accommodating the various life-histories and habitat requirements is best suited by a spectrum of MPA sizes. Genetic diversity and adaptive potential, particularly of weak and highly fluctuating populations, is sensitive to small sizes. Population bottlenecks lead to genetic bottlenecks on a local scale. In a metapopulation context lost local diversity might be recovered from neighbouring populations. Extinctions and recolonizations (metapopulation dynamics) should remain open at all times (Hamm and Burton, 2000).

Spacing: In an evolutionary sense, isolation-by-distance patterns prevail in marine organisms, such that spatial continuity is a crucial feature of MPAs. For example, duration of larval stage and genetic dispersal are correlated exponentially (Siegel *et al*., 2003). They may be linked to local physical characteristics (river flow for sole Le Pape *et al*., 2003, frontal zones for herring) which are limited in availability. In an intragenerational context, larvae disperse and adults actively move around as part of the life-long migration triangle (Harden Jones, 1968). Spawning grounds are lekking sites for reshuffling of heritable information

In the long term, the potential to adapt or else move latitudinally, will affect gene flow.

Coverage: the coverage of MPAs ideally matches the full range and pays attention to population structure. The size of ecosystems has to buffer the current requirements of maintaining viable populations and ensure the long-term requirements of offering opportunities to evolve. Effective population sizes are several orders of magnitude smaller than the census populations (spawning biomass), which provides a strong argument for sufficient coverage to lower fishing mortality. Only then the evolutionary impacts of intensive fishing (fisheries induced evolution) will have a chance to recover (Jørgensen *et al*., 2007). Estimates of the coverage of MPAs varies from a few

per cent over 10 (Toropova *et al*., 2010) and 30 (Airamé *et al*., 2003; FSBI, 2001) to 50 % (Gaines *et al*., 2010). From a science-based perspective coverage of at least 20% seems to be required to enjoy the full advantages of protection, spillover and seeding.

2.2.7 Major knowledge gaps

Despite good progress on the science basis of MPAs, many knowledge gaps remain to be addressed to provide solutions and strategies for a good science base. The following list includes bottom–up and top–down components of the science based approach:

1) Knowledge of average effective dispersal envelopes of larvae (Sale *et al*. 2005); A network of MPAs should maximize connectivity between individual reserves to ensure the protection of ecological functionality and productivity. Proper connectivity is necessary to ensure both the persistence of local populations and the export of adults/larvae outside the boundaries of the MPAs.

2) Knowledge of dispersal of juveniles and adults (Sale *et al*., 2005); migration triangle; spillover and seeding effects.

3) Knowledge of the variability of the genetic population characteristics. This inherent variability must be taken into account when designing MPAs as not a single strategy will affect all species in a community evenly (Halpern and Warner, 2003).

4) Knowledge of habitat/seascape characteristics and dispersal, for example the behaviour of water masses along complex coastlines (Sale *et al*., 2005), locations of reserves by considering patterns of connectivity in view of source/sink populations and habitat fragmentation.

5) Benefits from fisheries reserves (Gell and Roberts, 2003), for example knowledge of the shift from effort to area based management, the mitigation of the evolutionary impact of fishing (Jørgensen *et al*., 2007); Size of MPA protects against fisheries based selection (Baskett *et al*., 2005)

6) Need for well designed experimental studies of no-take reserves (Sale *et al*., 2005)

7) Benefits from conservation areas ; Impact of size and location of MPAs could be great as future management will be area and time-dependent (and not effort dependent; Nielsen, 23.02.2011)

8) Comparison of MPA strategies between biomes

9) Emergent benefits from MPAs (Gaines *et al*. 2010)

2.2.8 Recommendations based on the best available evidence:

1) That ICES stimulates a multidisciplinary modelling and experimental approach to formulate the genetic principles on the design and implications of MPA networks

2) That the ecosystem implications of designs of MPA networks for the connectivity and evolutionary requirements of species and communities are validated

3) That the common benefits between exploited resources and biodiversity oriented MPAs are evaluated within the perspective of STIGMSP

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2.3 ToR c) Review the issues and challenges associated with the utilization of SNPs as markers in population genetic studies with special attention to data handling and statistical tools

Paulo Prodöhl and Phillip McGinnity

Over the past two decades, exceptional advances in molecular analytical methodologies have resulted in a myriad of new types of genetic markers. Single Nucleotide Polymorphisms (SNPs) have been one of the latest additions to the molecular toolbox (reviewed by Allendorf *et al*., 2010). The rate of SNP development and genotyping, particularly its potential for non-model organisms, has been greatly accelerated by the advent of Next Generation Sequencing (NGS) techniques, which have been extensively reviewed recently, within special issues of Molecular Ecology (Tautz *et al*., 2010) and Molecular Ecology Resources (Seeb *et al*., 2011).

The unprecedented amount of genetic information provided by SNPs, make them the marker of choice for studies ranging from individual, family and population identification, to the discovery of genes and genomic regions affecting adaptive phenotypic variation (introduced by Seeb *et al*. 2010). While the potential usefulness of SNPs is not disputed, illustrated by the inexorable shift in popularity from fragment length polymorphism (FLP) analysis towards NGS and SNP techniques by most labs to address fisheries management and conservation questions, there are still a number of issues that need to be resolved. These include: ascertainment bias (e.g. Bradbury *et al*. 2011; Helyar *et al*., 2011; Seeb *et al*. 2011); cost (Allendorf *et al*. 2011); SNP number i.e. specific to project type – 100 v 100,000 (Paschou *et al*. 2007, Helyar *et al*. 2011), ease of analyses, including software options (Helyar *et al*., 2011) screening platform (e.g. Affymetrix, SNPstream, TaqMan, Sequenom, Illumina); SNP choice, e.g. neutral vs. non-neutral SNPs (refs), nuclear v mtDNA, including reliable identification of non-neutral SNPs (Brieuc and Naish 2011), also matching SNPs to the specific question (Allendorf *et al*. 2011), ease of validation; technical genotyping issues: including genotyping errors and missing allele call; necessity of pre-screening of SNP for linkage level assessment (i.e. linked can be useful for certain application e.g. QTL identification but are not appropriate to population structure analysis), database construction; data mining approaches (e.g. bio-informatic pipeline for SNP discovery especially for species without a reference genome).

