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Contribution to the Themed Section: '*Beyond ocean connectivity: new frontiers in early life stages and adult connectivity to meet assessment and management*'

Review Article

Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish

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Recent advances in the application of stock identification methods have revealed inconsistencies between the spatial structure of biological populations and the definition of stock units used in assessment and management. From a fisheries management perspective, stocks are typically assumed to be discrete units with homogeneous vital rates that can be exploited independently of each other. However, the unit stock assumption is often violated leading to spatial mismatches that can bias stock assessment and impede sustainable fisheries management. The primary ecological concern is the potential for overexploitation of unique spawning components, which can lead to loss of productivity and reduced biodiversity along with destabilization of local and regional stock dynamics. Furthermore, ignoring complex population structure and stock connectivity can lead to misperception of the magnitude of fish productivity, which can translate to suboptimal utilization of the resource. We describe approaches that are currently being applied to improve the assessment and management process for marine fish in situations where complex spatial structure has led to an observed mismatch between the scale of biological populations and spatially-defined stock units. The approaches include: (i) status quo management, (ii) "weakest link" management, (iii) spatial and temporal closures, (iv) stock composition analysis, and (v) alteration of stock boundaries. We highlight case studies in the North Atlantic that illustrate each approach and synthesize the lessons learned from these real-world applications. Alignment of biological and management units requires continual

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monitoring through the application of stock identification methods in conjunction with responsive management to preserve biocomplexity and the natural stability and resilience of fish species.

Keywords: biocomplexity, connectivity, fisheries management, population structure, spatial structure, stock assessment, stock identification.

Introduction

In recent years, substantial advances have been made in research to identify and delineate biologically discrete fish populations. These research efforts have demonstrated that marine fish with little population structure and essentially homogeneous genetic and phenotypic characteristics are the exception rather than the rule (Waples and Gaggiotti, 2006; Reiss *et al.*, 2009; Ames and Lichter, 2013; Ciannelli *et al.*, 2013). It is now clear that the population structure of marine species falls along a continuum from panmictic (e.g. American eel *Anguilla rostrata*, Côté *et al.*, 2013; European eel *Anguilla anguilla*, Als *et al.*, 2011) to numerous distinct populations (e.g. herring *Clupea harengus*, Ruzzante *et al.*, 2006; Hatfield *et al.*, 2007; Geffen *et al.*, 2011), with the majority of species exhibiting complex structure within this range (e.g. horse mackerel *Trachurus trachurus*, Abaunza *et al.*, 2008; redfish *Sebastes mentella*, Cadrin *et al.*, 2010; cod *Gadus morhua*, Smedbol and Wroblewski 2002; Wright *et al.*, 2006, Kelly *et al.*, 2009).

The mechanisms of fish population differentiation and connectivity within the marine environment are complicated, and for many species better understanding of the factors that restrict and promote the exchange of individuals is needed. Oceanographic and environmental features (e.g. currents, fronts, eddies, and temperature and salinity gradients) as well as the bio-physical attributes of eggs and larvae (e.g. buoyancy and swimming capabilities) can promote retention or dispersal, and have been identified as principal factors in structuring marine fish populations (e.g. Iles and Sinclair, 1982; Jørgensen *et al.*, 2005; Cowen *et al.*, 2006). Fish behaviour (e.g. natal homing, spawning site fidelity, straying, entrainment, resident or migratory life history strategies) and habitat requirements across the life cycle of fish act as other key processes affecting population differentiation and connectivity (Petitgas *et al.*, 2010, 2013; Secor, 2015). Additionally, adaptation to local environmental conditions can act as an important selective pressure maintaining population structure (Pampoulie *et al.*, 2006; Kovach *et al.*, 2010).

Population structure can have significant consequences, including mediating species responses to fishing and environmental change and playing a key role in species persistence. The seminal research on this topic examined the impact that spatial structure and connectivity could have on the persistence and recovery of populations (e.g. 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). In more recent years, there has been a shift toward examining questions that are relevant to the temporal scales addressed by fisheries scientists (Kritzer and Sale, 2004). The questions now focus on how populations might function to support the resilience and stability of marine resources and the implications of the loss of biocomplexity over ecological rather than evolutionary time scales (Secor *et al.*, 2009; Kerr *et al.*, 2010a,b, 2014b).

From a traditional fisheries management perspective, single species advice is provided for individual stock units. It is assumed that stocks are discrete units with homogeneous vital rates (e.g. growth, natural mortality) and that specific stocks can be exploited independently of each other (unit stock assumption, Secor, 2014) or that catches can be assigned to their stock of origin (Cadrin *et al.*, 2014a). Violation of the unit stock assumption (i.e. mis-classification of the appropriate spatial scale of management) could introduce significant problems affecting stock assessment and fisheries management that can impact sustainability of the resource, profitability of the fishery, resilience of fishing communities, and impede conservation or biodiversity goals. In some cases, what is assumed to be a homogeneous stock may in fact be a mixed stock, composed of populations with unique demographics and dynamics (Cadrin and Secor, 2009; Kell *et al.*, 2009; Hintzen *et al.*, 2015). Thus, short-term recommendations (e.g. total allowable catch, TAC) and long-term strategies (e.g. rebuilding targets and harvest control rules) produced from the stock assessment may be based on an erroneous perception of stock structure and not account for differentiation in productivity among population components. In this context, the harvest of a mixed stock, composed of unique populations of a single species, can potentially lead to overfishing less productive populations and under-fishing more productive populations (Ricker, 1958; Frank and Brickman, 2000; Fu and Fanning, 2004; Cadrin and Secor, 2009). Additionally, management units that are only a portion of a self-sustaining population can also pose problems for assessment and management due to difficulty in estimating biomass and providing catch advice for a portion of a population which may vary in its representation in a stock area over time (e.g. transboundary species that exhibit connectivity between United States and Canadian waters such as winter skate, Frisk *et al.*, 2008; and Atlantic halibut, Shackell *et al.*, 2016). Thus, understanding the spatiotemporal scale of population structure for a species in relation to management units is important for effective long-term sustainable management (Goethel *et al.*, 2011).

