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Executive summary

The Workshop on the Implications of Stock Structure (WKISS) met at ICES Headquarters 5–7 April 2011, chaired by Lisa Kerr (USA) and Niels Hintzen (The Netherlands) to examine the implications of complex stock structure on fish resources, fisheries, stock assessment and management. The workshop was attended by 15 participants from eight member states, including five members participating over WebEx. The workshop primarily focused on the advances in modelling to represent complex stock structure.

From a fisheries perspective, it is assumed that stocks are discrete units and that specific stocks can be exploited independently of each other or at least catches can be assigned to the stock of origin. This assumption is fundamental to ICES single species advice. In reality, however, this assumption is often violated and may pose problems affecting fish resources, fisheries, stock assessment and management. Modelling exercises to test the implications of stock structure across these scales were reviewed and extensively discussed during the workshop. Terminology was discussed at the outset of the meeting, as many of the terms used to describe complex population structure are ambiguous.

In principle, the goals of complex population modelling can be divided into two classes: (1) models designed to estimate population attributes relevant to management, of which stock assessment models, using tagging data or biological samples to estimate migration rates or stock mixing, form a major group, and (2) simulation models designed for hypotheses testing, where the results are most often compared against alternative scenarios. In both classes iterative simulation contributes to the understanding of stock complexity.

Over the past decade, several large stock identification projects were carried out to understand the structure of fish stocks in the North Atlantic Ocean. In general, these projects resulted in a better understanding of spatial-temporal dynamics of the metapopulation studied. In some instances, information on stock identity has been used to develop biologically realistic operating models and model simulation has been used to examine the behaviour of population components and the broader metapopulation under a range of scenarios (e.g. changes in the level of exploitation). Further, these same operating models can be used to simulate the outcome of alternative management strategies, which can help to inform fishery managers of the implications of management options. One important lesson to be learned from these projects was that stock assessment scientists need to be involved in stock identification projects to ensure that biological information gets incorporated or considered in the assessment and management of the stock.

A mismatch between management and biological units can affect the fish resource, stock assessment, fishery, and management. Of major concern at the biological level is the potential for overexploitation of spawning components, resulting in a loss of productivity or even extirpation of certain components. Further, ignoring stock structure may affect the accuracy of the stock assessment, possibly resulting in an inaccurate description of stock status and inappropriate level of harvest for sustainable fisheries management. Fisheries may be affected by a misperception of stock productivity and the appropriate scale of management; with the potential for a loss of yield when spatial structure is ignored.

Sustainable management options should aim to conserve diversity and avoid local depletion of components. In cases where there is a lack of understanding of stock

structure, managing for protection of the least productive component should be applied. The understanding gained from the analysis of stock structure and its influence on dynamics can inform the basis for comprehensive ecosystem management.

1 Opening of the meeting

Participants in the Workshop on the Implications of Stock Structure (WKISS) met at ICES Headquarters, 5–7 April 2011 to examine the implications of complex stock structure on fish resources, fisheries, stock assessment and management. ICES science to support sustainable use of fishery resources requires understanding of population structure and ICES advice assumes that fishery management units represent single, self-sustaining populations. When this assumption is violated, there may be adverse effects on the resource and the sustainability of the fishery. In WKISS we addressed how we can use the tool of simulation modelling and biological information gathered from stock identity projects to evaluate implications of complex stock structure for provision of reliable advice. WKISS acknowledges the substantial scientific progress made by previous initiatives (including SIMWG, ICES; 2010c) to address the issue of stock structure and have used this work as the basis to advance our understanding of the stock structure implications.

WKISS participants were composed of a diverse group of scientists including experts in stock identity, stock assessment and population modelling. The diverse composition of the workshop participants was essential to accomplishing the goals of WKISS and highlights the need to bring biologists and modellers together to effectively transfer relevant biological information into stock assessment and fisheries management.

2 Adoption of the agenda

The agenda for the workshop was developed prior to the meeting and presented for approval of the group at the start of the meeting. During the meeting, reviews of stock structure synthesis, modelling to represent stock structure, and other issues relevant to the terms of reference of the workshop were presented and discussed, and a workshop consensus was developed on each agenda item. After the meeting, workshop members continued to work by correspondence to draft the report.

3 Introduction

Substantial investments have been made into interdisciplinary research to identify and delineate biological populations. These research efforts indicate that the classic paradigm of marine fish being essentially homogeneous with little population structure does not hold for many ecologically and commercially important species. Increasingly, we find examples of spatial structure within fish stocks and movement between populations that may influence their productivity and dynamics. In some cases, consideration of spatial structure and movement may be necessary to resolve the internal and external influences affecting local and regional population dynamics. For example, differences in vital rates and asynchrony in the dynamics of populations can function to dampen variability of recruitment success at the metapopulation level (Hanski, 1998; Kerr *et al.*, 2010). Connectivity between populations that differ in productivity and dynamics under different environmental conditions may contribute to persistence at the local (i.e. rescue effects preventing local extirpations) and regional population level (Hanski, 1998; Kritzer and Sale, 2004; Secor *et al.*, 2009).

Sustainable fisheries management can be hindered when management units are not aligned with the biological structure within a stock. A misidentification of stock can result in stock assessments that do not accurately reflect the status of the stock. In this case, what is assumed to be a homogeneous stock may in fact be a mixed-stock, consists of populations with unique demographics and dynamics (Cadrin and Secor, 2009; Kell *et al.*, 2009). Thus, the short-term recommendations, such as total allowable catch, and long-term strategy, such as biological reference points, produced from the stock assessment may be incorrect. In this context, the harvest of a mixed-stock, consists of unique populations of a single species, can potentially lead to overfishing less productive populations and under fishing more productive populations (Cadrin and Secor, 2009). Recent research has revealed many examples of fish species within the North Atlantic for which there is a mismatch between the scale of biological population structure and spatially defined management units (Reiss *et al.*, 2009). Despite recognition of population structure and connectivity in the biological literature, many stock assessments ignore these phenomena. Often this is a necessity due to a lack of understanding of these phenomena or when there is understanding, a lack of sufficient survey data on a fine enough spatial scale to run a more spatially explicit assessment (Cope and Punt, 2011). When consideration of structure and movement are demonstrated to be important to the assessment and management of a fished stock, redefinition of the temporal and spatial scales of management units may be needed (Frank and Brickman, 2001). In some cases management units can be re-defined to reflect biological population structure, however, other populations are too complex to be spatially delineated, and many fisheries target mixed-stocks.

Simulation modelling is a useful and flexible approach that can allow exploration of the consequences of population structure and connectivity to the resource, assessment outcome, and management goals. Through simulation we can incorporate the best available empirically derived data to bring biological realism to dynamic models of fish stocks. We can use simulation to: 1) evaluate model performance, examining how the model performs under a wide range of population and fishery conditions and whether we have emulated the system of interest as closely as possible, 2) estimate population attributes by simulating a range of potential values for a specific attribute (e.g. connectivity rates between populations) and determine the simulated population trajectory for which the observed data are most likely, and 3) evaluate

population behaviour, examining how incorporating spatial structure and connectivity affect our perception of the population and impacts short-term (total allowable catch) and long-term projections (reference points).

The Workshop on Implications of Stock Structure (WKISS) was initiated to consider the implications of stock structure on fish resources, fisheries, assessment and management. Specific objectives of WKISS were to:

- a) Review and report on advances in population modelling to represent spatial population structure and movement of fisheries resources;
- b) Identify best practices for simulating populations with complex population structure;
- c) Synthesize information on biological stock structure for ICES management units;
- d) Examine the ecological, fisheries and management consequences of a mismatch between management units and biological stock structure and present modelling approaches to investigate these issues,
- e) Identify sustainable management options for complex population structures

3.1 Definitions of words and phrases used in the WKISS Report

There are a number of words in this report that are used in different ways in the specialist and non-specialist literature. To ensure that anyone reading this report understands the meaning and context of these words as used in this report they are defined here.

When referring to populations/groups of individuals or stocks we use the following meanings:

Biological population – a self-sustaining group of individuals from a single species which may have a number of spawning locations but form a single constituent part of a metapopulation. The term biological stock has also been used synonymously.

Components (of a metapopulation) – a term used to describe an identified or accepted part of a metapopulation. These are sometimes referred to in the literature as stocks or subpopulations, with the designation here of component meaning that they are probably part of a larger unit.

Deme – genetic sub unit within a metapopulation (Heath *et al.*, 2008).

Metapopulation – interacting biological populations (used in the variety of form given in Harrison and Taylor (1997) such as classical (Levins) mainland-island, patchy population, etc.).

Management Unit – a geographically delineated fishery resource that is based on practical or jurisdictional boundaries for operational stock assessment and fishery management that may or may not reflect biological population structure.

Spawning (contingent) aggregations – a group of individuals that utilize or are found on a single spawning ground. A biological population may utilize a single or a number of spawning grounds.

Stock – here we are utilizing the term in relation to a fishery (i.e. a fishery exploited unit). A stock may have a single spawning aggregation, be a biological population or even a metapopulation. In the fishery sense it is assumed that stocks are discrete and

that specific stocks can be exploited independently of each other or at least catches can be assigned to the stock of origin.

On the question of spatial distributions and locations of individuals and fisheries the following terms are used:

Natal homing – this term refers to individuals returning to spawn on the grounds they were spawned (McQuinn, 1997).

Reproductive mixing (straying, entrainment) – individuals that were spawned in one location and subsequently spawn in a different location (i.e. they join a different population). The processes by which they join a different population can be by ‘straying’ (drifting to a new location) or being ‘entrained’ (following the movement of individuals from a different spawning group; e.g. McQuinn 1997; Huse *et al.*, 2002; Heath *et al.*, 2008).

Spatial/temporal overlap – this refers to a location where two or more populations or stocks occur at the same time. There can also be spatial overlap without temporal overlap in the situation of spawning grounds being used at different times of the year (e.g. autumn, winter and/or spring-spawning populations).

The term ‘mixed’ with a qualifier we have reserved for fishery related factors:

Mixed-catches – not necessarily a targeted fishery but the composition of a catch that contains a number of different stocks or populations of a single species.

Mixed-fishery – a fishery that targets either a number of species or a number of stocks or populations of a single species.

Other definitions:

Connectivity – used here to mean there is a ‘link’ between two life-history stages, populations, locations, etc. In this sense the two points can be considered as linked by a ‘thread’ which can be traced from one end to the other (Secor and Rooker, 1995).

Productivity – productivity describes either biomass or recruitment and informs about the importance of the presence and abundance of a population within a given ecosystem.