Notwithstanding the issues above, an increasing number of studies have been reporting on the potential of SNPs for fisheries management. For instance, Freamo *et al*. (2011) demonstrated that a subset of 14 non-neutral SNPs, selected from a panel of 320 SNPs, can be reliably used (85% accuracy) to identify Atlantic salmon from both the inner and outer Bay of Fundy in Eastern Canada, an area targeted for conservation efforts given declining population trends. Discrimination between inner and outer Bay of Fundy stocks was previously problematic using FLP markers given low levels of divergence. Karlson *et al*. (2011), identified a panel of 60 SNPs sourced from a pool of 7,000 SNPs, which collectively are diagnostic in distinguishing individual wild or farmed Atlantic salmon irrespective of their populations of origin. Hess *et al*. (2011) compared the performance of 13 microsatellite loci in relation to 92 SNP loci for fine resolution GSI analysis in the Columbia River Basin. The authors found that the microsatellites outperformed the SNP panel in resolving fine-scale relationship, but the maximum power for GSI was only achieved when all 105 were considered together.

The objective of this TOR was to consider the issues above, and to provide recommendations that would provide best practice for application of SNPs for fisheries management. Also, to discuss optimal solutions and analytical routines for SNP screening that can be used for general fish population genetics application that are effective and represent good value for money, in both government and university environments, including funding agencies and policy-makers (e.g. ICES).

Recommendations:

1) We recommend and encourage that timely investment of scientific resources be used in testing, developing and deploying the technology.

2) We recommend SNPs be considered as a complementary tool to other available markers rather than a replacement for other makers.

3) Issues pertaining to ascertainment bias, cost, SNP choice, ease of analyses, screening platform, technical aspects related to genotyping, data management, and broader technological and statistical approaches should be further considered by members of this working group on an ongoing basis.

2.4 ToR d) Exploring opportunities for the integration of genetic data into fisheries management resulting from the European Union Data Collection Framework Regulation

Jochen Trautner, John Gilbey, John Benzie, Andone E. Recalde and Jann Th. Martinsohn

Background

In its user guide on the Common Fisheries Policy (CFP) (EC, 2009) the European Commission underlines that fisheries management in the EU relies on scientific advice, and is therefore dependent on accurate, relevant and up-to-date data. Since 2001, the CFP has set aside funding to help national authorities collect both economic and biological data related to fisheries management. Originally Council Regulation (EC) No 1543/2000 established a Community framework for the collection and management of the data needed to conduct the common fisheries policy ("The Data Collection Regulation" – DCR), for which Commission Regulation (EC) No. 1639/2001 determined Community programs for the collection of data in the fisheries sector and laid down detailed rules for the application.

Several practical shortcomings, such as a non-optimal aggregation level of data, *i.e.* an insufficient availability of raw data, and a legally fixed short-term storage of data in a central database, constituted an impediment to efficient uptake of data into scientific advice and led to an overhaul of the CFP data collection legislation. In 2008 the Council Regulation (EC) No 199/2008 was published ("The Data Collection Framework Regulation" – DCF) Council Regulation (EC) No 199/2008 establishing a Community framework for the collection, management and use of data in the fisheries sector and support for scientific advice regarding the Common Fisheries Policy. Implementation is ensured through Commission Regulation (EC) No. 665/2008, under which EU Member States are required to collect data on Biological and Economic aspects of many European fisheries and related fisheries sectors. Details of the Multiannual Community Programme in support of the DCF are set out in Commission Decision 2008/949/EC.

This document has been structured in the following modules:

- Module of evaluation of the fishing sector;
- Module of evaluation of the economic situation of the aquaculture and processing industry sectors;
- Module of evaluation of the effects of the fishing sector on the marine ecosystem.

The current data collection framework will run until 2013, providing € 50 million a year for national programmes. Table 2.4.1 provides a rough overview on modules and data type covered by the Data Collection Framework. Details are laid down in Commission Decision 2008/949/EC where data requirements are specified in the annex.

The DCF covers a broad array of biological data that can be integrated in fisheries modelling and stock assessment and feed into fisheries management but there is currently no reference to genetic data. We believe this absence of genetic data coverage to be unfortunate and counterproductive as genetic data can and has been applied to address questions of immediate relevance to fisheries management (Waples *et al.*, 2008). An example is the assessment of the extent to which economically exploited stocks match biological, evolutionary meaningful, populations (Waples and Gaggiotti, 2006). Genetics can also be used for estimating the effective populations size (Ne) of populations. This is, in broad terms the number of those individuals of a given population which reproduce and thereby contribute to the fitness and resilience of future generations. Recent evidence has shown that for marine fish, effective population size can be orders of magnitude smaller than census population size (the total number of individuals of a population). Where this is the case, demographic size may give a very false impression of population resiliency. These and other applications of genetics for marine fisheries management of a variety of species are discussed in detail in recent reviews (Hauser and Seeb 2008; Waples *et al.*, 2008) and below. In addition genetic information is increasingly important in aquaculture development as highlighted recently in the global aquaculture conference in Phuket (FAO and NACA, 2010). Beyond the use of genetic data for fishery management and aquaculture, the collection of genetic data has an added value as it can also be used to support the EU biodiversity strategy 2020 (EC, 2011). Also the initiative by the FAO for the assessment of the state of the world's aquatic genetic resources planned by the FAO for 2014 preservation stresses the importance of genetic information (FAO, 2007).

Despite examples clearly demonstrating the value of genetics for marine fishery management, routine use of genetic information in this field remains exceptional. A variety of reasons are responsible for the conspicuous absence of genetics. Some are historical; others arise due to a lack of communication between fish geneticists, fisheries managers and regulators. Also, integral to the problem, the current management infrastructure is not conducive to the uptake of genetics: Fish(eries) genetics remain confined largely to the academic realm, and research projects where there is a lack of long-term perspective and funding. As a result there is no central data-hub available for this type of information and it is not routinely collected and updated (Verspoor *et al.*, 2010).

These issues present inherent impediments to an efficient transfer of genetic data and insights into fisheries management. In order to be overcome, these must be addressed directly and involve all stakeholders, as was recently pointed out in a contribution of the FishPopTrace consortium to the Common Fisheries Policy reform consultation (FishPopTrace 2009). The DCF could in principle provide a platform to integrate ge-

netic data into EU fisheries management under the CFP remit. However, prior to this happening a variety of conditions have to be fulfilled, which are further delineated below

To address these issues, it is also important to understand how the DCF is currently implemented and how data from it is fed into fisheries management decisions. Figure 2.4.1 depicts how relevant data is centrally stored and made available for scientific assessments and management advice. The European Commission Directorate General Mare (DG Mare) makes requests for specific data from EU member states, by launching data calls, that are published on the DG JRC[1] website (https://datacollection.jrc.ec.europa.eu) and take into account advice and feedback from the STECF[2] subgroup RN (SGRN), an example of this is the call for Mediterranean data published April 2010. This call covers data on landings, catches, length and age compositions, fishing effort, trawl and hydro-acoustic surveys in the Mediterranean Sea. The data will be used to assess the status of European hake, red mullet, striped red mullet, deepwater rose shrimp, giant red shrimp, red shrimp, Norway lobster, anchovy, picarel and sardine and their fisheries in the various GFCM GSAs[3]. The data needs were previously defined during a preparatory STECF sub-group meeting, and assessments will be carried out by another STECF sub-group.