Despite increased recognition of complex population structure and stock mixing, the disparities between population structure and current management units have not been reconciled (Reiss *et al.*, 2009). The lack of integration of information on biological population structure in the assessment and management process is partly due to a lack of understanding of the consequences and costs of ignoring these phenomena. Furthermore, depending on the geographic location, there may be political, legal, cultural, and social pressures that prevent revision of stock boundaries or adding complexity to stock assessments. For example, in Europe, sampling units and intensities are currently fixed by regulation through the relatively inflexible data collection framework (EU, 2008), which creates financial consequences for member states when sampling methodology is altered to accommodate a new stock area design. In the United States, allocation of fishermen's quota is linked to historical patterns of fishing by stock area. Thus, there are important implications for the fishing industry and consequent challenges for fisheries management in changing management unit boundaries (e.g. Annala, 2012). However, it is

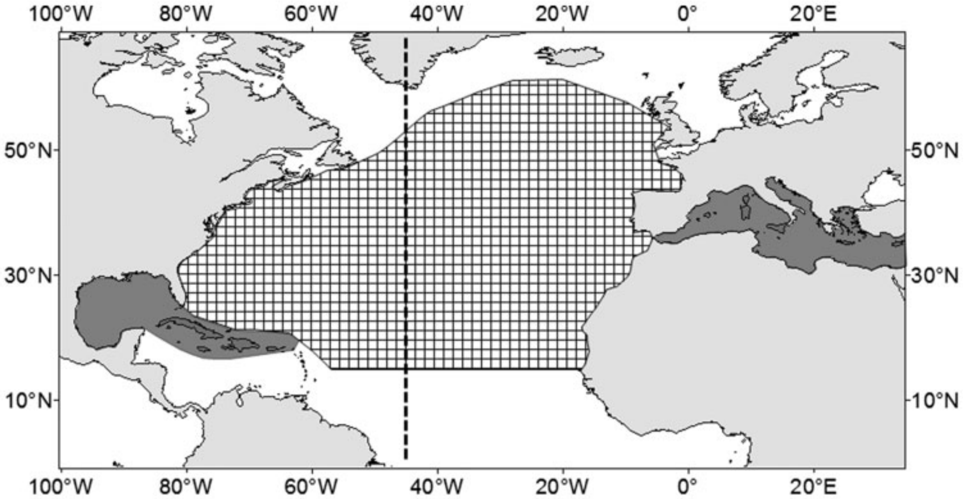

Figure 1. Illustration of spawning habitat (dark grey) of western and eastern origin Atlantic bluefin tuna (*Thunnus thynnus*) and range of overlap (hatched area) relative to the ICCAT management boundary (dashed line).

important to highlight that there are a range of management strategies that could be adopted or changes that could be incorporated in the stock assessment process to address complex spatial structure without changing management boundaries (Kritzer and Liu, 2014).

In recent years, there has been an increase in the application of simulation models to evaluate alternative approaches to address misalignment of biological and management units (e.g. Kell *et al.*, 2009; Cope and Punt, 2011; Ying *et al.*, 2011; Kerr *et al.*, 2014b). Management strategy evaluation (MSE) is currently considered the state-of-the-art in fisheries management decision-making and involves simulating a range of management options (e.g. the scale of assessment and management) in order to illustrate the potential biological and economic consequences (Sainsbury *et al.*, 2000; Kell *et al.*, 2006; Pastoors *et al.*, 2007; Kraak *et al.*, 2008). MSEs simulate the managed system as a whole (e.g. population dynamics, data collection, stock assessment, and policy implementation) including error associated with each stage (e.g. observation error, process error, and implementation error) and quantitatively evaluate the performance of each alternative management strategy (Sainsbury *et al.*, 2000; Bunnefeld *et al.*, 2011). Developing spatially explicit MSEs can provide insight regarding the potential consequences of ignoring population structure and demonstrate what type of management strategy might work best for any given situation (e.g. whether incorrect stock boundaries are truly detrimental to achieving sustainable harvest or if alternate management actions such as spatiotemporal closures might be sufficient).

We provide a review that summarizes the spectrum of approaches that have been applied to integrate new information on complex population structure and mixing of marine fish into assessment and management. Focus is placed on current applications and the lessons learned from their implementation in the North Atlantic based on our experience as contributors to the International Council for the Exploration of the Sea (ICES) Workshop on Implications of Stock Structure (WKISS). We have limited our review to real-world applications, whereas the full breadth of potential techniques that could be used to address mismatches in scale was previously reviewed by Goethel *et al.* (2011), Kerr and Goethel (2014), Kritzer and Liu (2014), and Goethel *et al.* (2016). We conclude with a summary of best practices and lessons learned in integrating new information on biological population structure into assessment and management.

Approaches applied to address misalignment of biological and management units

There are a range of approaches to improve assessment and management in situations where a mismatch in spatial scale occurs and the degree of overlap between biological populations and mixed stock composition of the fisheries are key determinants of the appropriate management strategy. We selected case studies that illustrate each approach and, in the case of approaches (ii) to (v), were specifically implemented with the goal of aligning assessment or management based on new information on population structure. It is important to note that these approaches are not mutually exclusive and in many cases multiple techniques have been applied over time (e.g. North Sea herring and bluefin tuna). We have arranged the approaches in a gradient of complexity with respect to implementation from relatively simple to complex.

(i) Status quo management—there is insufficient information to change the current management practices.

(ii) "Weakest link" management—there is some knowledge of spatial structure, but insufficient information exists to explicitly manage all spawning components. The assumed weakest spawning component is protected through management measures.

(iii) Spatial and temporal closures—there is knowledge of spatial structure, but insufficient information exists to alter the scale of assessment. Spatial and temporal closures are used to protect spawning populations.