Recruitment – is defined with a life stage on each occasion it is mentioned. Most often the term refers to a life stage that occurs after the first winter or after settlement in the juvenile period. It is not necessarily related to recruitment to the fishery/exploitation.

Settlement – The process of moving from a predominantly pelagic way of life to becoming classed as either demersal or benthic (Geffen *et al.*, 2007). This process may occur over a protracted period of time (i.e. months but involves a switch in habitats).

4 Review and report on advances in population modelling to represent spatial population structure and movement of fisheries resources

4.1 Review of past modelling approaches

Development of population and assessment models that include biological complexity characteristic of a system will allow us to simulate realistic population dynamics. Recognition of the potentially important impact stock structure can have on the ecology of a resource, and consequently the fishery and management of the species, has led to advances in population modelling to represent spatial population structure and movement of fish resources. Incorporation of complex structure of fisheries resources in population models typically takes three forms: 1) spatial heterogeneity, 2) movement (i.e. spatial overlap), and 3) reproductive isolation/mixing (Cadrin and Secor 2009).

We can model spatial heterogeneity of a stock by dividing stock-specific data into smaller spatial (and/or temporal) units and modelling production of these units independently (Cadrin and Secor, 2009). Smaller units may be scaled to represent spawning populations or fine-scale spatial units (usually represented as cells of fixed size) within a region (e.g. Andrews *et al.*, 2006; Reich and Dealteris, 2009). This approach can allow us to account for spatial differences in vital rates within a fish stock when sufficient data are available. Spatially explicit vital rates can be estimated by selecting data from the appropriate spatial and temporal scale using GIS software and using model fitting techniques to fit models to data (e.g. growth and maturity models). Subsequently, we can calculate spawning-stock biomass for spawning populations or spatial units; including number-at-age, weight-at-age, and maturity-at-age information unique to that area or population. We can also characterize the dynamics of a stock on a finer spatial scale by utilizing data in a more spatially explicit manner, calculating recruitment indices for unique spawning populations and using this information to inform levels of recruitment variability on a finer spatial scale. When the data to estimate vital rates or inform dynamics on a fine spatial or temporal scale are lacking a simpler approach, namely geographic apportionment, can be used (Quinn and Deriso, 1999). Using this technique we model the population using a single set of population parameters, and then allocate the proportional abundance of the population to smaller areas based on some index of relative abundance (Quinn and Deriso, 1999). MacCall (1990) proposed another approach (termed the basin model) for modelling spatial heterogeneity of fish stocks that incorporates the influence of density and habitat suitability on the distribution and growth-rate of fish. The underlying theory of the basin model postulates that fish inhabit their optimal habitat at low population size and as population size grows they will increasingly utilize suboptimal habitat which will have adverse affect on per capita growth rate (MacCall 1990). An example of this application was the use of a general additive model to model the spatial distribution of yellowtail flounder as a function of environmental variables (i.e. depth, temperature and sediment type; Simpson and Walsh 2004). Classic metapopulation models, such as Levins' patch-occupancy model, are another type of model developed to characterize spatial differences across populations. In this case, the model focused on differences in the risk of extinction and probability of recolonization of populations in habitat patches (Levins, 1970). Although this classic form of the metapopulation model is not very useful in modelling fish population dynamics due to the emphasis on extinction risk (Kritzer and Sale, 2004), the extension of this concept has formed the basis for modern metapopulation models.

Movement between populations is a complex process to model as it can occur across life stages with the potential for planktonic dispersal during the egg and larval stage, juvenile movement to and from nursery areas, and adult feeding and spawning migrations. In many cases the spatial aspects of recruitment processes are ignored in population models and stock assessments. Individual based models (IBMs) linked to hydrodynamic models have been used to model egg and larval drift. In these models, egg and larval stage fish are modelled as Lagrangian particles with biological traits whose movement is driven by an ocean circulation model (see review by Werner *et al.*, 2001). Work is currently ongoing to integrate these models directly into the stock assessment framework (Goethel and Cadrin, 2010). Another approach is to utilize IBM results in an "offline" manner to model the proportion of successful recruits of a specific stock to a particular region and integrate this information into a population model (e.g. Heath *et al.*, 2008). Goethel *et al.* (2011) present a review of methods to incorporate adult movement into stock assessments and we have summarized some of the major points here. There are two distinct approaches to modelling adult movement, one focused on modelling the change in density of fish at a given point in space, an approach similar to models of random diffusion of gases, termed a dispersion model (Beverton and Holt, 1957), and one geared toward modelling movement across a stock or spatial boundary (i.e. box transfer model; Beverton and Holt, 1957). The dispersion model tracks the change in concentration of fish over time in x and y space as a function of a dispersion coefficient (which accounts for velocity of movement, number of movements, and mean free movement path; Beverton and Holt, 1957). This approach was used to model dispersal of juvenile plaice from inshore nursery grounds to offshore habitat in the North Sea (Beverton and Holt, 1957; Goethel *et al.*, 2011). The dispersion model was subsequently expanded upon to incorporate directional movement of fish, as well as diffusion, termed advective-diffusion-reaction models. Siebert *et al.* (1999) applied this approach in modelling the movement of skipjack tuna in the western Pacific. Using this model they were able to predict tag returns that matched their observed recaptures. The drawback of this technique is there are large data requirements to inform this type of model. The most frequently applied approach to representing movement in assessment and general population models is a variation on Beverton and Holt's (1957) box transfer model (Porch *et al.*, 2001; Goethal *et al.*, 2011). This model uses a transfer coefficient (Quinn and Deriso, 1999) to describe the probability or proportion of movement between (and fidelity within) stocks or spatial units. Utilizing this approach we can model movement whereby fish from one area move to another, but return to their natal area to spawn (also termed overlap following Porch *et al.*, 2001). We can also model reproductive isolation/mixing whereby fish from one area move to another and spawn there (also termed diffusion following Porch *et al.*, 2001). The process equations are essentially the same in modelling these two phenomena, but there is an important distinction in how fish are accounted for in each process (see review by Goethal *et al.*, 2011). Further subtleties, such as the mode of reproductive mixing (i.e. straying or entrainment), can be included in movement models. Straying represents the movement of individuals away from their natal population whereas entrainment involves the "capture" of individuals from one spawning group into another during a period of spatial overlap (Secor *et al.*, 2009). These processes can be structured as a unidirectional or bidirectional (in the case of straying) and as occurring randomly or in a density-dependent manner. Tag integrated assessment models are a relatively new development that allow for movement between stocks or populations within the framework of an assessment model (Goethel *et al.*, 2011). Full life-history metapopulation models represent the most sophisticated approach to modelling movement

across life stages and between populations. Heath *et al.* (2008) describes the development of a metapopulation model of North Sea cod that incorporates spatial heterogeneity and movement across life stages.

4.1.1 Evaluating the importance of spatial variation in life-history traits

Life-history traits have played an important role in stock identification, and therefore in understanding complex spatial structure of marine populations. But life-history traits are not only useful markers; they are also key drivers of population dynamics. Ever since the seminal paper by Cole (1954) that first examined linkages between life-history traits and population growth, a rich body of theory and data has emerged from the fields of ecology, biogeography and conservation biology that adds detail to Cole's original theory of the effects of changing rates of growth, mortality and reproduction on population dynamics. These insights have been enhanced by the emergence of life-history theory within the broader field of evolutionary biology that explains relationships and trade-offs among life-history traits (Roff, 1992).

The vast majority of these studies, however, address the implications of variation in life-history traits in a single population and our understanding of variation across a spatially structured metapopulation is less well developed. Understanding how changing a given life-history trait affects the dynamics of a single population can lend insights into the implications of variation in that trait across a metapopulation, but those insights will be limited because the settings have fundamental differences. More direct lessons from metapopulation models are needed. Critical questions include whether, when and how sub-populations with life-history traits associated with greater fitness (e.g. superior growth) are disproportionately important for the productivity, stability and resilience of the overall system.

Where the dynamics of spatially structured populations have been examined, models are often constructed in terms of aggregate population parameters (e.g. population growth rate, extinction probability) rather than the constituent life-history traits that determine those aggregate parameters. Furthermore, these studies have examined concepts and dynamics that are relevant to fisheries science and management, but not the full range of relevant issues. Key concepts that have been addressed include the extinction-recolonization dynamics of classical metapopulation theory (Levins, 1969, 1970), island-mainland structure (Simberloff, 1974), source-sink dynamics (Pulliam, 1988), and rescue effects (Gotelli, 1991). A common feature of these concepts is a focus on persistence of populations, or on dynamics at the low end of abundance and productivity. Those issues are certainly important to marine conservation (e.g. Watson *et al.*, 2010), and also to fisheries management when depletion is severe (e.g. Smedbol and Wroblewski, 2002). However, processes that determine abundance and productivity, and not solely persistence and recovery, are of particular interest in fisheries (Kritzer and Sale, 2004).

Models of marine protected areas (MPAs) represent one class of models that lend insights into the effects of spatial variation in life-history traits within a spatially structured population. MPA models essentially show the effects of disparities in mortality across a spatially structured population, albeit with the differences induced by management rather than occurring naturally. Within these models, total mortality, Z , is equivalent to natural mortality, M , within MPA boundaries, but increased elsewhere by the level of fishing mortality, F . Total mortality within MPAs can change if partial-take reserves (e.g. Baskett *et al.*, 2005) or noncompliance (e.g. Kritzer, 2004) are modelled. Regardless, a typical result is that MPAs contribute little, or even that total yield is less than without MPAs, when F is low, but that overall system productivity

is greater with MPAs when F becomes high enough. Understanding these effects can not only help determine the level of F that is high enough to warrant establishment of an MPA, but also the point at which natural differences in M render certain populations especially important to a larger metapopulation independent of anthropogenic effects.

Lessons about the importance of spatial variation in life-history traits other than mortality are rarer. Kritzer and Davies (2005) examined whether observed variation in asymptotic body size among populations of a tropical reef fish were significant for population dynamics under a variety of recruitment and connectivity scenarios. They found that including a sub-population with larger body size within the metapopulation had little effect, unless stochastic variability of recruitment was high, variability was synchronous among sub-populations, and recruitment followed a cyclical pattern above the stochastic variation. Those factors decreased overall abundance, and shifted the population structure toward older age classes where effects of the differences in growth are strongest. However, stronger effects might have been observed under other conditions had age- or size-specific increases in reproductive success been included (Berkeley *et al.*, 2004).