For the call formulation, STECF advises DG Mare on call components including the target region (sea area) to be covered, the issue being addressed, and the aggregation level needed to render a specific data set useful for scientific assessment purposes. The EU member states respond to the call by delivering the requested data to a database hosted by DG Joint Research Centre within a pre-defined time window. It is obvious that the EU member states must have the capacity to reply to the calls, *i.e.* they must have set-up databases that can host the data until it is called for. A major improvement in this approach, compared to the former data collection framework, is that data submitted by member states can now be stored indefinitely. Another major improvement is that the new framework obliges Member States to provide access to the data for fisheries management advice, scientific publications, public debate and stakeholder participation in policy development – i.e. the data is public domain. For genetic data this has to be taken into account: Currently genetic data is to a great extent generated through scientific projects addressing specific hypotheses and, generally, the data only becomes public after analytical results emerging from the data analysis have been published in scientific journals. It is unlikely that this procedure will change. However, there is no reason for this to be a major impediment. However, it existing mechanisms for biological sampling and data collection will often provide opportunities for cost-effective sampling in support of genetic data generation.

[1] European Commission Directorate General Joint Research Centre.

[2] Scientific, Technical and Economic Committee for Fisheries; Provides advice to the European Commission under Article 33 of Council Regulation EC 2371/2002.

[3] GFCM: General Fisheries Commission for the Mediterranean; GSA: Geographical sub-area.

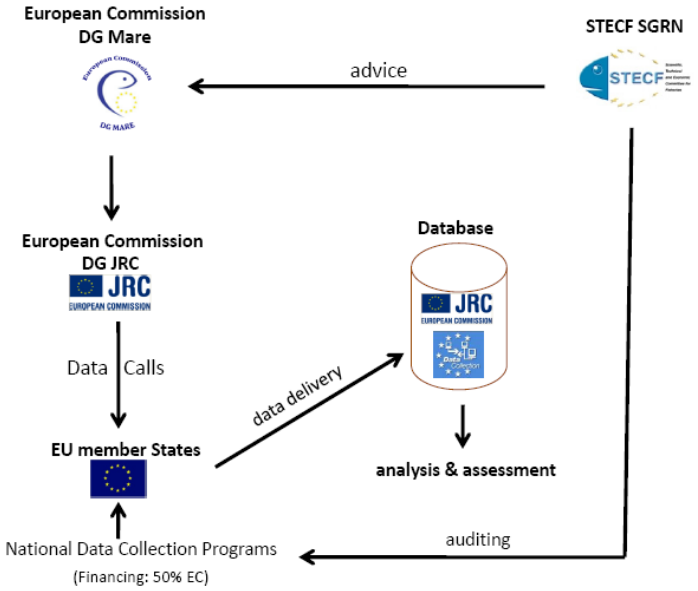

Figure 2.4.1. The Data Collection Framework. Process of data definition and delivery.

Requirements and needs to enable the integration of genetic data under the DCF remit

Historically, geneticists have struggled to communicate the value of genetic information for the successful management of aquatic biological resources to fisheries biologists and, especially, to fisheries managers. It was a long time before the first management plans were based on more than just assessment data using traditional parameters such as abundance, size, weight and age distributions and this is still rare. However, there are now a number of examples where genetics is being successfully applied as a tool in the management of marine fisheries. For example, Norwegian coastal cod are being managed in real-time using among other techniques, genetic screening of fisheries to define the origin of the stock proportions present. The fishery can then be opened or closed depending on the proportions found and the management needs to preserve important stock components (Geir Dahle, Institute of Marine Research Bergen, Norway – personal communication). Another example using the same techniques of mixed stock fishery analysis is the Atlantic salmon coastal and inshore drift net fisheries off the coast of Ireland. Here again samples are obtained from the fishery and the fishery opened or closed depending on the stock components found at a particular point in time. Together with such mixed stock fishery management scenarios genetics has also been utilized to help managers define stock structures (Hauser and Seeb 2008; Waples *et al.*, 2008).

Examples such as those referred to above have shown the benefits to be realised when genetics are integrated into the toolkit available to fishery managers. This information is often not taken into consideration in fishery management programmes, although there is a great deal of genetic information available for many species of interest in relation to both sustainable exploitation and the maintenance of biodiversity. This is in spite of the already stated positions of both ICES and the Scientific, Technical and Economic Committee for Fisheries (STECF), which provides scientific advice to the European Commission for the Common Fisheries Policy that have iden-

tified incorporation of genetic information as an important development in fisheries management (ICES, 2009), (STECF, 2011).

As pointed out previously, a shortcoming of most of the current genetic data on marine resources is that they are generated and stored on a project level, especially in cases where marine resources are exploited by several nations. As a result, the data are not collected through a longer time frame. Only within national programmes, and these are few in number, are genetic data collected on a broader time scale and only then for species where there is a specific national interest.

In order to realize the incorporation genetic information into routine management programmes genetic data have first to be integrated into the DCF. As with all other cases of integration of data from disparate sources, this will require the definition and agreement of standard procedures for collection, screening and analysis of the data. The existing mechanisms for the collection of biological information already being undertaken by EU member states, that underlay the data collection for the DCF, provide a cost effective basis for collection of samples to generate genetic data. If so, then genetic screening of samples will also need to be performed. This would be in member state laboratories and have to be according to an agreed set of laboratory protocols. Similarly, the analysis performed on the data generated would need to follow an agreed set of analytical techniques. Standard Operating Procedures such as these have successfully been developed in the past for techniques such as scale reading and otoliths analysis at ICES expert workshops.