(iv) Stock composition analysis—there is knowledge of stock mixing, but insufficient information exists to explicitly model connectivity within a stock assessment. Stock composition data are used to parse data (catches or samples) to

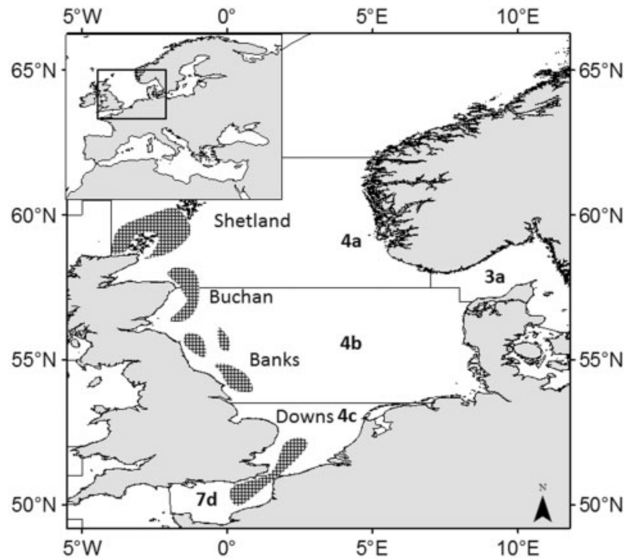

Figure 2. North Sea herring (*Clupea harengus*) are managed as a single stock (ICES Subarea 4 and Divisions 3a and 7d), but diverse spawning components (Shetland, Buchan, Banks, and Downs; hatched areas) are recognized and management is designed to preserve the Downs component. Map is modified from Bierman *et al.*, 2010.

the appropriate stock of origin before being input to the stock assessment or used in management.

(v) Alteration of stock boundaries—sufficient information is available on population structure and unique harvest stocks exist, which allows updating and redrawing stock boundaries to improve the alignment of biological populations and management units.

Approach I: maintain status quo

Case study I: Atlantic bluefin tuna

Atlantic bluefin tuna (*Thunnus thynnus*) is a highly migratory species composed of two spawning populations that exhibit natal homing with the western population spawning in the Gulf of Mexico and adjacent waters and the eastern population spawning in the Mediterranean Sea (Figure 1; Boustany *et al.*, 2008; Rooker *et al.*, 2008, 2014). However, there is also evidence of extensive migration of bluefin that results in mixing of these populations within the North Atlantic Ocean (Mather *et al.*, 1974, Mather, 1980; NRC, 1994; ICCAT, 2001, 2013; Block *et al.*, 2005; Rooker *et al.*, 2008, 2014). Otolith chemistry information has revealed a large contribution of eastern-origin fish to western fisheries (as high as 63% at times in the United States mid-Atlantic fisheries; Siskey *et al.*, 2016). There is also new evidence suggesting an additional spawning location within the western stock area in the Slope Sea (Richardson *et al.*, 2016). However, further information on the magnitude of spawning at this location and its role in population dynamics of the species is needed to understand the implications of this finding (Walter *et al.*, 2016).

Atlantic bluefin tuna were assessed and managed as a single stock historically, but recognition of stock structure led to separate assessments of eastern and western Atlantic stocks since 1980. The most recent assessments for Atlantic bluefin support significant differences in relative abundance and productivity between stocks with the eastern stock estimated to be an order of magnitude larger in biomass than the western stock (ICCAT, 2014). Given the magnitude of difference in relative abundance, even low rates of movement of fish from the eastern stock into the western stock area could have a large influence on the abundance and stock composition of fish in this region (Butterworth and Punt, 1994; ICCAT, 1994; NRC, 1994). Currently, the degree of stock mixing is considered an important source of uncertainty in the assessment of Atlantic bluefin tuna, particularly for the western stock unit (ICCAT, 2014). Stock assessments of Atlantic bluefin tuna have attempted to incorporate stock structure and mixing for decades, and models have been developed to reflect an expanding understanding of movement and stock mixing (e.g. the VPA 2-Box overlap model, Porch *et al.*, 2001, and the Multi-stock Age Structured Tag-Integrated model, Taylor *et al.*, 2011). These models have advanced understanding of the implications of stock mixing on estimates of stock biomass and sustainable yield, but lacked adequate data to provide credible or robust advice to management (ICCAT, 2008, 2012).

Despite increased awareness of population structure and mixing across the management boundary, the scale of assessment and management of Atlantic bluefin tuna has remained the same (i.e. *status quo* management that assumes no mixing) since the 1980s. In 2013, a workshop was convened to review existing information on population structure and stock mixing of Atlantic bluefin tuna, including information derived from otolith chemistry, genetics, tagging, and life history parameters (ICCAT, 2013). The workshop recommended that the effects of complex population structure on scientific advice should be evaluated and ICCAT has prioritized the need to develop and apply a MSE for Atlantic bluefin tuna.

Lessons learned

Ignoring stock mixing can result in inaccurate estimates of stock productivity and sustainable yield and misinterpretation of trends in abundance (e.g. Kerr *et al.*, 2014a; Secor 2015). This is particularly true for overlapping fishery resources that exhibit asymmetry in production, like Atlantic bluefin tuna populations. Existing information on stock mixing of bluefin tuna suggests that the current two-box view is inadequate and may impede sustainable management of western origin fish (Kerr *et al.*, 2014a). ICCAT is currently approaching this challenge using MSE, and plans are developing to test the performance of alternative approaches for meeting fishery management objectives (e.g. Carruthers *et al*, 2016). It is important to note that Atlantic bluefin tuna migrate across domestic and international boundaries and their management is characterized by complex, international politics which can make achieving the goal of sustainable management more challenging.