Baskett *et al.* (2005) used an MPA model to look at interactions among multiple traits (growth, mortality, age-at-maturity). They found that, although an earlier age-at-maturity typically increases productivity when all else is equal (Cole, 1954), it resulted in lower productivity when brought about by greater mortality and compromised growth. Conversely, a sub-population with older age-at-maturity (i.e. within an MPA) enhanced system productivity when maturity was linked to lower mortality and superior growth.

Although our understanding of the implications of spatial variation in particular life-history traits for metapopulation dynamics is limited, some general lessons are emerging. Traits that would seemingly contribute to greater productivity might have little effect on system dynamics in many cases. Instead, the significance of any observed variation will clearly depend on the magnitude of differences among populations, as well as other prevailing factors such as the nature and strength of recruitment variability, interpopulation connectivity and density-dependence. Furthermore, the effects of variation in one trait are not independent of the effects of other traits, with some combinations enhancing each other whereas others offset. Ultimately, it is important to understand these effects to determine when population-specific parameters need to be included in assessment models, to develop more effective spatial management strategies, and perhaps to establish management and monitoring targets linked to life-history traits, beyond simply gross biomass indices.

4.2 Ongoing work

During WKISS, several participants presented aspects of their ongoing work to represent complex structure of ICES and US fish stocks in assessment and general population models. Below are short summaries of their research.

4.2.1 A combined stock assessment of 2 herring stocks

Casper Berg, DTU Aqua – National Institute of Aquatic Resources Section for Fisheries Advice, Denmark

There are several different herring spawning components in the North Sea and surrounding waters. Spawning components are characterized by a unique time of spawning and spawning location. During their lifetime, however, these components

overlap spatially and are caught together by commercial fisheries. Traditionally, herring in the North Sea have been assessed and managed as two separate stocks, a North Sea autumn-spawning (NSAS) stock and a Western Baltic spring-spawning (WBSS) stock. ICES management area IIIa is used as nursery area for immature NSAS herring and feeding area for the WBSS herring. In this region the two stocks are exposed to a mixed fishery, which poses problems for single-stock assessment methods. The current practice is to split the catches in this region (commercial catches as well as catches from scientific surveys) between the two stocks according to the catch composition of samples, then perform separate assessments on the split data (ICES 2009c). Hence, catches taken in IIIa (the mixing area) must be reallocated to either the North Sea or the Western Baltic stocks, although only a small proportion of the catches are sampled to determine the stock composition.

An alternative assessment was presented in which catch data are not split between the two stocks in the model, but instead split into three areas: one area with NSAS, another area with a mix of NSAS and WBSS, and an area assumed to contain WBSS herring exclusively. Samples of catch composition were used as an input to the model. The size of each of the stocks, the sampled proportions, and the associated uncertainties in these numbers were combined within the model to estimate abundances for the two stocks. While the model does not explicitly account for within-year dynamics or migration, it is flexible to these dynamics, and can be viewed as a simpler alternative to models that explicitly incorporate migration. Besides the usual outputs from the single-stock assessments like estimates of SSB, F , and numbers-at-age, the model provides estimates of numbers-at-age, composition, and F in the mixing area as well, all of which can aid management decisions.

Surveys covering multiple areas, such that catchability parameters could be assumed equal across areas, were important in estimating the abundance in the mixing area. Variation in relative year-class abundances between stocks explained the variation in the observed composition in the mixing area, as opposed to changes in the spatial distribution of the two stocks between the three areas. Therefore, the model may provide better predictions for the following year's composition in the mixing area than the usual geometric averages, especially when unusual large cohorts in either stock are observed.

The output of the model was compared to the output from single-stock assessments, and the results were similar but not identical. The largest differences were found for the NSAS stock, which was estimated to have significantly lower SSB in the terminal years than in the single-stock assessment. The WBSS estimates of SSB were more similar between models. The survey indices used in the models differed substantially, so it is not clear whether the observed discrepancies in model output were mainly caused by the differences in input data or model formulation.

The modelled areas were chosen to coincide with the management units, which made it easy to distribute catches among areas (as this was already done) and allowed for interpretation of fishery mortalities in relation to management units. This did not address the problem of a possible mismatch between management units and biological population structures, but such a mismatch could be investigated by changing the area definitions and comparing model fits.

4.2.2 Integrating larval dispersal into a full life-history stock assessment model

Daniel R. Goethel and Steven X. Cadrin, UMASS-SMAST, USA

Many marine species exhibit complex spatial structure resulting from dispersal between populations (Cadrin and Secor 2009), yet many stock assessment techniques ignore the spatial heterogeneity resulting from adult movement and larval drift. In fact, many assessment models still assume closed population structure although dispersal between adjacent populations is often common. Ignoring the spatial complexities of population structure and mixing can not only impact assessment results (Aldenburg, 1975; Hart and Cadrin, 2004), but can be detrimental to sustainable fisheries management (Stephenson, 1999; Secor, 2002).

In recent years, major advances have been made in including complex spatial structure within stock assessments through the development of tag-integrated models (e.g. Maunder, 1998; Goethel *et al.*, 2011). These models allow for numerous populations with movement between them. A tag-recapture dataset is used as an input data source that is included directly within the objective function of the assessment model in order to help inform movement estimates. However, tag-integrated models often ignore the spatial complexities of recruitment processes and the impact of larval drift on year-class strength, thereby excluding a key component of the life cycle of marine species.

Although spatially explicit Individual Based Models (IBMs) of larval fish provide invaluable information on connectivity and distribution of early life-history stages, results are difficult to incorporate into management decisions. One way in which IBM outputs have been utilized is in full life-history simulations used to investigate spatial population structure or the effects of various management strategies (e.g. Heath *et al.*, 2008; Heifetz and Quinn, 1998). However, little work has been done to incorporate IBM results directly into a stock assessment framework (e.g. Bentley *et al.*, 2004). We developed a method for incorporating IBM estimates of larval mixing rates directly within the objective function of a forward projecting, multi-region statistical catch-at-age model. This model allows for full life cycle closure by allowing for larval drift and adult movement between populations. Larval IBM results are used as a 'data' source in the model and each IBM particle is treated as if it were a 'tagged' fish in a mark-recapture dataset. The objective function for the assessment model includes multiple data sources including catch-at-age, abundance indices, tag-recapture data, and larval IBM data.

Attempting to account for the complex spatial structure of marine species is a necessary part of creating a reliable stock assessment model. By providing spatially explicit abundance estimates and interactions between subpopulations at all life-history stages, this approach will improve spatial management of marine species. In addition, it provides an alternative to single-stock assessment and management when interstock interactions are occurring.

4.2.3 Testing hypotheses on fish stock structure using spatial simulation modeling: an application to Irish herring populations

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Knowledge of the underlying structure of fish stocks is fundamental to understanding population dynamics and management implication of fisheries operating on mixed-stocks. Atlantic herring (*Clupea harengus*) is a species with highly complex (and explicit) population structure due to the unique diversity in the timing and location

of spawning components. However, in many instances populations mix on summer feeding grounds and genetic analyses indicate a rather high level of gene flow in European waters (King *et al.*, 1987), despite a high level of spawning-area fidelity (Brophy *et al.*, 2006).

Recently, the metapopulation concept and model framework have been proposed as useful construct to describe the complexity of herring stock structure (McQuinn, 1997). In this study, herring within four main ICES assessment and management areas to the west of the British Isles (namely, VIaN to the west of Scotland, VIaS and VIIb,c to the northwest of Ireland, Celtic Sea and VIIj to the south of Ireland and the Irish Sea between Ireland and Great Britain) have been included in a metapopulation model. Each of these areas is assumed to represent a separate and closed stock unit (meaning that no exchange occurs between each stock). However, as there is no real physical barrier in the ocean, this representation is not likely biologically realistic and does not align with our understanding of herring population biology off the coast of Ireland. Here, simulation modelling was used to improve our understanding of herring population structure by testing the biological feasibility and consequences of different types and levels of exchange between stocks.

The metapopulation model was constructed as a series of linked age-structured models representative of ICES stocks (Secor 2009; Kerr *et al.*, 2010). Model parameters were derived from the most recent ICES stock assessments (ICES, 2010a). Recruitment dynamics were simulated as a stochastic process in the model, with the magnitude and correlation of recruitment variation between stocks based on indices of recruitment.

In this study, simulation modelling was used as a biological experiment within a computer, allowing for manipulation of processes not possible in the wild (Peck, 2004). Although the area under study has been the subject of intensive stock identification research (Brophy and Danilowicz, 2002; Campbell *et al.*, 2007; Hatfield *et al.*, 2007; ICES, 2010a), little is known regarding the type and degree (i.e. quantity) of stock mixing. Simulation modelling allowed us to test different hypotheses about the type and level of connectivity between herring stocks. Based on our biological understanding of herring populations in the area and the need for model simplification, we assumed connectivity was only possible between adjacent stocks and that the metapopulation under study was closed. Two types of connectivity (straying and entrainment) between stocks were investigated. Straying refers to individuals leaving one population to contribute to the productivity of another population either through random (as reference to the member-vagrant hypothesis, Sinclair and Iles (1989)) or density-dependent processes. Entrainment is a “learning-behaviour” process (Secor *et al.*, 2009) with individuals mixed in the feeding grounds following bigger schools during subsequent spawning migration. For each type of connectivity different rates of exchange, from low (5%) to high (30%), were tested. The metapopulation model outputs were compared to a baseline model where there was no connectivity between stocks. The productivity (i.e. SSB for each stock across years and simulations), and stability (i.e. coefficient of variation of SSB for each stock across years and simulations) of the parameterized simulated populations were used to test the biological realism of the model, which might ultimately result in an assumption of stock structure. Additionally, the productivity of the individual stock components of the metapopulation was monitored to inform management on its sustainable yield.

4.2.4 Advances on North Sea plaice population modelling

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Plaice (*Pleuronectes platessa*) is a well-studied flatfish found in locations around the world. The Institute for Marine Resources and Ecosystem Studies (IMARES) currently studies the spatial behaviour of plaice in the North Sea, where it has been a key target species for the Dutch fisheries. Due to its economic importance, it has received great scientific attention, resulting in a qualitative and quantitative understanding of its life-history characteristics and bioenergetics. This understanding has led to the development of Dynamic Energy Budget (DEB) models for plaice (see van der Veer *et al.*, 2003, 2009), integrating environmental drivers with growth.

In this application, the DEB model is incorporated into an Individual Based Model (IBM) seeking, through the use of an evolutionary model, to estimate the optimal movement strategy of plaice based upon bioenergetic constraints. The IBM approach adds increased biological realism to the modelling of plaice movement and results can be directly contrasted to individual observation of tagging and telemetry studies.