WGAGFM is convinced of the benefits incorporation of genetic data into the DCF can bring. In order to achieve this outcome it would be useful if at a political level ICES initiated an informative mutual dialogue on doing so with relevant stakeholders such as DGMARE, ICES Stock Assessment Working Groups, and national and local fishery managers. Such a dialogue might best be achieved at a workshop involving all relevant stakeholders. Such a workshop would allow geneticists to outline the potential of genetic data for informing management, managers to communicate particular questions where genetics may add useful insights, and for data format requirements to be discussed.

Recommendations

- We recommend ICES to support the integration of genetic data into the DCF.
- ICES should initiate a stakeholder workshop where the potential of genetic data to support management and its incorporation into the DCF is discussed.

Table 2.4.1. Modules and data type covered by the Data Collection Framework. Please note: this table is just providing a rough overview to demonstrate scope and complexity of the DCF. Definitions and details can be found in the Commission Decision 2008/949/EC {Commission, 2008 #1210} and on https://datacollection.jrc.ec.europa.eu/dcf-modules.

	DCF Modules							
	FISHING					Aquaculture & Processing Industry		Marine Ecosystems
	Economic Data	Biological Data		Transversal Data	Research Surveys at Sea	Aquaculture Econ.-Data	Processing Econ.-Data	
		Metier related	Stock related					
Variables	Fishing Enterp Employment Income Expenditure CapitalValue	Sampling must be performed in order to evaluate the quarterly length distribution of species in the catches, and the quarterly volume of discards.	e.g. individual information on age; individual information on length; individual information on weight; individual information on sex; individual information on maturity; individual information on fecundity;	Capacity Effort Landings	MEDITS Small Pelagic	See [2008/949/EC]	See [2008/949/EC]	See [2008/949/EC]

	DCF Modules							
	FISHING					Aquaculture & Processing Industry		Marine Ecosystems
	Economic Data	Biological Data		Transversal Data	Research Surveys at Sea	Aquaculture Econ.-Data	Processing Econ.-Data	
		Metier related	Stock related					
Disaggregation level	Member States are required to report economic parameters on an annual basis for each fleet segment (combination of fishing gear and vessel length) and supra region combination.	In order to optimise the sampling programmes, the metiers defined in Appendix IV (1 to 5) may be merged. When metiers are merged (vertical merging), statistical evidence shall be brought regarding the homogeneity of the combined metiers.	The necessary disaggregation levels as well as the collection periodicity for all variables and the sampling intensities for age are specified in Appendix VII. For sampling strategies and sampling intensities, the rules established in Chapter II section B (Precision levels and sampling intensities) shall apply.	Depending on the data, transversal parameters are required to be collected at varying aggregation levels,. Appendix VIII of 949/2008 provides a list of transversal variables and their corresponding minimum sampling specifications.	See [2008/949/EC]	See [2008/949/EC]	See [2008/949/EC]	See [2008/949/EC]

	DCF Modules							
	FISHING				Aquaculture & Processing Industry			Marine Ecosystems
	Economic Data	Biological Data		Transversal Data	Research Surveys at Sea	Aquaculture Econ.-Data	Processing Econ.-Data	
		Metier related	Stock related					
Sampling strategy	Member States are required to describe the methodologies used for estimating each economic variable, including quality aspects, in their national programmes.	For landings: 1. The Member State on whose territory the first sale take place, shall be responsible for ensuring that biological sampling occurs according to the standards defined in this Community Programme.. 2. For sampling purpose, only the major metiers need be considered.	When possible, age-reading shall be performed on commercial catches to estimate the age composition by species and, where relevant, growth parameters. Where this is not possible, Member States shall justify why in their national programs.	Tansversal data should be collected in an exhaustive way. Where not possible, Member States are required to specify the sampling procedures within their national programmes.	See [2008/949/EC]	See [2008/949/EC]	See [2008/949/EC]	See [2008/949/EC]

	DCF Modules							
	FISHING					Aquaculture & Processing Industry		Marine Ecosystems
	Economic Data	Biological Data		Transversal Data	Research Surveys at Sea	Aquaculture Econ.–Data	Processing Econ.–Data	
		Metier related	Stock related					
Precision levels	Member States are required to include in their annual report information on the quality (accuracy and precision) of estimates.	Landings: The precision level 2 shall be targeted at the stock level for both Group 1 and Group 2 species. If necessary, specific stock-based samples shall be added if metier-based sampling fails to provide the appropriate precision for length distributions at the stock level. Discards: Data related to quarterly estimates of discards length and age composition for Group 1 and Group 2 species must lead to a precision of level 1. Weight estimates of Group 1, 2 and 3 species must lead to a precision of level 1. Recreational fisheries: Data related to annual estimates of the catches in	See [2008/949/EC]	Member States are required to include in their annual report information on the quality (accuracy and precision) of estimates.	See [2008/949/EC]	See [2008/949/EC]	See [2008/949/EC]	See [2008/949/EC]

	DCF Modules							
	FISHING					Aquaculture & Processing Industry		Marine Ecosystems
	Economic Data	Biological Data		Transversal Data	Research Surveys at Sea	Aquaculture Econ.-Data	Processing Econ.-Data	
		Metier related	Stock related					
Exemption rules	See [2008/949/EC]	If Member States cannot reach required levels of precision or only at excessive costs, they can obtain, based on STECF recommendation, derogation from the Commission to reduce the precision level, sampling frequency or to implement a pilot survey provided this request is fully documented and scientifically proven.	See [2008/949/EC]	See [2008/949/EC]	See [2008/949/EC]	See [2008/949/EC]	See [2008/949/EC]	See [2008/949/EC]

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2.5 ToR e) Genomic approaches of adaptation of marine organisms in changing environments: what can populations tell us about genes underlying phenotypic changes and what can genes tell us about adaptive evolution of populations?

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Justification: Genomics of marine organisms can contribute to better understand how they can adapt to variation of environmental factors in the wild or under aquaculture conditions. In the wild, environmental variation can result from climate change, acidification of oceans, increasing levels of pollutants or fisheries. In aquaculture, adaptation can result from changes in rearing practices or to the extension of new pathogens. Adaptive responses can have phenotypic and genetic components that must be disentangled to model the evolutionary response of species.