Despite knowledge that complex spatial population structure exists, data and modelling limitations often impede successful application of assessment and management frameworks that can match the scale of biological processes. *Status quo* management is not optimal, but, in situations of high complexity and limited data (typical for many highly migratory species), it often represents the default option. Furthermore, Porch *et al.* (1998) demonstrated through simulation analysis with a bluefin-like species that if spatial structure and movement are directly incorporated into the assessment, incorrectly specifying movement can potentially lead to more biased assessment results than if movement is ignored. Thus, in certain instances, it may be more risk averse to ignore complex population dynamics in the stock assessment framework than attempting to include dynamics that are not fully understood. In these cases, however, enhanced monitoring (e.g. stock composition analysis of samples collected through robust statistically designed surveys and fishery-dependent sampling) is critical to track changes in the relative abundance of unique populations. Furthermore, implementation of alternate spatiotemporal management measures (e.g. to protect spawning components) can be useful (e.g. Gulf of Mexico spawning closures; Armsworth *et al.*, 2010).

Approach II: "weakest link" management

Case study II: North Sea autumn spawning herring

North Sea herring are managed as a single stock (spatially delineated as ICES Subarea 4 and Divisions 3a and 7d), but diverse spawning components (Shetland/Orkney, Buchan, Banks, and Downs) are recognized and their preservation is considered important (Figure 2, Bierman *et al.*, 2010). The North Sea herring stock collapsed during the 1970s, resulting in a moratorium on the fishery until 1981 (Dickey-Collas *et al.*, 2010). During the rebuilding phase, measures were put in place to ensure that one of the minority spawning components of the stock, the Downs component (herring that spawn in December and January in the southern North Sea and eastern English Channel), was protected from being targeted during spawning.

Regional quota for the spawning area of the Downs component was set at a fixed proportion (11%) of the total North Sea herring allowable catch (Dickey-Collas *et al.*, 2010). The fixed allocation of this separate quota was not based on robust science, because the size of this component was unknown and no monitoring was in place to ascertain its temporal dynamics. The aim of this management strategy was to conserve what was perceived as the weakest component of the stock. The Downs component has recovered to a substantial degree since the implementation of conservation measures (ICES, 2009a). However, the extensive rebuilding time of the Downs component (∼25 years), given the relatively short generation time of herring, indicates the management strategy did not have an immediate impact (Dickey-Collas *et al.*, 2010). Today, however, the spawning component is considered to be an integral contributor to the autumn-spawning stock (Dickey-Collas *et al.*, 2010).

Lessons learned

"Weakest-link" management is a practical approach to account for biocomplexity and preserve critical spawning components when limited data are available to directly assess mixing or yield from a sub-stock unit (Reiss *et al.*, 2009; ICES, 2010a). Minority components within a stock complex can be adversely impacted if the fishery exploits the resource without regard for component productivity (Fu and Fanning, 2004; Ruzzante *et al.*, 2006; Dickey-Collas *et al.*, 2010; Payne, 2010; Ying *et al.*, 2011). Less productive components may not be as valuable to the fishery, but can help maintain regional stability (particularly in the context of a metapopulation). They can also protect against collapse of the resource through the "portfolio effect", whereby diversification reduces the overall species extinction risk (Secor *et al.*, 2009; Kerr *et al.*, 2010a,b).

Although fairly easy to adopt by managers, the "weakest link" approach can also lead to under-utilization of the remaining population components and will not be effective in optimizing the long term yield (Ricker, 1958; Punt and Donovan, 2007). A "weakest link" approach can result in displacement of fishing effort to other more productive components, which may be important to stock productivity, and may result in an overall reduction in biomass and decrease in yield (Tuck and Possingham, 1994). Additionally, monitoring minority populations or spawning components may be difficult and costly as survey samples may be dominated by the more productive populations or components. A critical decision for "weakest link" management is defining which components of the population are "valuable" in a biocomplexity context and, therefore, require conservation. Since the implementation of separate quota management, the Downs component has recovered and substantial variation in the strength of this spawning component has been documented (ICES, 2009a; Payne, 2010). This example demonstrates that even with very little science, a precautionary measure can bring about conservation success, but potentially at the cost of foregone utilization. Thus, from a management perspective this approach may be deemed suboptimal, because potential fishing opportunities and yield were lost.

Approach III: temporal and spatial closures

Case study III: Gulf of Maine stock of Atlantic cod

Two genetically distinct spawning populations of Atlantic cod (*G. morhua*) have been identified within the Gulf of Maine stock area: (i) a spring-spawning complex, which spawns in inshore Gulf of Maine waters from Massachusetts Bay to Bigelow Bight in spring; and (ii) a winter-spawning complex, which spawns within the inshore Gulf of Maine and southern New England waters in winter (Kovach *et al.*, 2010). These two populations overlap spatially outside of the spawning periods and for assessment and management purposes are lumped together within the Gulf of Maine stock unit (Kerr *et al.*, 2014b).

Due to perceived declines in the Gulf of Maine cod stock and the relative ineffectiveness of other management efforts (e.g. trip limits and restrictions on days at sea) to halt declines in stock biomass, management measures based on fine scale spatial restrictions were enacted to protect coastal spawning groups (Dean *et al.*, 2012; Armstrong *et al.*, 2013). Closures of three areas to both commercial and recreational fishing effort during spawning were enacted in Massachusetts state waters including: (i) Massachusetts Bay Winter Cod Conservation Zone (enacted in 2003), (ii) Massachusetts Bay Spring Cod Conservation Zone (enacted in 2009), and (iii) the Gulf of Maine Cod Spawning Protection Area (Figure 3). Seasonal rolling closures aimed at protecting coastal spawning components in US federal waters from April-June preceded these closures (i.e. the rolling closures were in effect beginning in the late 1990s), but they did not exclude recreational exploitation which expanded in the early 2000s (Figure 3, Armstrong *et al.*, 2013). Furthermore, a larger scale year-round closure, the Western Gulf of Maine Closure, was implemented in 1998 to reduce mortality of Gulf of Maine cod (Figure 3). However, recreational fishing has also been permitted within this closed area.