Knowing which environmental factors play a key role in determining plaice behaviour is essential in determining and preserving habitats essential to the life cycle of the species. Furthermore, a mechanistic understanding of the spatial distribution of plaice will enable us to better predict how climate changes might affect the productivity of the stock. Overall, models, such as the DEB model incorporated into IBMs, that increase our understanding of fish movement behaviour and spatial habitat use will help us achieve our goal of sustainable fisheries management.

4.2.5 Ecological and fisheries consequences of a mismatch between biological population structure and management units of Atlantic cod in US waters

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A prerequisite of sustainable fishery management is that the scale of management action matches the scale of biological processes (Begg *et al.*, 1999; Reiss *et al.*, 2009). Application of a single management approach to a “mixed-stock”, consisting of populations that differ in their productivity and dynamics may have profound consequences to the persistence of the resource and the fishery it supports (Frank and Brickman, 2001). Here, we used simulation modelling as a tool to examine ecological and fisheries consequences of a mismatch between management units and genetic population structure of Atlantic cod in US waters. We hypothesized that recognition of fine-scale population structuring of Atlantic cod in the Northwest Atlantic would revise our perceptions of the productivity, stability, and sustainability of the regional population. Specifically, we compared a model of Atlantic cod in US waters based on the current spatially defined US management units (Gulf of Maine and Georges Bank) with another based on genetic population structure (northern spring-spawning, southern winter/spring-spawning, and Georges Bank spring-spawning populations; Kovach *et al.*, 2010). We took care to construct the models in a similar fashion, using the same data sources and age-structured model framework, so that they would be comparable. The parameters of the management unit model were derived from the most recent stock assessments for Gulf of Maine and Georges Bank management units (Working Group on Re-Evaluation of Biological Reference Points for New England Groundfish 2002, NEFSC 2008). This model reflected the assumption that fishery management units represent single, self-sustaining populations (i.e. no connectivity was modelled between management units). The biological unit model

was informed by parameters estimated using data from the appropriate spatial and temporal scale for each spawning complex. Connectivity rates between populations were estimated from genetic information (F_{st} values; Kovach *et al.*, 2010) and incorporated in the model. Recruitment variability and correlation in recruitment between populations was calculated from trawl survey data (Northeast Fisheries Science Center, 1970–2007). We simulated the response of both models to changes in fishing mortality (F : 0 to 1) and examined response metrics, namely productivity (spawning-stock biomass), stability (coefficient of variation of SSB), and maximum sustainable yield. Productivity, stability, and maximum sustainable yield of the biological unit model was greater than that of the management unit model due to consideration of unique vital rates and dynamics of spawning groups, and connectivity between them. Recognition of biological structure indicated higher regional productivity of cod and may contribute to a more productive fishery. By considering population structure, we gain a spatially explicit view of productivity in the region and by incorporating spatial management of fishing pressure may increase the yield of this fishery and better protect the Gulf of Maine cod stock from overexploitation.

4.2.6 A model of meta-population dynamics for North Sea and west of Scotland cod – the dynamic consequences of natal fidelity

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The summary that follows describes work published in Heath *et al.* (2008).

It is clear from a variety of data that cod (*Gadus morhua*) in the North Sea do not constitute a homogeneous population that will rapidly redistribute in response to local variability of exploitation. Hence, local exploitation has the potential to deplete local populations, perhaps to the extent that depensation occurs and recovery is impossible without recolonization from other areas. This carries the risk of consequent loss of genetic diversity. The oceanographic, biological and behavioural processes which maintain the spatial population structures are only partly understood, and one of the key unknown factors is the extent to which cod exhibit homing migrations to natal spawning areas.

The nature of the problem clearly requires a spatial population modelling approach in order to provide strategic analysis of management options. Spatial modelling of physiologically structured populations is a well known source of numerical difficulty (McKendrick, 1926; von Foerster, 1959). A number of numerical implementations are available to represent the development of homogeneous populations comprising distinct age-based developmental stages (Gurney and Nisbet, 1998). Most fish stock models currently in operational use for European waters are of this type. However, none of these can readily accommodate space dependent development. This is because cohorts will have different development histories at different locations in space, and the average which results from advective or diffusive mixing does not represent the state of all of the constituents.

Alternative modelling approaches require that the life-history be divided into discrete stages based on size or some other measure, with the transition between stages being defined by a probability distribution. By assuming that all individuals within a stage are indistinguishable, the scheme can be expanded to accommodate spatial structure (Neubert and Caswell, 2000). An example of the use of this method for planktonic taxa is Bryant *et al.* (1997). However, the weakness of the Neubert and Caswell approach is that each development class is considered to be homogeneous. This means that with a uniform time-step for updating the population, the distribu-

tion of stage durations is highly sensitive to the number of stages. Various methods are available for more or less controlling the numerical diffusion which increases as the number of stages is decreased. For fish, where body size ranges over many orders of magnitude over the life cycle, this is a serious problem.

Gurney *et al.* (2001) developed a different approach to resolve these difficulties. Update intervals for development classes were independent of transport, such that in each spatial grid cell all the members of a development class were transferred to the next class at the same time. Hence the update interval for development will vary in space and time, but numerical diffusion is eliminated. Spatial dispersal by migration, advection and diffusion are updated independently by reference to a redistribution matrix which defines the proportion of individuals from each location which are to be transferred to all other locations. The scheme works best when spatial dispersal updates are widely spaced in time compared to the slowest developmental updates. Gurney *et al.* (2001) illustrated the method by developing a population model of *Calanus finmarchicus* in the northeastern Atlantic. The spatial redistribution matrix was determined by an external particle tracking model. Comparisons between the new Eulerian grid method and a Lagrangian based approach showed high conformity across a range of grid scales.

The Gurney *et al.* method was used by Andrews *et al.* (2006) to develop a spatially resolved population dynamics model of cod in European waters. The model represented a biologically homogeneous population of cod throughout the model domain, combining spatially resolved mortality, growth and reproduction with larval drift, and migrations by juvenile and adult fish. The spatial scheme had a resolution of approximately 60 km over the shelf region extending from Brittany in the south to the northern limit of the North Sea. Andrews *et al.* (2006) fitted various structural alternatives of the model, representing different hypotheses about migration behaviour, to spatial and temporal data on cod abundance then used the fitted parameterization to explore the consequences of various spatial measures applied to fishing mortality. However, whilst the model was capable of simulating spatial dynamics which compared favourably with observations, the results cannot be used to make any inferences about the degree of natal fidelity. To do this would require a significant increase in complexity, by resolving a set of separate genetic populations or demes and their potential interactions, each of which would have to be simulated in parallel.

Resolution of discrete demes was a key objective of the METACOD modelling effort. To achieve this, spatial resolution, representation of mixing, and spatial dependence of development rates were considered. The key simplifying assumption was that all individuals in a given deme are endowed at birth with the same future growth trajectory, which they follow regardless of where they eventually live in the model domain. This allowed an age-based, discrete time methodology for simulating the population dynamics, without the penalties associated with most spatial versions of such types of model.

The knowledge of cod metapopulation structure in European waters was caricatured in terms of 10 interlinked demes, each representing groups of fish with a common natal origin. The spawning locations of fish in each deme are governed by a variety of rules concerning oceanographic dispersal, migration behaviour and straying. Numerical experiments were carried out with the model and the results compared with observations. These led to a conclusion that active homing is probably not necessary to explain some of the population structures of European cod. Separation of some sub-populations is possible through distance and oceanographic processes affecting

the dispersal of eggs and larvae. However, other evidence suggests that homing may be a necessary behaviour to explain the structure of other sub-populations.

The consequences of taking spatial population structuring into account for fisheries management are complicated. For example, recovery or recolonization strategies require consideration not only of mortality rates in the target area for restoration, but also on the source areas for the recruits, which may be far removed depending on the oceanography. The model has an inbuilt capability to address issues concerning the effects of climate change, including temperature change, on spatial patterns of recruitment, development and population structure in cod.

5 Identifying best practices for simulating populations with complex population structure

One of the goals of WKISS was to identify best practices for simulating populations with complex population structure. In discussing this topic, we concluded that the goal of a particular simulation (i.e. the specific hypotheses being tested or questions explored, which might be biologically or management oriented) determines the structure and data requirements of the model used. For example, some simulation studies might aim to be predictive and to help establish management measures, others might aim to explore the implications of management alternatives in a relative or comparative sense, and still others might aim to explore ecological processes independent of management decisions. Hence, best practices relevant to all applications cannot be readily determined. General guidelines, however, can be identified. When modelling complex population structure, the choices and assumptions we make at each stage of model development are important to the outcome of simulation modelling. Therefore, careful consideration of how one defines, characterizes, and simulates the system of interest is a useful exercise regardless of purpose. Also, techniques to validate models are valuable to most if not all applications in order to strengthen the faith in model outcomes and take-home message of the modelling exercise.

Some important considerations in modelling spatial structure and movement include:

Definition of the system:

- Appropriate scale of the metapopulation, i.e. geographic extent of the network of interacting populations
- Number of relevant interacting populations to be included in the model

Characterization of the system:

- Incorporation of spatially explicit differences in demography and dynamics
 - Approach to simulating recruitment dynamics (mechanistic model or simulation of observed pattern of recruitment variability)
 - Identification and modelling of synchrony/ asynchrony in recruitment dynamics between stocks
 - Life stages to be explicitly modelled
- Inclusion of temporal differences (e.g. seasonality of spawning)
- Representation of connectivity in the model
 - Pattern of movement (i.e. spatial overlap or reproductive mixing)
 - Estimation of connectivity rates (e.g. tagging, genetics, otolith chemistry)
 - Life stage (age) at which occurs
 - Mode of population connectivity (i.e. straying or entrainment)

Simulation of the system:

- Purpose of simulation (exploratory, hypothesis testing)
- Incorporation of stochasticity (random, density-dependent)
- Different scenarios to be simulated (e.g. exploitation or climate scenarios)
- Definition of a baseline model
- Details of model runs

- Number of model runs
- Time to equilibrium
- Initial conditions

Evaluation of Model Output:

- Relevant response variables to examine
 - Productivity (spawning-stock biomass)
 - Yield/Maximum Sustainable Yield
 - Fishing mortality at MSY
 - Stability (coefficient of variation of spawning-stock biomass)
 - Resilience (number of years to rebuild population above certain threshold)
 - Extinction risk/probability of recolonization
 - Population richness and evenness
- Verification or validation of the model
 - Sensitivity analysis of model parameters
 - Comparison of output to independent datasets

6 Synthesize information on biological stock structure for ICES management units

The synthesis of information on biological stock structure can improve our understanding of the dynamics of fish populations and stocks. This information can also be critical in meeting objectives of fisheries management, such as sustaining yield, avoiding recruitment failure, rebuilding overfished stocks, and conserving endangered species (Cadrin *et al.*, 2005). Topical initiatives, such as conserving biodiversity, applying a 'precautionary approach', ecosystem-based fishery management, and marine protected areas, place even greater emphasis on understanding the spatial aspects of populations (Cadrin *et al.*, 2005). In recent years there has been a substantial investment in interdisciplinary research to identify and delineate biological structure for ICES stocks. Despite the value of this information and the research investment in this arena, the results of these projects are not always incorporated into the assessment and management of the studied stocks. Here, we have summarized the major stock structure identification efforts on ICES stocks and examined whether the results of the synthesis were translated into the assessment or management of the stock.