Firstly, **genetically based phenotypic differences between wild or culture populations** have been demonstrated in many marine species. In these cases, **genome scans**, based on large numbers of genetic markers using high throughput genotyping technology, can identify regions of the genome associated with these differences and therefore resulting from response to differential selection pressures. When mapped on the genome, these markers contribute to identify QTLs and the genetic architecture of the concerned traits. Secondly, analysis of **sequence variation of coding and**

non-coding parts of the genome can be used to infer the role of selection on the shaping of the observed molecular diversity. Thirdly, **transcriptome sequencing,** revolutionized by the new generation of sequencing technologies, strongly facilitate the identification of genes differentially expressed in organisms exposed to different environmental conditions, or resulting from divergent selection in the wild or under aquaculture conditions. Candidate genes should then be validated using functional genomics approaches (i.e. reverse genetics, mutagenesis, RNAi...). They can be used for gene assisted selection or for population management purposes. Finally, both approaches (i.e. genome scans and transcriptome studies) can be **merged combined through eQTL** and genetical genomics studies, inferring genetic and environmental variance components associated with transcriptional abundances underlying adaptive traits. Such approaches provide further links between adaptation of marine organisms and the molecular bases of the concerned traits.

Novel genomics approaches aiming to better describe and understand these processes will be reviewed in the present ToR and study cases concerning fish and shellfish will be presented. Current developments will be described, highlighting the potentials and limitations of these approaches to contribute to better manage marine biodiversity.

Adaptation is a key component of sustainability in a changing environment. For living organisms, two main components must be distinguished: (1) phenotypic plasticity of an individual facing variable environmental conditions and (2) genetic polymorphism within a species allowing its potential adaptation to a given range of environments. Distinction between adaptive and non-adaptive evolution and elucidation of the genetic basis of adaptive population divergence is a goal of central importance in evolutionary biology. Genetically based polymorphism for traits involved in spatial or temporal adaptation can lead to differentiation over time or space if other evolutionary forces, such as gene flow, do not counterbalance the effect of local selection. Direct demonstration of the effect of selection – relative to other evolutionary forces - on local adaptation is one of the goals of evolutionary biology. Studies have long been – and still are – based on the analysis of phenotypic traits varying between populations in space or time. The increasing ability to obtain genomic information has opened novel possibilities to distinguish adaptation from other evolutionary forces by tracing its footprints at the molecular level. Establishment of functional links between the phenotypes and genotypes is also greatly facilitated by genomics and reverse genetics. Different approaches can be distinguished to demonstrate adaptive processes. They can be classified in two different groups:

- At the phenotypic level, the comparison of individuals sampled in different populations under common environmental conditions, often referred as 'common garden experiments' aim at minimizing non-genetic components of variation of the studied traits to reveal genetically based differences. Phenotypes can cover a variety of traits of different natures from morphometric measurements to quantification of gene expression. The "genetic architecture" of these traits can be obtained by QTL mapping.
- At the genome level, investigations are based on allele frequencies at given loci or – more directly – on DNA sequence data. In most cases, signature of selection on the genome provides indirect evidence, as alternative hypotheses cannot be totally ruled out. As a result, a question that often remains is to know if the observed differences between genotypes is really adaptive or results from other factors.

Linking phenotypes and genotypes at given loci is needed to provide direct evidence for response to local adaptation. However, cases for which direct links between observed variation for traits, DNA polymorphism and selective forces have been demonstrated remain rare. This is often due to the complex relationship linking DNA variation to the resulting phenotype as illustrated by (Dalziel *et al.*, 2009). Current progress in genomics of non-model organisms increases rapidly the number of well documented cases in marine species.

Common garden experiments: the phenotypic approach

Common garden experiments aim at disentangling environmental and genetic components of observed phenotypic differences. Under a "common garden", variations due to environmental factors are assumed to be minimized and the observed remaining variance is therefore presumed to be genetically based. The comparison of traits recorded on individuals originating from different locations or generations aims at identifying those putatively under differential selection. Such experiments are however strongly constrained by biological characteristics of the studied species and remain unfeasible for many marine species. In a first step, comparisons of specimens collected in natural populations can be performed, assuming that environmental differences encountered before the experiment will not significantly influence the recorded traits. In that case, a period of acclimatization to the common experimental condition is commonly used to reduce this bias. The efficiency of such acclimation period is however rarely assessed. Preferably, comparisons can be performed on progenies of individuals to be studied. By this way, common environment can be ensured but this approach implies that reproduction of the studied species is well mastered and that the development timing is rapid enough so that progenies reach the stage in which they will be phenotyped. This breeding step under controlled conditions minimizes influence from maternal or developmental effects originating from sampling the individuals directly in nature. Such a step may, however, strongly reduce the number of marine species where this approach can be applied. One additional difficulty related to this approach is that the tested progeny is representative of the studied population. This assumes that a large enough number of parental individuals are used with minimized variance of their reproductive success to avoid random drift.

Environmental conditions under which phenotypic characterization is undertaken can strongly influence the recorded traits. In case of significant genotype x environment interactions, different environmental conditions should be preferably tested. This will also allow estimating the genetic bases of plasticity of traits, which can be an important component of adaptiveness. Ideally, reciprocal transplant experiments will ideally reveal local adaptation. However, this is often most unpractical for marine species such as pelagic fish. The development and use of marine mesocosms for such studies remain challenging for most species and should be encouraged.

The development of transcriptomics studies, based on microarrays other high throughput approaches opened the possibility to score hundreds of traits as gene expression levels. In most cases, the genetic basis of these expression levels remains to be studied. In a first approach, this can be assessed by recording expression profiles of progenies resulting from crosses within and between individuals sampled in the studies populations. Intermediate levels of expression in "hybrid" progenies supporting additive variance genetic components. In a further step, heritability of expression level can be estimated in a similar way than morphometric traits.

Mapping adaptive traits within genomes: the QTL approach

Mapping of quantitative trait loci (QTLs) is commonly based on the analysis of experimentally controlled populations (e.g. F_2 progenies from a cross between inbred lines or more complex schemes involving on related individuals). Our working group reviewed QTL mapping in fisheries and aquaculture in 2008. When generation time is too long to allow such approaches, "whole-genome association studies" (WGAS) can be performed. These studies rely on linkage disequilibrium (LD) to detect an association between genotypes and phenotypes. The power and precision of these WGAS depend on the extent of LD in the studied population, which notably depends on its effective size (the smaller, the easier) and the number of loci scored. This is notably currently performed in cattle using SNP arrays (e.g. MacLeod *et al*., 2010). It such approaches, the use of phenotypic variation is a starting point and the statistical association of this variation with markers is the resulting goal. This approach therefore assumes that the adaptive traits have first been identified and measured.