The seasonal and year-round closures enacted for Gulf of Maine cod were effective in protecting spawning activity and a portion of the cod resource (although the extent is unknown; Zemeckis *et al.*, 2014a), but these protections were not enough to

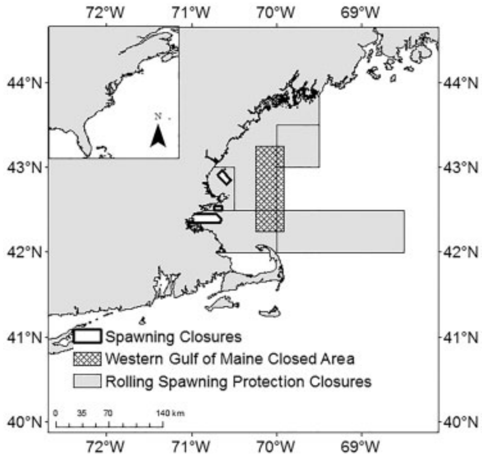

Figure 3. Closures designed to protect the Gulf of Maine cod stock (*Gadus morhua*), including spawning closures within state waters, a year-round western Gulf of Maine closed area, and rolling spawning protection closures.

halt the decline in cod abundance (NEFSC, 2014). A key factor influencing the lack of response may have been recreational exploitation, which was permitted within the federal closed areas (Armstrong *et al.*, 2013). Although, the year-round closure did not appear to enhance local abundance or biomass within the closed area (Kerr *et al.*, 2012), measurable recovery of the population age structure within the closure did occur (as evidence from comparisons of age structure inside and outside of the closure; Sherwood and Grabowski, 2016), which should act to enhance long-term stock productivity given the disproportionate reproductive value of older and larger fish (Berkeley *et al.*, 2004).

Lessons learned

Alternative spatiotemporal management options have the potential to contribute to sustainable management by conserving fine-scale population structure (Kraak *et al.*, 2012; Rijnsdorp *et al.*, 2012). By focusing on the spatial aspects of the fishery resource and accounting for biological sensitivity of defined-areas at specific times of the year (e.g. spawning aggregations or nursery grounds), closures can eliminate direct exploitation of vulnerable life stages, while protecting them from disturbance (i.e. the latter has been shown to increase reproductive success for species that form spawning aggregations like cod; Dean *et al.*, 2012; Armstrong *et al.*, 2013). In many instances, fishermen are aware of the sensitivity of various life stages and can be a valuable source of information for identifying fine-scale spawning aggregations and contribute as key partners in implementing conservation measures.

It is challenging to assess the impact of spawning and mortality closures at the stock-level, because fishing pressure outside the closures along with ecosystem changes may have a stronger impact on long-term stock trajectories (Pershing *et al.*, 2015; Hare *et al.*, 2016). Seasonal closures designed to protect Atlantic cod spawning in the Firth of Clyde off the Scottish west coast (ICES Area 6a) implemented in 2001 also did not show evidence of local recovery, but implementation was most likely too late to be useful in the short-term (Clarke *et al.*, 2015). Similarly, a closed area designed to protect juvenile haddock on the central Scotian Shelf did not demonstrate its intended benefit (Frank *et al.*, 2000). The lack of response was attributed to several factors: (i) the low proportion of juveniles protected by the closed area, (ii) the closed area was not closed to all gear types (fixed gear was permitted), and (iii) the combined influence of historical over-exploitation and environmental change on resident haddock (Frank *et al.*, 2000).

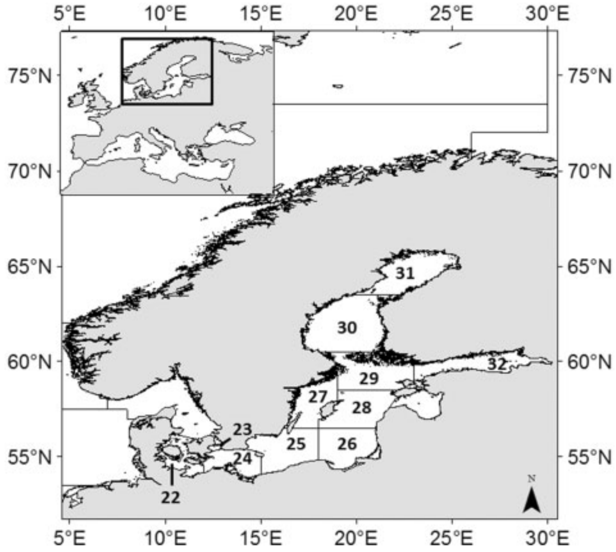

Figure 4. Eastern Baltic (ICES SDs 25-32) and western Baltic cod (ICES SDs 22-24) stock areas. The area of significant stock mixing is located in the Arkona Basin (ICES SD 24).

Seasonal and area closures have great potential to be effective tools in the management of spatial complexity, but, in order to have broad-scale (i.e. stock-level) impact, these tools must be applied early, at the appropriate scale, and in a way to effectively reduce total fishing pressure (Kritzer and Lui, 2014). Spatiotemporal closures alone cannot guarantee management success, especially if spatial population structure is being misinterpreted at the scale of assessment (e.g. lumping or splitting of unique spawning populations; Kerr *et al.*, 2014b). In the case of northwest Atlantic cod, stock assessment models and broad-scale management measures (i.e. stock-specific TACs) did not account for the existing population structure within the Gulf of Maine stock unit, which likely impeded the potential success of the implemented spatiotemporal closures.

Approach IV: integration of stock composition analysis in assessment and management

Case study IV: eastern and western Baltic cod

Two genetically distinct cod (*G. morhua*) populations occur in the Baltic Sea and are assessed and managed as separate stocks: eastern Baltic cod (ICES SDs 25–32) and western Baltic cod (ICES SDs 22-24, Figure 4). Stock mixing has been documented in the Arkona Basin (ICES SD 24) and has apparently increased due to increasing abundance of the eastern population in recent years (Eero *et al.*, 2014). Because of the substantially lower stock size of western Baltic cod compared to eastern Baltic cod, concern exists about the potential for local depletion of the western Baltic cod stock, and it was deemed necessary to incorporate stock mixing dynamics into management decisions (Hüssy *et al.*, 2013).