6.1 Horse Mackerel Stock Identity Synthesis (HOMSIR)

The overall objective of the HOMSIR project was the identification of biological stocks of horse mackerel (*Trachurus trachurus*) throughout its distributional range, from the Northeast Atlantic to the Mediterranean Sea. This project integrated established and innovative stock identification approaches, such as genetic markers (allozymes, mtDNA, msDNA and SSCP), biological tags (morphometry, parasites), and life-history traits (growth, reproduction and distribution; Abaunza *et al.*, 2008c).

The project involved sampling horse mackerel throughout the majority of their range at 20 sampling locations. At least 200 hundred fish were collected per sampling site (taking spawning season into consideration) with temporal replication over two years (a total of 4,400 specimens). The sampling design was such that all approaches were applied on the same specimen (Abaunza *et al.*, 2008b). The results from genetic approaches (Multilocus Allozyme Electrophoresis, mtDNA sequencing and msDNA) showed a very weak genetic differentiation among sampling sites (Cimmaruta *et al.*, 2008; Comesaña *et al.*, 2008; Kasapidis *et al.*, 2008). Thus, the gene flow along the entire area of distribution is an important evolutionary force for horse mackerel species. Horse mackerel showed high genetic variability and a stable genetic structure over time.

Several approaches supported a separation between the Atlantic Ocean and Mediterranean Sea horse mackerel populations, although the westernmost Mediterranean area could also be connected with the Atlantic populations (MacKenzie *et al.*, 2008; Mattiucci *et al.*, 2008; Murta *et al.*, 2008; Stransky *et al.*, 2008). In the Northeast Atlantic, three main biological stocks were distinguished: the west Atlantic coast of the Iberian Peninsula (southern stock); the west coasts of European countries from north Spain to Norway (Western stock), and the North Sea stock (MacKenzie *et al.*, 2008; Mattiucci *et al.*, 2008; Murta *et al.*, 2008). This information implied the revision of the boundaries of what were previously classified as southern and Western stocks. The southern boundary of the southern stock is unclear, given the lack of samples from the Moroccan coast. However, horse mackerel from the Mauritanian coast were clearly separated from other sampling sites according to several of the methods (body morphometry, parasites, growth and fecundity; Abaunza *et al.*, 2008a; MacKenzie *et*

al., 2008; Murta *et al.*, 2008). The population of horse mackerel in the Mediterranean Sea is structured in at least three main units: western, central and eastern Mediterranean (MacKenzie *et al.*, 2008; Murta *et al.*, 2008). Horse mackerel from the Tyrrhenian Sea (central Mediterranean) is particularly different from the rest of the Mediterranean areas. The synthesis of information on stock identification enhanced the assessment and management of horse mackerel in EU waters (Abaunza *et al.*, 2008c).

6.2 Sardine Stock Identity Synthesis (SARDYN)

The main objective of the SARDYN project was to improve the basis for management advice provided for sardine (*Sardina pilchardus*) in Atlantic European waters (Anon., 2006). Specifically, two major questions regarding stock identity raised in the 1999 assessment WG meeting (ICES, 2000) were addressed: (i) are there multiple biological stocks within the assessed area (ICES areas VIIIc and IXa)? and (ii) is there immigration/emigration between the current stock and adjacent areas?

The project focused on sardine off the coast of the Iberian Peninsula and adjacent regions, although data were collected opportunistically from most of the species' range. Key topographic features and oceanographic processes that could potentially act as barriers to mixing across the area were described and hypotheses of spatially and temporally discrete spawning which could promote reproductive isolation were examined. A comprehensive analysis of the spatial structure of sardine was undertaken, including examination of variation in genotypic (microsatellite DNA, mitochondrial DNA and allozyme markers), phenotypic (morphometry) and life-history traits (growth, maturation, spawning). The results were used to formulate hypotheses on the spatial structure and dynamics (e.g. synchronicity in egg production and recruitment, movements between areas) of sardine in the region of study and to develop multi-area assessment models (i.e. statistical catch-at-age, Bayesian state-space age structured model, biomass dynamic model).

The project conclusions with most relevance to Atlanto-Iberian stock structure were:

- Genetic properties indicated the existence of five genetic populations. The Iberian fisheries stock is part of a large Northeast Atlantic genetic population, distributed between the North Sea and the Agadir area off Morocco, showing a pattern of isolation by distance;
- Life-history patterns generally corroborated the genetic findings. Spawning dynamics promoting reproductive isolation were not identified, although clinal variation in phenotypic and life-history traits suggest the degree of population mixing declines with distance;
- Specific oceanographic features that could act as barriers to sardine gene flow were not identified and mesoscale circulation likely promotes mixing of early life stages at small spatial scales;
- The spatial patterns of age structure, recruitment and egg production dynamics suggested three major localized, partly independent recruitment areas in southern Bay of Biscay, northern Portugal and Gulf of Cadiz; young fish are relatively sedentary but mobility increases as fish grow as also shown by otolith elemental composition. Thus, recruitment areas supply fish to adjacent areas and older fish tend to mix across the whole Iberian peninsula;
- Assessment trials using area-disaggregated data corroborated size-related migrations within the stock area (namely from the western recruitment

area to both northern and southern Iberia), while also showing temporal variation in migration direction and intensity;

- The Bayesian model indicated net immigration of age 1 sardine from southern Bay of Biscay into the stock area: preliminary estimates of the proportion of the Iberian stock biomass resulting from immigration were in the range 1–4%; when only the East Cantabrian Sea was considered this proportion was around 19%.

Overall, the SARDYN results indicated sardine from ICES management areas VIIIc and IXa do not comprise multiple stocks. Different dynamics among stock areas (namely between the northern, western and south coasts of the Iberian Peninsula) are due to spatial differences in spawning intensity, recruitment strength and temporal variation in migration directions and intensity. There was some evidence of immigration of recruits across the northern limit (Cantabrian Sea) and the possibility of egg and larval mixing across the southern border. The ICES WGHMSA considered the SARDYN results improved knowledge of the spatial structure and dynamics of sardine populations in the Iberian-Biscay region (ICES, 2006). Although moving towards area-based assessment would be a natural follow up of the SARDYN project, the results were not conclusive with respect to the level of migration between management areas and across the stock limits. Multi-area assessments were highly dependent on assumptions on spatial structure and migration. Given the clear links among areas within the stock, the WG decided to pool data from the acoustic surveys covering different parts of the stock (northern Spain and Portugal+ Gulf of Cadiz) in a single tuning series.

6.3 Atlantic Herring Stock Identity Synthesis (WESTHER)

WESTHER's overall goal was to describe the population structure of herring stocks to the west of the British Isles, to enable the production of a set of improved guidelines for the conservation and management of biodiversity and stock preservation by incorporating findings into the assessment processes for western herring. Analysis of a multidisciplinary suite of characters (including body and otolith morphometry, parasites as biological tags, otolith microchemistry and genetics) was carried out on herring collected from spawning aggregations, nursery areas and adult non-spawning feeding aggregations in the study area. The results revealed temporally distinct spawning grounds in the area, with each being populated by a group of herring with a level of site fidelity. There was strong evidence that juveniles from separate spawning areas mixed in some of the nursery areas sampled. There was also evidence to suggest mixing of adults from separate spawning components, especially in the area to the west of Scotland (VIa North). The science, therefore, suggested links between areas, with fish spawning in different areas mixing, to varying extents, on feeding grounds. The results from WESTHER suggested that under the current stock assessment units, two basic assumptions of stock assessment (the stock is a closed unit, and the data used in assessments are representative of the entire stock) are violated.

The significant mixing, mostly in VIa North, appeared to be between the currently defined three northern stocks (VIa North, VIaS and VIIb,c and Irish Sea) at various periods in their life history. WESTHER recommended merging these three stocks in the assessment. The recommendation to combine the three northern stocks and assess them as a new stock unit recognized the complexity of the stock structure. It was hoped that a combined assessment would reduce the uncertainty surrounding the current individual stock assessments, lead to the provision of more precise scientific advice, and a better understanding of the dynamics of the herring exploited in the

area. The results of WESTHER indicated that the current Celtic Sea and VIIj stock are more discrete and it was recommended that this stock unit be retained in its current form.

The opportunity to examine the consequences of the recommended changes to management units for herring was beyond the scope of WESTHER. WESTHER was, however, able to report its findings directly to the ICES Herring Assessment Working Group (HAWG) as several of the WESTHER consortium were members. The recommendations were perceived to be of sufficient importance to warrant examination and a study group (SGHERWAY) was set up under the auspices of ICES to examine them in detail. The results of that group are reported in ICES (2008, 2009, 2010a) and summarized in Section 8.

6.4 Redfish Stock Identity Synthesis (WKREDS)

The Workshop on Redfish Stock Structure (WKREDS) was convened to review existing information on the stock structure of *Sebastes mentella* in the Irminger Sea and adjacent waters. The goal of this project was to identify the most likely definition of biological stocks and to recommend practical management units in the Irminger Sea and adjacent waters. Of particular importance was reconciling new genetic results with all previous information on stock structure of *S. mentella*. Prior to the workshop, ICES provided advice for *S. mentella* fisheries as two distinct management units: 1) a demersal unit on the continental shelf and 2) a pelagic unit in the Irminger Sea and adjacent areas. However, concern about the resource grew with the development of a pelagic deep-sea fishery. At the time the relationship between the demersal and shallow-pelagic resource (the traditional target fisheries for *S. mentella*) and the resource being targeted by the newly developed pelagic deep-sea fishery was unknown. Further, there was spatial overlap in the deep-sea and demersal fishery, whereas the shallow pelagic fishery is separate.