Tracking the footprints of adaptation within genomes

The identification of variation at the DNA level of polymorphisms leading to presumed adaptive phenotypic variants has benefited in the recent years of the expansion of genomic technology. It should however be noted that, in several cases, early allozyme-based "classical" population genetics studied led to the identification of loci presumed to be under selection. For example, clinal variation of such markers along environmental clines can be indicative of local adaptation. They can however result from other evolutionary phenomena such as secondary contacts zones (e.g. in mussels: Boon *et al*., 2009).

Genome scans can be performed to identify loci or parts of the genome that appear under directional selection at the population level without phenotypic information. The detection of adaptive evolution at the molecular level essentially relies on indirect inferences. Direct inferences can of course be established if further information can be obtained regarding the functional role of those loci. "F_{st} ouliers" are defined as loci showing significant deviation from the other loci. Different methods and associated statistical tests have been proposed to identify outliers (Vitalis *et al.,* 2001; Foll and Gaggiotti, 2008).

It must be underlined here that a loci showing significantly higher (or lower) genetic differentiation and others is not necessarily under direct selection. They can be the result of associative effects, adaptive evolution leaving footprints on the pattern of neutral diversity by "hitchhiking". There are many similarities between the way demography and selection shapes genetic diversity. However selection only acts on the chromosomal neighbourhood of the site targeted while demography affects the whole genome. Population differentiation has an influence on hitchhiking: from "local effects" in the neighbourhood of favourable mutation to "global effects" (Bierne, 2010). As a result, scanning whole genomes (i.e. scoring large number of markers) is needed to discriminate between different causal factors of evolution.

Hierarchical testing is a way to increase confidence of candidate genes detected from genome scans. Starting out with a genome-wide distribution of genetic markers (preferably >100), one can perform genome scans to attain an initial set of candidates for selection (Figure 2.5.1). However, most outlier tests suffer from various levels of type I and II errors (Narum and Hess 2011). In order to further increase confidence in findings of natural selection at certain candidate markers, a range of "follow-up" approaches can be applied as far as data allows. First, if the underlying sequence of a

marker is known, annotation can be made to infer potential functions of gene regions underlying the genetic polymorphisms suggested outliers (Figure 2.5.1).

For populations genetically adapted to different environments (e.g. different temperature or salinity regimes) one would expect to find stronger correlations between important environmental drivers and the actual genes targeted by selection compared to neutral genes. An array of landscape genetics approaches allow to test for correlations between various environmental variables with each genetic marker independently (Joost *et al.* 2008; Coop *et al.* 2010). A pattern of stronger and more frequent landscape correlations for outlier markers than neutral markers will first of all suggest a potential evolutionary role of the particular variable, but also add confidence towards a true adaptive role for candidate markers showing such correlations (e.g. Narum *et al.* 2010). Increased support for a true adaptive role of candidate markers can be added if the study design allows for independent replication of tests (also referred to as parallelism in recent literature; Figure 2.5.1; Fraser *et al*. 2011).

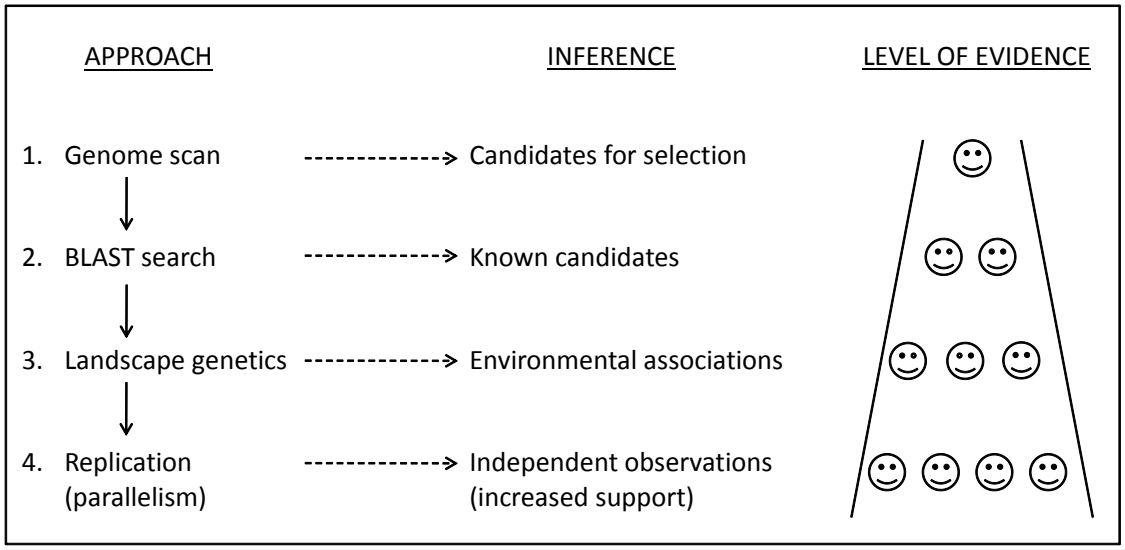

Figure 2.5.1. Conceptual diagram of a hierarchical approach for inferring in-direct evidence of selection at genetic markers (see text for more details).

Case studies and novel "model" species

Bradbury *et al*. (2010) followed the hierarchical approach outlined above for studying adaptations to temperature in Atlantic cod (*Gadus morhua*). They sampled cod populations along two independent temperature clines along either side of the Atlantic Ocean. Cod assemblages at either side of the Atlantic are expected to have followed independent evolutionary trajectories since they diverged between 100–150,000 years ago (Carr and Marshall 2008). However, the study by Bradbury *et al*. (2010) demonstrated a range of congruent outliers for divergent selection also showing strong correlations with temperature. BLAST annotations further suggested a range of different physiological processes to be associated with local temperature regimes. All together, this study found strong support for an adaptive role of the candidate genes underlying these congruent outliers. Currently, the study by Bradbury *et al*. (2010) demonstrates one of the most convincing findings of local adaption in a non-model marine fish following the indirect genotype based approach.

Understanding the functionality of evolution through genomic and transcriptomic analyses of commercial fish species is benefiting greatly from a few models. While reflecting scientific, historical (Wootton, 2009) and socio-economic determinants of choice, models have become accepted and have been shown to be very valuable. Current small fish models commonly used in ecology and evolution include the three-spined stickleback (*Gasterosteus aculeatus*), guppy (*Poecilia reticulata*) and mummichog (*Fundulus heteroclitus*). They are cited in the literature with about the same intensity, although reflect somewhat different scientific interests. For various reasons the small fish models of developmental developmental biology (the zebrafish *Danio rerio*) and medaka *Oryzias latipes*) have never attained a status of significance in eco-evolutionary research. Key traits for a model fish include generation time and lab footprint, experimental cost per animal, tolerance of broad environmental conditions, access to background biology (Bell and Foster, 1994), genomic tools (Oleksiak, 2010), the size of the research community, scientific literature (Östlund-Nilsson *et al*., 2007), tradition and experience.