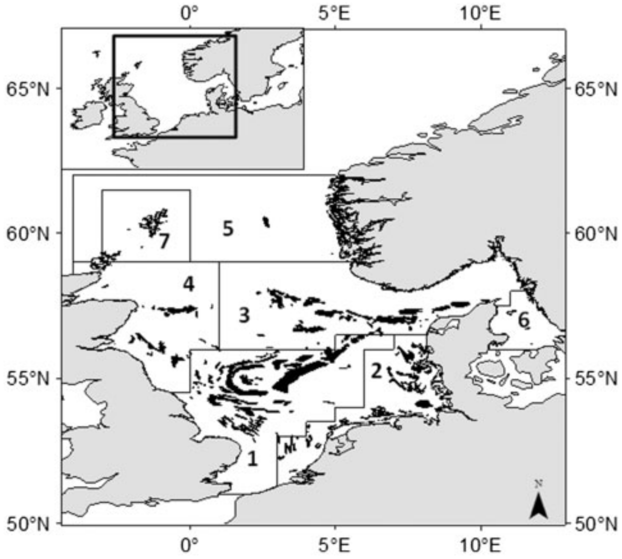

Figure 5. Sandeel (*Ammodytes spp.*) management areas (1-7) and spawning habitat (black). Figure modified from ICES (2014).

Otolith shape analysis has been identified as a useful method in mixed stock analysis of Baltic cod, providing a high degree of accuracy in the discrimination of fish stocks (Hüssy *et al.*, 2016). Otolith shape analysis is a phenotypic stock identification technique, which in this case was validated using genetic markers (single nucleotide polymorphisms, Hüssy *et al.*, 2013). Application of this method to archived otoliths has resulted in a time series of estimated proportions of eastern and western Baltic cod within the Arkona Basin since 1996 (ICES, 2015a). Hüssy *et al.* (2016) documented a temporal trend in the proportion of eastern Baltic cod in the Arkona Basin with an increase from ~30% before 2005 to >80% in 2011. In 2015, eastern and western Baltic cod stock assessments incorporated information on the proportion of eastern fish within the western stock area. Prior to 2015 all fish within the western Baltic geographical area (SDs 22–24) were attributed to the western Baltic cod stock regardless of their natal origin (ICES, 2015a). This revision provided a more realistic view of western Baltic cod stock status, indicating biomass is stable at low abundance (ICES, 2016a).

Lessons learned

Geographic stock boundaries cannot delineate sympatric populations. In such cases, mixed-stock analysis is a powerful tool that provides information on the stock composition of current fisheries, and also offers insights on temporal changes in population proportions in catches and the causes of those changes (Cadrin *et al.*, 2005). Mixed stock analysis of Baltic cod allowed for parsing of survey and catch data back to the stock of origin. In the absence of mixed stock analysis, the increase in the Arkona Basin would be attributed solely to the western stock and the resulting harvest strategy would be based on a misperception of western Baltic cod biomass (Hüssy *et al.*, 2016). Parsing of data using improved analytical tools such as otolith shape analysis as validated through use of genetic markers enabled a more representative assessment of the populations and the ability to more closely track the magnitude and trends in population dynamics of the individual stock components (Hüssy *et al.*, 2016). Stock composition analysis based on age structures (e.g. otoliths) takes advantage of samples that are routinely collected during a survey and based on a robust statistical design in order to represent age composition. However, analysis of otoliths requires increased resources, which should be weighed against the benefits offered for the given application. As high throughput genetic analysis becomes less expensive, this method of stock composition analysis can be more thoroughly utilized to supplement less costly methods (e.g. otolith shape analysis), and can be collected regularly in the same way that traditional catch length or age composition are sampled.

Approach V: alteration of stock boundaries and the spatial-scale of assessment

Two case studies, sandeel in the North Sea and redfish in the Irminger Sea, are highlighted to demonstrate this approach. These case studies profile species with different life histories (i.e. sedentary sandeel compared with semi-pelagic redfish) and complexity of population structure (i.e. metapopulation structure in the case of sandeel and genetically distinct populations for redfish). Additionally, different approaches are applied in redefining stock boundaries from relatively simple (i.e. implementing more fine-scale management units within the current stock boundaries for sandeel) to more complex (i.e. overhauling the stock units of redfish).

Case study Va: sandeel (Ammodytes spp.) in the North Sea

Sandeel (*Ammodytes* spp.) are a key component of the North Sea ecosystem serving as a major prey item for many fish, marine mammal, and seabird species as well as being a target fishery species. Local depletions of sandeel populations in the vicinity of breeding bird colonies have had catastrophic consequences to seabird reproductive success and brought considerable public and political attention to the issue of sandeel management (Frederiksen *et al.*, 2005). Sandeel exhibit a pelagic larval phase with settlement occurring on suitable sand habitat where they burrow during daylight periods to avoid predation (Wright *et al.*, 2000). Post-settlement sandeels are largely sedentary and demonstrate high site fidelity (Wright *et al.*, 2000), which results in the formation of local subpopulations in the North Sea due to the limited exchange of adults between areas. Larval drift models suggest that the North Sea consists of a spatial mosaic of self-recruiting populations. Additionally, the patchy geographic distribution and regional growth differences of sandeel suggest that the unit stock concept does not apply to sandeel in the North Sea (Christensen *et al.*, 2008).

Sandeels in the North Sea were managed historically as four stocks [(i): northern North Sea, (ii) southern North Sea, (iii) Shetland Island, and (iv) Skagerrak–Kattegat area] until 1995 when management units were revised to three units (i.e. the northern and southern North Sea stocks were combined into a single stock unit). In 2010, ICES modified the spatial scale of assessment and management from three to seven areas to better reflect the sub-population structure, and allow for spatial management measures that could mitigate potential depletion of local populations (Figure 5). Of these stock areas, three have analytical assessments, one is classified as data limited and managed based on an index of abundance, and the remaining three only have catch statistics available (ICES, 2015b).