Studies examining the stock structure of *S. mentella* in the Irminger Sea and adjacent areas were reviewed and synthesized to determine the most parsimonious view of stock structure. The research reviewed included multiple approaches to stock identification, such as examinations of geographic distribution (e.g. fishing grounds, survey data of early life stage, juveniles and adults), genetic variation (e.g. allozymes, mitochondrial DNA, nuclear DNA), phenotypic variation (e.g. life-history traits, morphology, fatty acid composition) and connectivity (e.g. larval dispersal, natural tags and artificial tags). This review resulted in an interdisciplinary synthesis on the most likely stock structure of *S. mentella* in the Irminger Sea and adjacent areas.

Based primarily on genetic information (i.e. microsatellites), and supported by other information on stock structure, WKREDS concluded that there are three biological stocks of *S. mentella* in the Irminger Sea and adjacent waters:

- 1) a 'Deep Pelagic' stock (NAFO 1-2, ICES Vb XII XIV >500m),
- 2) a 'Shallow Pelagic' stock (NAFO 1-2, ICES Vb XII XIV <500m), and
- 3) an 'Icelandic Slope' stock (ICES Va XIV).

Although the biological stocks of *S. mentella* were redefined, in part, by depth, WKREDS recognized that depth-defined management units would not be practical and instead recommended new spatially defined management unit boundaries that were located to minimize mixed-stock catches. The three recommended management units were:

- 1) a 'Deep Pelagic' management unit in the northeast Irminger Sea (defined by the spatial distribution of the deep, pelagic fishery)
- 2) a 'Shallow Pelagic' management unit in NAFO areas 1 and 2, ICES areas Vb, XII, XIV (outside the deep, pelagic area), and
- 3) an 'Icelandic Slope' management unit that is north and east of the existing' redfish line.'

Based on the view of *S. mentella* biological stock structure that emerged from the review and the recommendations of WKREDS, ICES revised its advice for management of *S. mentella* fisheries in the Irminger Sea to the three proposed management units. In 2009, advice for the shallow-pelagic stock was "given the very low state of the stock, the directed fishery should be closed", and for the deep-pelagic stock "given the reduced abundance of this stock in recent years, a total catch limit of no greater than 20 000 tonnes should be implemented in 2010". The difference in advice for the two stocks illustrates the importance of stock identification for fishery management. The recommendations of WKREDS were based on a synthesis of all stock identification information available, and the synthesis could be used to develop an operating model to reflect redfish populations and simulate alternative management units would help to inform fishery managers of the implications of alternatives. However, the general uncertainty in demographic information (e.g. age determination, growth, ontogenetic movements) would present challenges for developing accurate operating models and representative management strategy evaluations.

6.5 Sandeel Stock Identity Synthesis

No dedicated EU research project has been carried out on sandeel stock structure. However, the EU-FP6 project PROTECT investigated the application of MPAs for sandeel conservation and protection against local depletion. Further, sandeel distribution, biology and stock dynamics have been investigated in several national Danish, Norwegian and UK projects, some of them with support from the EFF and other EU foundations. The work involved international collaboration with close links to several ICES workshops and study groups (AGSAN, AGSANNOP, AGSAN2). The main aim of this research was to account for biological stock structure in the provision of advice on long-term management strategies for the fishery. Earlier management regimes failed to account for regional differences in productivity and catch rates and resulted in local depletion in many areas. In preparation for a benchmark process, different ICES groups revisited sandeel stock structure. The potential for local depletion and proposals for management measures to prevent such depletion were investigated. A Benchmark Workshop on Sandeel in Subarea IV (excluding the Shetland Islands) was conducted by ICES in 2010 (ICES, 2010d). The benchmark resulted in a change in the scale of assessment, from single-stock to multiple stock components based on structure identified from information on larval distribution, connectivity (Christensen *et al.*, 2007, 2008, 2009), and growth differences (Boulcott *et al.*, 2007). Seven separate stock components were identified, although analytical assessments are only possible in four areas due to limitations of fisheries data and monitoring. Management scenarios were investigated at WKSAN and applied to the different management units. Data were insufficient to evaluate whether the management scenarios could be implemented in all areas. Improving the assessment will require further spatial stratification, including providing natural mortality rate estimates by area. Current natural mortality rate estimates were derived from predator stomachs collected 20 years ago region-wide. A new stomach collection study is required to provide updated, area-specific mortality estimates. Additional research priorities

include studies of the relationship between sandeel biomass and predator condition, growth, and recruitment success. This information will improve knowledge for setting reference points which provide for species effects on predator populations.

Industry representatives attended WKSAN and provided useful information throughout the workshop. Industry representatives also provided details on marine spatial planning issues that could potentially affect the sandeel fishery in future (e.g. windfarms, Natura 2000). Their participation was not only welcome, but also necessary.

6.6 Summary of lessons learned from stock identification projects

In reviewing the approach and outcome of stock identification projects on ICES stocks we found that some included significant biological sampling and application of multiple stock identification methods, whereas others focused mainly on the information gained from genetic analysis. In a few cases, these efforts incorporated modelling as a tool to examine the consequences of the identified stock structure. Some of these synthesis projects brought about a change in the scale of management, but simulations would have helped to inform fishery managers on the implications of the change in management units.

The large-scale EU projects HOMSIR, WESTHER, REDFISH, and SARDYN were set up in the early 2000s as part of ongoing research agendas to understand the dynamics of commercially important species. The conservation of biodiversity was one of the main drivers in the establishment of the WESTHER and HOMSIR projects. The SARDYN project was initiated in 1999 following issues raised in the stock assessment; different trends in the survey abundance used to tune the assessment model were identified in surveys off northern Spain and Portugal. Each of these projects involved extensive sampling efforts and generally included time consuming methods of data collection and analysis. The time for analysis and presentation of results, however, was often short. Further, when problems were identified there was often not enough time to address them fully. These projects provided information from a large range of disciplines. It was hoped that the analysis of data from each stock identification method could be carried out in a similar way, but at the time it was often difficult to combine information from these different disciplines in a quantitative manner.

The results of these stock identity projects provided information which could be incorporated in the assessment and management of the species. In general, when the same people were involved in the synthesis project and the stock assessment it was easier to communicate the results of a stock identity project to the assessment working group. Recommendations from the HOMSIR project were taken up and a change in the boundaries of the management units followed. The SARDYN project provided information related to spatial structure of sardine and mixing between areas, however, because there was no strong evidence that the assessment was biased by this mixing there were no changes to existing management units. Results from the REDFISH project were considered by WKREDS to recommend revised management units. The WESTHER project recommendations were taken up by the SGHERWAY project and an evaluation of assessment and management strategies of the western herring stock was carried out.

The METACOD project is another example of EU collaboration aimed at identifying and understanding the biological stock structure of fish, in this case North Sea cod. Researchers examined the structure of cod stocks around Iceland and to the west and

north of Scotland where there was little understanding of biological structure. This project focused on the use of advanced genetic techniques (i.e. single nucleotide polymorphism) to characterize population structure in the region. Based on this work, three cod stocks are now defined in the region. Simulation modelling of possible metapopulation structure in the region was included as part of this project. However, the findings of this work have not yet been incorporated into the assessment.

HERGEN is an example of another EU project aimed at investigating the conservation of diversity and examine spatio-temporal variation in the genetics of herring in the North Sea and adjacent areas. This project did not recommend any changes to management areas and all spawning components continue to be assessed together.

Our current understanding of North Sea sandeel stock structure is based on observed differences in life-history traits and larval dispersal. A benchmark assessment was carried out on sandeel and the scale of assessment was changed from a single stock to multiple stock structures based on stock identity information. In this case, the close collaboration between scientists, managers, and industry in the benchmark process was critical to changing the management structure for North Sea sandeel.

We propose that the inclusion of simulation modelling as a last step in stock identity projects, such as those discussed above, would be informative. A diversity of scenarios or hypotheses could be explored relative to the objective of the study, such as whether ignoring stock structure could introduce bias to the assessment or at what scale we should conserve biodiversity for continued population persistence and productivity.

7 Ecological, Fisheries, and Management Consequences of a Mismatch between Biological and Management Units

For a number of species, the existing biological structure does not coincide perfectly with the defined management unit. For example, the scale of biological structure may extend across management unit boundaries or multiple populations of a species may be lumped into one management unit. Below, we elaborate on the ecological, fisheries and management consequences of a mismatch and present simulation and estimation approaches to investigate these issues.

7.1 Ecological consequences related to spatio-temporal scale

For fish species, a mismatch in the scale of biological and management-defined units may have ecological consequences. Unique spawning components may act as buffers to regional productivity, with each experiencing optimal recruitment success under a specific set of environmental conditions. When management units are larger than biological units, the under and overfishing of local spawning components may affect this buffering capacity. Overfishing of components that exhibit high integrity and isolation in spawning behaviour (e.g. by homing) could result in local depletion and under more extreme circumstances local extirpation. At the end of this continuum of adverse responses to loss of unique spawning components is the potential for meta-population extinction. Under-fishing portions of the regional population is also a real possibility when the scales of biology and management are not aligned. A combination of under-fishing and overfishing components of a regional population could result in more homogeneous composition, disturbing the balance biocomplexity confers to the system, and making it more unstable. Thus, an understanding of the spatial scale of biological processes in relation to the management scale for a species is crucial to a full understanding of local and regional dynamics.

New genetic methods enable detection of population differences at finer scales. This raises the question of what the appropriate scale of biological complexity is that we need to conserve to maintain a sustainable level of population biomass. For example, microsatellites could detect three major genetically distinct components of herring in the North Sea region (Ruzzante *et al.*, 2006); however, application of new genomic methods (e.g. single-nucleotide polymorphisms) may identify finer detail in stock structure in the near future (Gomez-Uchida *et al.*, 2011). From a biological perspective, we may view complexity as an essential characteristic of the system; however, we must recognize that there is an upper spatial bound to the scale of management. Additionally, there are limitations to the scale of assessment. Typically this is determined by the spatial and temporal scale on which we collect data, but there are also computational limits to the level of spatial complexity we would want to include in a model.

Simulation modelling can serve as a useful tool to evaluate the consequences of a mismatch between the scale of biological and management unit structure on both ecological, including impacts on local and regional productivity, stability, and resilience to disturbance, and evolutionary time-scales (i.e. persistence of the local and regional population). Using simulation modelling we can explore specific questions regarding the sustainable level of harvest for populations and the outcomes of under or overfishing certain components within a stock. Additionally, we can examine the optimal scale of biocomplexity to conserve and identify components that are essential to the persistence and productivity of the system.