Three-spined stickleback represents an outstanding model in eco-evolutionary research. It has contributed prominently to long standing questions such as the mechanisms of parallel evolution, sympatric speciation, directional selection, hybridization, the pace of evolution and eco-evolutionary dynamics. It is also a model in biomedical research for bone formation (Chan *et al*., 2010) and pigmentation (Miller *et al*., 2007). A nice case of the power of a small fish model is the pleiotropic effects of single gene changes (Pitx1- Peichel *et al*., 2001; Eda – Colosimo *et al*., 2005 and Kitlg – Miller *et al*., 2007). Small genomic changes may lead to large changes in phenotype, for example the presence of pectoral spines and lateral plates, and changes in pigmentation. Few cases have been documented in non-model species, such as the Pantophysin I gene in cod (Pogson and Mesa, 2004).

Whether selection acts on standing variation originate from a new mutation has been an issue for a long time (Schluter and Conte, 2009). The evolution of plateless stickelbacks in freshwater has its origin in the rare presence of an Eda allele in marine populations (Colosimo *et al*., 2005). Moreover, the process of divergence may act fast, as shown by the tolerance of cold. Fast evolution has also been proven in Atlantic silverside *Menidia menidia* (Conover and Munch, 2002) and guppies (van Wijk and Carvalho, pers. comm.), but remains largely to be documented in commercial fish (but see Jakobsdottir *et al*., 2011).

The maturation of technical developments in genomics and transcriptomics has led to considerable progress. In a short time genome scans, which look for signatures of selection in the genome, have expanded from not being possible to implement in a natural setting over a small set of markers (Makinen *et al*., 2008; Raeymaekers *et al*., 2009) to an almost full screening of the genome (Hohenlohe *et al*., 2010). The latter study found in a representation library of 100 different individuals signatures of genome-wide selection in freshwater and marine populations. Excellent knowledge of field gradients and experiments have facilitated the interpretation of the genomic data. At the moment the sequencing of 10 freshwater and 10 marine genomes collected worldwide is in progress by the Kingsley lab in California. This will lead to an even more detailed analysis of adaptation and selection, for example allowing understanding the functionality of selection.

While genome scans allow identifying gene regions and genes of interest, the functionality of these genes and gene regions remains largely unknown. Therefore research on a growing list of candidate genes has identified several interesting and

significant aspects (Colosimo *et al*., 2004; Miller *et al*., 2007; Wegner *et al* 2006). For example the regulation of the Pitx gene determines to a large extent the lateral plates of sticklebacks, of which the low plated morphotype has so remarkably colonized in parallel the rivers of the northern hemisphere. Body armour influences mobility and hence determines predation risk. Other strategies to identify candidate genes are transcriptomics, where the transcripts of the genes are studied for presence/absence, and more importantly up and down regulation (McCairns and Bernatchez, 2010). Increasingly a shift is occurring from single transcript screening (Peichel *et al*., 2001; McCairns *et al*. 2010), to full genome screening with micro-arrays (Leder *et al*., 2009) and currently also to whole genome transcriptome shotgun sequencing.

Understanding the full meaning of high throughput –omics approaches is backed by more traditional biology. Classical genetics including the heritability of traits (body armour - Mazzi *et al*., 2002; cold tolerance - Barrett *et al*., 2010, spine size - Barrett *et al*., 2008), and the mapping of traits (phenomics; Peichel *et al*., 2001, Shapiro *et al*., 2004). Behaviour (Pike *et al*., 2011) and comparative functional biology (Kitano *et al*., 2010) allow characterizing genomic changes, which often happen at the level of transcript regulation.

Marine fish and fisheries population genomics have largely developed in parallel with the findings in model species such as threespined stickleback (Nielsen *et al*., 2009 - review), although they have been constrained by good field data and experimental opportunities. A most striking finding is the molecular evidence for evolution induced through fishing. Although suspected for a long time (Rijnsdorp *et al*., 1996), confirmation is available from a remarkable allele shift in the pantophysin I gene of Icelandic cod populations over a period of only 55 years (Jakobsdottir *et al*., 2011).

With the arrival of affordable single-genome sequencing, the integration of information from genome, transcriptome, metabolome, physiology, life-history traits and ecology in field and experiment becomes increasingly feasible. Fish and fisheries biology has now more than ever before the means to understand the causes of evolution.

An elegant example of how insights in modes of selection and adaptive evolution can be obtained using genetic approaches is photic adaptation in the sand goby *Pomatoschistus minutus*. Polymorphisms were found for the rhodopsin gene RH1, initially selected as a candidate gene, which reflected water photic conditions rather than phylogeographic pattern. This suggests selection at the RH1 gene is involved in adaptation to light environments (Larmuseau *et al*., 2009). Additionally, synonymous and non-synonymous SNPs were compared between Baltic and North Sea regions. High levels of polymorphism were observed in the temporarily variable turbid conditions of the North Sea, whereas in the Baltic, where conditions are stable over time but photic conditions strongly differ between areas, signatures of stabilizing selection were observed. It is noteworthy that within one gene, synonymous and non-synonymous polymorphisms showed different modes of differentiation and this patterning could be used to infer both different modes of selection and demographic history (Larmuseau *et al*., 2010).

Recommendations

It is clear that monitoring of the genetic components of local adaptation in fisheries and aquaculture is required in view of changing selective pressures such as global change and fisheries induced evolution affecting productivity. Understanding of the dynamics of fitness, an important determinant of local adaptation in populations,

requires the integration of the various levels linking genotypic to phenotypic variation. Therefore we recommend:

1) Given the complexity of such undertaking, focusing on a few key aquatic species, providing well documented examples relevant to other species of interests for fisheries and aquaculture.

2) The incorporation of genome-wide genotyping as a tool in population studies.

3) Combining complementary approaches to minimize false positive markers and maximize the likelihood of identifying genes underlying adaptive processes in the wild.

4) The development of massive multi-trait phenotyping methods under natural and aquaculture conditions.