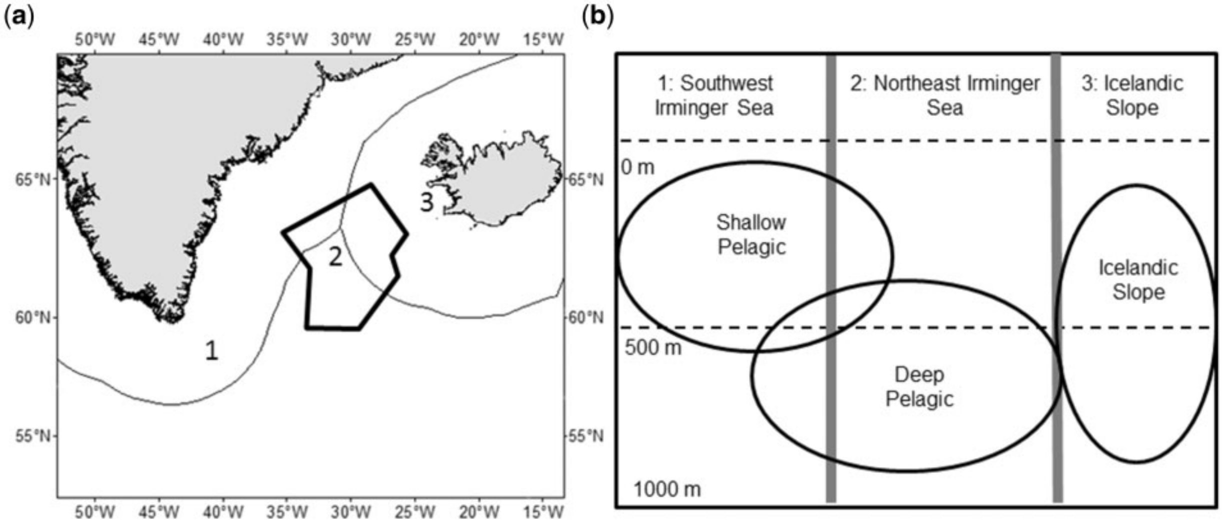

Figure 6. a) Redfish (*Sebastes mentella*) management areas in the Irminger Sea and adjacent waters (1: Southwest Irminger Sea, 2: Northeast Irminger Sea, 3: Icelandic Slope). b) Diagram of distribution of biological stocks by depth, including shallow pelagic, deep pelagic, and Icelandic slope as well as their respective stock areas (1-3). Figures modified from ICES, 2009.

Current catch advice for North Sea sandeel stocks is area specific in order to protect individual units, and these stocks are subject to annual TAC constraints, 'in-year' adjustments to projected TACs, and area-specific rotational fishery closures. The approach allows maintaining fishing on the more productive units, while protecting the smaller units that are more susceptible to overharvest (e.g. there is a quota for area 3, while no fishing is allowed in area 7; ICES, 2016b).

Lessons learned

Spatially explicit management is appropriate and essential for species which are sessile or semi-sessile. In the case of sandeel, it was recognized that fisheries targeting specific areas have the ability to extirpate parts or all of a local population. Due to the unique dynamics of local sandeel populations and the potential for local extirpation of spawning populations, there is a necessity for assessment and management plans to be area specific. The shift to more spatially explicit assessment and management of sandeel allowed for varying advice across local populations. By adjusting the management boundaries to conform to the substock structure, the potential for overexploitation when units were lumped, as was historically done for North Sea sandeel, was reduced. Simultaneously, foregone yield from underexploitation of more productive units also declined, which demonstrates the benefit of redefining spatial units as opposed to simply managing and protecting the weakest stock component.

Case study Vb: redfish (S. mentella) in the Irminger Sea

Population structure of beaked redfish (*S. mentella*) and the appropriate management units for this resource have been an issue of controversy over the past two decades (Cadrin *et al.*, 2010). Prior to 2009, ICES provided advice for redfish fisheries as two distinct management units: (i) a demersal unit on the continental shelf, and (ii) 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 in the mid-1990s. At the time, the relationship between the demersal and shallow-pelagic resources (the traditional target fisheries for redfish) and the resource being targeted by the newly developed pelagic deep sea fishery was unknown. Furthermore, there was spatial overlap in the deep-sea and demersal fishery, whereas the shallow pelagic fishery was more spatially distinct (Cadrin *et al.*, 2010).

In 2009, ICES convened a Study Group on Redfish Stock Structure in the Irminger Sea and adjacent waters (WKREDS) to review existing stock structure information, define the most likely biological stocks, and recommend practical management units (ICES, 2005, 2009b). All available studies related to stock structure of redfish in the region were reviewed and synthesized to determine the most parsimonious view of population structure. The review included multiple approaches to stock identification, such as examinations of geographic distribution (e.g. fishing grounds and survey data of early life stages, juveniles, and adults), genetic variation (e.g. allozymes, mitochondrial DNA, and nuclear DNA analyses), phenotypic variation (e.g. life history traits, morphology, and fatty acid composition characterizations), and connectivity (e.g. larval dispersal, natural tags, and artificial tags; Cadrin *et al.*, 2010).

Based primarily on genetic information (i.e. microsatellites), and supported by other information on stock structure, WKREDS concluded three biological stocks of redfish exist in the Irminger Sea and adjacent waters (Cadrin *et al.*, 2010):

(i) "Deep Pelagic" stock (NAFO 1-2, ICES 5b, 12, 14 >500 m),
(ii) "Shallow Pelagic" stock (NAFO 1-2, ICES 5b, 12, 14 <500 m), and
(iii) "Icelandic Slope" stock (ICES 5a, 14).