7.2 Fisheries consequences

Fishers adapt to changes in fish distribution and abundance and are primarily concerned when they lose opportunities to catch their target species. Loss of harvest opportunities may result from a mismatch in the scale of biological and management units. When several stock components are managed within a single large unit there may be problems with ownership as well as conservation of local components, thus an overall TAC may lead to local depletion and loss of overall productivity.

When the scale of management and assessment units are not aligned with biological structure of fish, fishers may be faced with modelled views of stock status and catch limits that do not match their first-hand view of the fish resource. This can erode their faith in the underlying science and lead to contentious relationships between fisheries stakeholders. In a number of EU projects effort has been made to bridge the gap between science and fisheries (e.g. GAP1, GAP2, and JAKFISH). This work was geared towards moving from micro-management to result-based fisheries management through development of modelling tools that may be generally applied so that stakeholders (including fishers) would be able redo or set up alternative analyses that will elucidate the biological dynamics and the consequences of different fishing activities. Much of this work has been focused on the development of single-stock models; however, this platform could be used to evaluate stock structure and multistock models. In this context, modelling could be useful in informing stakeholders on the spatio-temporal scale of fish ecology and its impact on the fishery. Furthermore, this sharing of information could facilitate agreement between fisheries stakeholder on the appropriate scale of management.

7.3 Management consequences

Management units that do not encompass the scale of fish biology can make meeting goals of sustainable management (e.g. maintaining or rebuilding stock biomass) difficult. Simulation modelling can be a useful tool in determining when it is biologically meaningful to alter management unit boundaries or manage at a finer spatial scale. Management may construct harvest rules to operate at any given spatial scale; however, a change in the scale of management may result in complex political issues regarding the ownership of the resource. Thus, the alignment of management units with biological structure requires information on stock identity as well as political cooperation.

Examples of fine-scale spatial management typically include species with limited migration or patchy and/or local distribution. For example, American lobster management occurs on a small scale, but the science (assessment and analysis of management plans) to support specific decision is not currently available on this scale. In the case of the Chilean abalone fisheries, a TURF (Territorial Use Rights for Fishing Programme) system, where groups of fishers are granted exclusive access to publicly owned benthic resource, have been effective at recovering populations to intermediate catch rates, whereas the overall management of this fishery has failed. Another example of the application of local management measures occurs in the UK scallop fisheries.

Management of highly migratory stocks that cross several management units is often difficult due only in part to uncertainty about the stock structure. The monitoring of these stocks is a major task requiring internationally coordinated effort and the possibility to identify and assess stock structure is often at the limit of fisheries science. Changes in the distribution patterns of pelagic fish, such as herring or mackerel, is

sometimes seen by fishers and even national authorities as new stock components to be exploited without reference to the nature of the stock complexity in the region (Cunningham *et al.*, 2007). Atlantic bluefin tuna is an example of a pelagic species with complex population structure as well as complex politics surrounding its international management. Without proper management actions, conservation of the endangered Atlantic bluefin tuna may be at risk of failure (MacKenzie *et al.*, 2008). A better in depth understanding of the complicated stock structure and migration patterns is necessary for scientists to convincingly model the probable outcome of optimal management measures (Porch, 2005).

Simulation modelling has been used to examine management effects North Sea cod, currently managed as a single stock, exhibited a severe decline during several decades and has, in the last ten years, been exploited below safe biological limits. A lack of understanding of stock structure may have contributed to this decline. A number of management measures have been applied at different geographical scales with limited effects. The cumulative evidence supports the existence of genetically distinct sub stocks (Hutchinson 2008) with different life-history characteristics and productivity (Holmes *et al.*, 2008). As a part of the METACOD project Heath *et al.* (2008) modelled North Sea cod using a full life-history metapopulation model. This simulation model framework allowed for investigation of combined scenarios of spawning behaviour and oceanographic features and thus is a useful instrument in the analysis of management effects, including regionally different fishing mortalities

Both assuming stock structure at a spatial scale where it does not exist or ignoring the existence of different stock components may influence the results of management. In general, science should strive to bring reality into stock structured models. It should apply a stochastic approach that will yield confidence limits to different predictions as well enabling analyses of risks involved in management decisions or omitting taking action.

8 Identifying sustainable management options for complex population structures

Complex population structure of fish makes achieving our goal of sustainable management a challenge. One of the most complicated issues to account for in a management context is fisheries that target multiple population units and the impact this may have on the population and yield from the fishery. Simulation modelling is a useful construct to evaluate the impact of potential management options and derive the best approach for sustainable management. Here, we present a case study where due to the mixed nature of the fishery providing management has been difficult. Additionally, important aspects of sustainable management are identified that can guide future stock structure implication studies.

8.1 Sustainable management options under a mixed catch scenario (WKWATSUP)

Western Baltic spring-spawning herring (WBSS) and North Sea autumn spawning herring (NSAS) are assessed as separate stocks and the fisheries are managed by herring TACs per area. Herring from these stocks migrate between the western Baltic and the North Sea and herring catches within mixing areas (Division IIIa (Skagerrak and Kattegat) and parts of the eastern North Sea) are made up of a mixture Western Baltic spring spawners (WBSS) and North Sea autumn spawners (NSAS). In the biological advice, the level of mixing between the stocks is measured and used to calculate a total TAC for herring in the separate areas (ICES, 2010b).

A long-term management plan for the NSAS has been agreed on between the European Union and Norway, and a long-term management plan for WBSS is being developed as part of a wider initiative on long-term management plans for pelagic stocks in the Baltic. These plans would be used to fix the overall TACs for the respective stocks, but they do not provide advice on the appropriate level of TAC for the mixed-stock in Skagerrak and Kattegat. A workshop on procedures to establish the appropriate level of the mixed herring TAC (WBSS and NSAS stocks) in Skagerrak and Kattegat (Division IIIa; WKWATSUP) was held at ICES in 2010.

The overall outcome of WKWATSUP was an alternative TAC setting procedure. The WKWATSUP suggested that the TAC should first be set for the WBSS according to the F_{MSY} or F_{MSY} transition framework for WBSS alone. If the NSAS is greatly impacted by management of the WBSS, this rule would need to be re-evaluated. Following this, the fraction taken in the eastern part of the North Sea (parts of Subdivisions IVb and IVaE) should be subtracted from the total TAC for the WBSS before sharing the TAC between Division IIIa and Subdivisions 22–24. Subsequently the best estimates of the proportions of the NSAS and WBSS in the catch should be used to calculate the combined catch options in compliance with the targeted catch for WBSS.

Currently, there is a 50:50 share of the WBSS TAC between Division IIIa and Subdivisions 22–24. This split was not specifically evaluated by WKWATSUP as it was viewed as a political choice. Thus, all evaluations of TAC setting procedures were performed applying a 50:50 share of the TAC between areas. However, three different approaches as how to include the share taken in the North Sea were explored. Ultimately, WKWATSUP recommended a seasonal closure of the herring fishery in parts of the eastern North Sea and until the closure is implemented, the TAC setting procedure suggested by WKWATSUP should be applied.

At the end of the workshop it became clear that the interpretation of the ToRs was ambiguous. Despite initial discussions between all participants (scientists, stakeholders, managers), industry representatives had a different interpretation of the ToRs. It became clear that taking all possible biological, political and economical scenarios/interests into account made the task of providing advice extremely difficult. Thus moving away from single-stock advice and a strict TAC regime may be the way forward for giving advice in such complex population structures such as WBSS and NSAS in IIIa and adjacent areas.

8.2 Sustainable management options for a metapopulation scenario (SGHERWAY)

In the SGHERWAY project (see ICES, 2008, 2009, 2010a), a Management Strategy Evaluation (MSE) was executed to evaluate the conditions under which exploitation of the perceived herring metapopulation west of the British Isles was still considered to be sustainable, given the complexity in survey sampling, spatial overlap and the mixed nature of the fishery.

Currently, herring to the west of the British Isles are fished, managed and assessed separately as four ICES stocks 1: VIa North; 2: VIaS and VIIb,c; 3: VIIaN and 4: Celtic Sea and VIIj. Analytical assessments for VIa North are accepted by ICES in most years and the last two assessments have been accepted for the Celtic Sea and VIIj stocks. Analytical assessments have been rejected by ICES for VIaS and VIIb,c or VIaN stocks for many years. Because the WESTHER project indicated the possible existence of a herring metapopulation, SGHERWAY decided to add more population complexity to the management strategy evaluations and move away from single independent stock approaches.

The tools evaluated did not, under all conditions, suffice to manage the components of the metapopulation sustainably. The results showed that managing metapopulations is only possible with detailed fisheries independent data. Additionally, when components of the metapopulation differ considerably in abundance, sustainable management is impossible for the smallest component. Thus, in this specific case study, the VIIaN ICES stock (a component of relatively low abundance) should continue to be assessed and managed separately. Further, where there is uncertainty in stock identification, fishing mortality should be kept at low levels. If the success rates of stock identification of survey and catch samples increase, fishing mortality may also be increased. Hence, there are strong trade-offs between the uncertainty in biological processes, classification of these processes, and sustainable levels of exploitation. Figure 1 indicates these trade-offs and how management could respond to a change in spatial overlap of the components, or the success in the classification of spawning origin.