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Annex 2: Agenda

Wednesday 4 May 2011

09.00	Registration
09.30 – 09.50	Welcome by local host, welcome and updates from WG chair
09.50 - 11.00	Presentation of position papers for the different ToR's, including a preliminary discussion
11.00 - 11.20	**Coffee**
11.20 - 13.00	Presentation of position papers for the different ToR's, including a preliminary discussion (cont.)
13.00 - 14.00	**Lunch**
14.00 - 17.00	Presentation of position papers for the different ToR's, including a preliminary discussion (cont.)
17.00 - 18.00	Open session. (Present results, projects, management problems)

Thursday 5 May 2011

09.00 - 12.30	Group discussions of the different ToR's
13.00 - 14.00	**Lunch**
14.00 - 16.30	Presentation of revised ToR reports
16.30 – 17.00	SALSEA-MERGE
17.00 - 18.00	SSGHIE and other ICES related issues

20.00 WG-dinner at Blue Sky Café, Bangor High Street

Friday 6 May 2011:

09.00 - 11.00	Final adjustments of TOR reports – Recommendations
11.00 - 12.00	Suggestions for new TOR's for 2012 and future meeting venue
12.00 - 12.30	Election of Chair person for the next three years
12.30 - 13.00	Evaluation and closing of meeting.

Annex 3: WGAGFM terms of reference for the next meeting

The **Working Group on the Application of Genetics in Fisheries and Mariculture** (WGAGFM), chaired by Dorthe Bekkevold*, Denmark, will meet in Bilbao, Spain, 1–3 May 2012 to:

a) Parasites and pathogens as "magnifying glass" for fish stock characterization;

b) Adaptive markers - Consider the issues pertaining to the use of adaptive SNPs and other markers for genetic identification of populations (breeding stocks);

c) Continuing assessment of the SNP-technology.

WGAGFM will report by 31 May 2012 for the attention of SCICOM.

Supporting information

Priority	The current activities of this Group will lead ICES into issues related to the ecosystem affects of fisheries, especially with regard to the application of the Precautionary Approach. Consequently, these activities are considered to have a very high priority.
Scientific justification	Term of Reference a) Parasites and pathogens as "magnifying glass" for fish stock characterization Justification: Stock discrimination is at the core of fisheries management. It is achieved through a combination of tools, including morphometrics, genetics and otolith characterization. However, when neutral genetic differentiation in the fish population is low, assignment becomes difficult. For a long time parasites and pathogens have been used as biological tags for stock assignment, but success was sometimes limited. Recent progress in genetic characterization of parasites and pathogens has now revealed unprecedented levels of resolution. Due to the usually short generation time (and higher mutation rate), they accumulate mutations much faster than their host, providing a 'magnifying glass' to study their host's evolutionary history. We will review the current information on parasites and pathogens as a tool in stock discrimination. As symbiotic microbes of the digestive system have also been shown characteristic of the host, they will be included in the review. Term of Reference b) Adaptive markers - Consider the issues pertaining to the use of adaptive SNPs and other markers for genetic identification of populations (breeding stocks) Justification: For microsatellites, there are substantially lower Fst values (as a measure population differences) among populations of marine species, compared with freshwater or anadromous species, at presumed neutral markers. Markers influenced by directional selection often show higher Fst values among populations of marine species than neutral markers. If selected markers are used for population identification, questions arise; e.g. what is time-scale of their usefulness (long enough for management?) and how is the likely lack of temporal stability to be accommodated? With the advent of large-scale SNP screening by next generation sequencing of genomic DNA, it is now possible to consider suites of neutral and directionally selected markers for population discrimination independently. Thus it is timely to consider the issues pertaining to the use of adaptive markers in population genetics applications, with particular reference to marine species.

	Term of Reference c) Continuing assessment of the SNP-technology Issues pertaining to ascertainment bias, cost, SNP choice, ease of analyses, screening platform, technical aspects related to genotyping, data management, and broader technological and statistical approaches should be further considered by members of this working group on an ongoing basis.
Resource requirements	None required other than those provided by the host institute.
Participants	The Group is normally attended by some 15–25 members and guests.
Secretariat facilities	None.
Financial	No financial implications.
Linkages to advisory committees	SCICOM
Linkages to other committees or groups	SIMWG , WGECO, WGMAFC, WGMASC
Linkages to other organizations	Linkage with the EC Joint Research Centre at Ispra, Italy

Annex 4: Recommendations

Recommendation	For follow up by:
1) We recommend multidisciplinary methods- e.g. genetic, direct tagging, demographic, behavioural, and oceanographic are integrated to address population connectivity	SCICOM, WGAGFM
2) We recommend spatio-temporal sampling schemes are carefully planned (micro-, local, regional scales) and should incorporate empirical knowledge or predictions from oceanographic models, e.g. distributions/habitat requirements of different life stages	SCICOM, WGAGFM
3) We recommend analytical approaches (e.g. Approximate Bayesian Computation) are integrated into the generation and testing of alternate models of mechanisms driving population genetic structuring in marine organisms	WGAGFM
4) Long-term empirical studies of genetic and environmental data are instigated to evaluate rare extreme events (such as ENSO, hurricanes etc).	WGAGFM
5) That ICES stimulates a multidisciplinary modelling and experimental approach to formulate the genetic principles on the design and implications of MPA networks	SGMPAN
6) That the ecosystem implications of designs of MPA networks for the connectivity and evolutionary requirements of species and communities are validated	SGMPAN
7) That the common benefits between exploited resources and biodiversity oriented MPAs are evaluated within the perspective of STIG-MSP	SGMPAN/STIGMSP
8) We recommend and encourage that timely investment of scientific resources be used in testing, developing and deploying the technology.	WGAGFM
9) We recommend SNPs be considered as a complementary tool to other available markers rather than a replacement for other makers.	ICES,WGAGFM
10) Issues pertaining to ascertainment bias, cost, SNP choice, ease of analyses, screening platform, technical aspects related to genotyping, data management, and broader technological and statistical approaches should be further considered by members of this working group on an ongoing basis.	WGAGFM

11) We recommend ICES to support the integration of genetic data into the DCF	ACOM
12) ICES should initiate a stakeholder workshop where the potential of genetic data to support management and its incorporation into the DCF is discussed	ACOM
13) Given the complexity of such undertaking, focusing on a few key aquatic species, providing well documented examples relevant to other species of interests for fisheries and aquaculture.	ICES, WGAGFM
14) The incorporation of genome-wide genotyping as a tool in population studies	WGAGFM
15) Combining complementary approaches to minimize false positive markers and maximize the likelihood of identifying genes underlying adaptive processes in the wild	WGAGFM
16) The development of massive multi-trait phenotyping methods under natural and aquaculture conditions.	WGAGFM