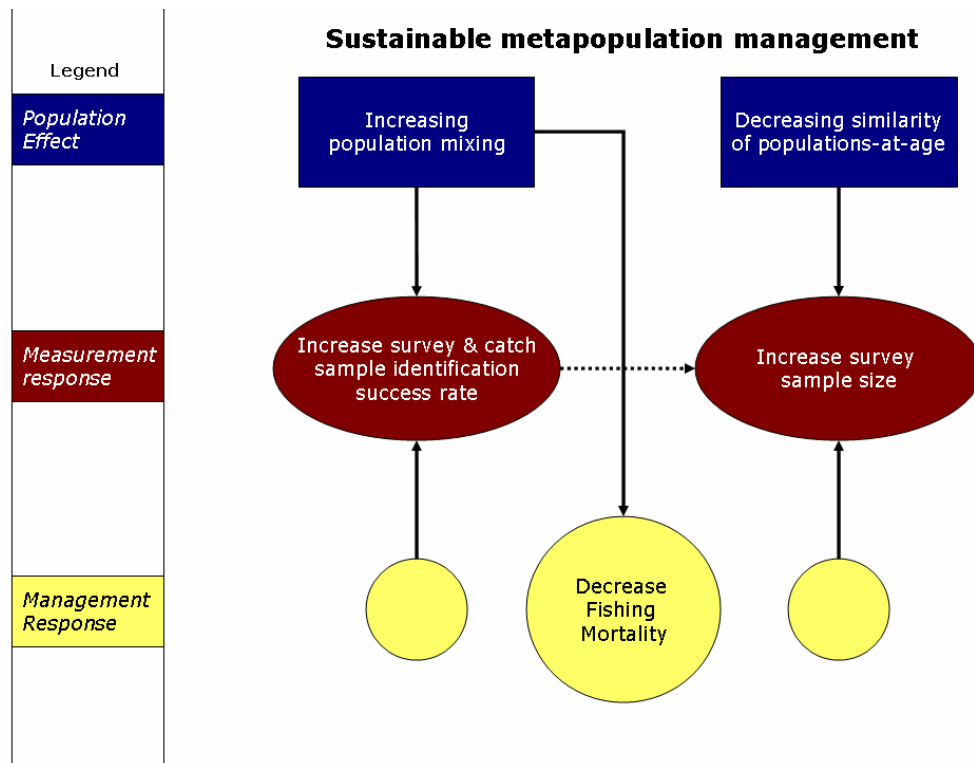


Figure 1. Population and management relationships for sustainable metapopulation management. Square boxes represent the biological subcomponents of the metapopulation. The ovals represent measurements taken from the metapopulation while the circles indicate possible management responses. Solid arrows represent direct cause-and-effect relationships while dashed arrows indicate possible cause-and-effect relationships to improve sustainable metapopulation management. The multiple arrows originating from the ‘increasing population mixing’ box can exist next to each other.

8.3 General lessons learned on sustainable management options for complex population structures

Management of complex population structure should ensure that spawning components are maintained at sufficient abundance to play a continued role in the ecosystem and provide services to society. Whilst fluctuations in abundance must be expected, to maintain resilience, diversity must not be allowed to decline and local depletion of stock components should be avoided. When giving management options in the ICES community, we need to consider how yield can be optimized following sustainable principles, essentially the application of the MSY approach in an ecological perspective.

The simplest way to manage a complex population and preserve all components is to manage according to the weakest link. Thus, in situations where knowledge and supporting data are limited the status of the weakest component may set management objectives. Though fairly easy to adopt by managers, this approach will lead to underutilization of the remaining population components and will not be effective in optimizing the long-term yield. Additionally, this approach requires definition of the components of the population which are considered ‘valuable’ in terms of biological diversity and require preservation beyond any political influences.

The state-of-the-art in management advice includes giving a range of management options that illustrate the consequences of diverse management scenarios. These scenarios could potentially incorporate the fate of population components under differ-

ent management decisions. Alternative management options, like seasonal closures, closure of juvenile nursery grounds, or directed fisheries on spawning grounds (or another 'pure' aggregation of the population) could facilitate sustainable management of complex population structure. This would represent a paradigm-shift in management, whereby management involves measures other than TAC advice. An example of this approach in a multispecies context is the management of the pollack fishery in the Bering Sea, where the industry uses real-time information on Chinook salmon bycatch to avoid reaching the bycatch limit, contributing to conservation of the species, and allowing for harvest of the TAC for pollack. With respect to management of a single species comprising of multiple population components, we can envision scenarios whereby fishing in mixing areas is avoided in favour of a spatio-temporal of distribution of fishing effort designed to target separate populations and ensure sustainable management of each unique population components. Approaches like a fully documented fishery (Kindt *et al.*, 2011) could potentially be applied to manage at such fine-scales, bearing in mind that such management needs full support from all parties involved.

Ideally, the choice of assessment model should reflect the choice of management regime (i.e. whether it is an effort based management, strict single-species TAC management, or a spatial-temporal closure approach). In the effort to manage complex population structures, the simplicity of models often diminishes as we try to encompass aspects of the life history of populations (e.g. migration). Applying spatio-temporally resolved management of a complex of populations could potentially facilitate precautionary management. In this case, the output of the assessments would be estimations of the potential take of the various life stages and/or population components at a given time and space. This approach could pave the way for an optimized fishery on various components under safe biological limits if combined with models of optimized economical yield, illustrating the effectiveness of spatially explicit harvest (catching the optimal part of the population in market-terms, reducing fuel costs).

Such a management regime requires solid knowledge of the life-history of the species and the spatio-temporal distribution of the various life stages. An example could be the North Sea herring stock complex, where four different spawning components are currently managed as one unit under a TAC regime. Due to differences in life-history, the weakest stock could be adversely impacted if the fishery exploits the resource without regard for component-strengths (Payne *et al.*, 2009, Payne, 2010). Currently, the fishery is considered to exploit the resource uniformly, although this may be far from the truth. Thus, assessment models should consider the spatial aspect of exploitation (i.e. spatially variable F).

Moving towards integrated advice for ecosystem-based approaches to management (Sissenwine and Murawski, 2004), researchers and scientific advisors are trying to respond to the changing demands of society (Rice, 2005). For this move to succeed it must involve all stakeholders and be based on incentives and not control (Hilborn 2004, Makino *et al.*, 2009). Thus fishers, scientists, and managers of complex fish populations need to be well informed of the breath of potential management options and the consequences of management decisions. Further, scientists need to take into account the political issues associated with and potential management responses to advice; otherwise the advice given may be completely ignored or even worse contradicted in management action.

In order to make an ecosystem approach to fisheries operational, a hierarchy of objectives needs to be defined, ranging from high-level policy goals to more specific operational objectives (FAO, 2003). Indicators related to ecological, social, economic, and governance aspects of ecosystem management provide a framework for monitoring and evaluating the performance of management in terms of achieving both the operational and higher level objectives (e.g. Garcia and Staples, 2000; FAO, 2003; Cury and Christensen, 2005). One potential ecological objective of an ecosystem approach is to “characterize and maintain the natural spatial structure of fish stocks” (Francis *et al.*, 2007). This would require information on stock structure as well as alignment of the scale of assessment and management with the natural spatial scale of the population (Francis *et al.*, 2007). Because spatial distribution patterns of various species often overlap (nursery areas, spawning habitat, feeding grounds), specific knowledge of the spatial structure of species could play an important role in informing the development of ecologically relevant ecosystem boundaries. Furthermore, a first step to optimize the harvest of the ecosystem could be based on multispecies meta-population models.

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Annex 1: List of participants

Ten participants attended the workshop at ICES Headquarters, Copenhagen, 5–7 April 2011 and five participated in the meeting remotely through WebEx.

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Annex 2: Agenda

Agenda

Workshop on the Implications of Stock Structure (WKISS)

Copenhagen, 5–7 April 2011

Tuesday 5 April

Morning (09:00–13:00)

9:00–9:30

1. Opening –Chairs – L. Kerr and N. Hintzen
2. Introductions + notifications from ICES secretariat

9:30–10:00

3. Background (terms of reference, meeting objectives, meeting products) – N. Hintzen
4. Adoption of agenda and timetable

10:00–11:00

Term of Reference a) Review and report on advances in population modelling to represent spatial population structure and movement of fisheries resources

1. Review of approaches to modelling spatial population structure and movement
 - a. Introduction to ToR a) – L. Kerr
 - b. Presentation on review work – L. Kerr

11:00–11:20 BREAK

11:20–12:30

- c. Discussion of ongoing work/missing points in review
 - i. C. Harma
 - ii. L. Kerr
 - iii. J. Kritzer

12:30–13:00

2. Present Paper review setup
3. Writing session on ToR a)

Tuesday 5 April

Afternoon (14:00–18:00)

Term of Reference c) Synthesize all information on biological stock structure for ICES management units (e.g. cod in the North Sea and adjacent areas, North Sea whiting, sandeel) through simulation modelling

5. 14:00–14:05

1. Opening – L. Kerr
2. Introduction to ToR c) – L. Kerr

14:05–16:00

3. Lessons learned from interdisciplinary stock identification (e.g. outcome of projects, how can we best inform models with biological information, incorporation of information into management)
 - a. HOMSIR project – A. Murta
 - b. REDFISH project – L. Kerr/S. Cadrin
 - c. WESTHER project –E. Hatfield

16:00–16:20 BREAK

16:20–17:30

4. Discussion – L. Kerr, moderator, rapporteur N. Hintzen
5. Summary and Conclusions

17:30–18:00

6. Writing session on ToR c)

**Wednesday 6 April
Morning (09:00–13:00)**

Term of Reference: d) Use simulation modelling as a tool to examine the ecological and fisheries consequences of a mismatch between management units and biological stock structure; and develop biologically realistic operating models for use in management strategy evaluation

9:00–9:15

1. Introduction to ToR d) – N. Hintzen

09:15:00–10:15

2. Examples
 - a. SGHERWAY – N. Hintzen
 - b. Multistock assessment models – C. Berg

10:15–11:00

3. Discussion – L. Kerr, moderator, rapporteur N. Hintzen

11:00–11:20 BREAK

11:20–12:00

4. Summary and Conclusions

12:00–13:00

5. Writing session on ToR d)

**Wednesday 6 April
Afternoon (14:00–18:00)**

Term of Reference b) Identify best practices for simulating populations with complex population structure

14:00–14:15

1. Introduction to ToR b) – N. Hintzen

14:15–15:00

2. Presentations of Ongoing work:
 - a. J. Kritzer
 - b. D. Goethal
 - c. M. Heath

15:00–16:00

3. Discussion – N. Hintzen moderator, rapporteur L. Kerr

16:00–16:20 BREAK

16:20–18:00

4. Writing session on ToR b)
5. Summary and Conclusions

19:30 SOCIAL DINNER

**Thursday 7 April
Morning (09:00–13:00)**

Term of Reference: e) Identify sustainable management options for complex population structures

9:30–9:15

1. Introduction to ToR e)– N. Hintzen

9:15–11:00

1. Presentation on WKWATSUP – H. Mosegaard / L. Worsøe Clausen
2. Discussion – N. Hintzen, moderator, rapporteur L. Kerr

11:00–11:20 BREAK

11:20–12:00

3. Summary and Conclusions

12:00–13:00

4. Writing session on ToR e)

**Thursday 7 April
Afternoon (14:00–18:00)**

14:00–17:00

1. Develop WKISS Report
 - a. Assign tasks and develop timelines
2. Summary and Conclusions

Annex 3: Recommendations

Recommendation	Addressed to
1. WKISS recommends that information on commercial catch, discards and biological sampling is made available at the highest spatial and temporal resolution possible.	PGCCDBS