Although the biological stocks of redfish were in part redefined by depth and habitat, WKREDS recognized that depth-defined management units would not be practical and instead recommended new spatially-defined management unit boundaries that were redrawn to minimize mixed-stock catches. The three recommended management units included a (Figure 6; Cadrin *et al.*, 2010):

(i) "Deep Pelagic" management unit in the northeast Irminger Sea (defined by the spatial distribution of the deep, pelagic fishery),

(ii) "Shallow Pelagic" management unit in NAFO areas 1 and 2, ICES areas 5b, 12, 14 (outside of the deep, pelagic area), and

(iii) "Icelandic Slope" management unit that is north and east of the existing 'redfish line'.

Based on the view of redfish biological stock structure that emerged from the review and the recommendations of WKREDS, ICES revised the management units of *S. mentella* fisheries in the Irminger Sea and now provides specific advice based on the perception of the status of the three newly defined management units (Figure 6).

Lessons learned

When biological units overlap with new or developing harvest stocks and historical data can be parsed to the appropriate unit, a revision of the existing stock units may be the most appropriate and practical approach to improve the accuracy of assessment and effectiveness of management. The definition of management units usually cannot exactly match biological boundaries, because the latter are not precisely known and the spatial resolution of fishery management (e.g. reporting of fishing effort, monitoring of catch, and enforcement of regulations) is limited. There are also challenges to maintain pragmatic management areas, when biology brings new concepts into the separation of stock units (i.e. separation by depth).

Because ICES advice is now provided for three geographically defined management units for redfish, the more vulnerable shallow pelagic stock can be directly protected from overharvest without foregone yield from the other units (Cadrin *et al.*, 2010). The potential for improved advice for the three stocks illustrates the importance of stock identification for fisheries management. However, the situation for redfish was fairly unique in that harvest stocks aligned with population units and there was limited mixed stock catches, which allowed redefinition of stock units that overlapped with the developing fishery.

Best practices in integration of biological population structure into assessment and management

Below we outline a process for improving assessment and management in situations where there is a mismatch between the scale of biological population structure and spatially-defined stock units. This stepwise process is intended to reflect best practices and includes:

(i) Holistic review of available stock identity information by a group of experts,

(ii) Identification of alternative assessment and management options that consider biological structure,

(iii) Consideration of the practical limitations of alternative approaches, and

(iv) Quantitative evaluation of outcomes of alternative assessment and management options relative to biological, economic, and social objectives through MSE.

Review of stock identity information

In recent years there has been an increase in the application of a diversity of approaches to identify and delineate biological structure of fishery resources. In some cases, single methods are applied to resolve issues of stock structure (i.e. genetic markers), but increasingly multiple approaches (e.g. otolith chemistry and genetic markers; Tanner *et al.*, 2016) are applied to identify and delineate biological structure (Cadrin *et al.*, 2014b; Zemeckis *et al.*, 2014b). Because population structure is influenced by processes that vary across ecological and evolutionary time scales and are characterized by both genetic and phenotypic variability, information from multiple stock identification approaches is recommended as the most robust approach to draw conclusions regarding stock identity (Abaunza *et al.*, 2008; Cadrin *et al.*, 2014b). The application of more than one stock identification method increases the likelihood of correctly identifying and describing population structure (Cadrin and Secor, 2009; Cadrin *et al.*, 2014b).

Cadrin *et al.* (2014b) outlined a five step process for interdisciplinary evaluation of population structure and recommended that a summary statement be developed after each sequential step:

(i) Define the current spatial assessment and management units and their scientific or practical justification.

(ii) Identify all *a priori* hypotheses about population structure, including the current management units.

(iii) Conduct a comprehensive review of available information on the population structure of the fishery resource and summarize conclusions by discipline (e.g. geographic variation in genetic composition, phenotypic traits, movement patterns, otolith microchemistry, and parasitic infection).

(iv) Synthesize information across disciplines through an interdisciplinary evaluation with the goal of identifying congruent results and reconciling apparent differences.

(v) Test whether information supports or rejects *a priori* hypotheses of population structure and draw a final conclusion on population structure that is consistent with the best available science.

The ICES Stock Identification Methods Working Group is an example of an expert group that reviews questions of stock structure specifically for ICES stocks. A key aspect of this group is that the members include experts across the range of disciplines used to identify biological units in space and time, including genetics, life-history, tagging, otolith chemistry, morphometrics, parasites, and statistics. Through its reviews of the best available science and resultant recommendations (e.g. ICES, 2015c), the group strives to play a significant role in developing improved approaches to define stock units and incorporating explicit knowledge of population structure into assessment and management.

Identifying alternative assessment and management options

A range of approaches are available to improve assessment and management in situations where a mismatch in scale occurs between biological population structure and management units including: (i) changing the scale of the stock assessment or parsing "mixed" data prior to use in the assessment, (ii) changing the scale of management, or (iii) changing both the scale of assessment and management. Ideally, the scale of assessment models should coincide with the scale of management; however, this is not always feasible. The degree of spatial isolation or overlap between populations along with the stock composition of catches are important determinants of the appropriate strategy.

When mixing occurs among population components, naïve stock assessment techniques can give an inaccurate perception of the fishery resource and lead to overexploitation of unique spawning components, and loss of yield or other fishing opportunities. Development of assessment models that align with our understanding of biological structure can provide a more realistic assessment of population status and trends (Kerr and Goethel, 2014). Spatially-explicit models can account for connectivity within and across stock boundaries, but these models can be data intensive, add increased costs to monitoring (e.g. collection of tagging data for tag-integrated models), and require extensive knowledge of population structure in order to provide unbiased estimates (Porch *et al.*, 1998, 2001; Goethel *et al.*, 2015a,b). The application of spatially explicit stock assessment models is quite limited (e.g. management applications are only common in a handful of tropical tunas) and, to our knowledge, have not been used as the basis for management advice in any North Atlantic fisheries to date (see Goethel *et al.*, 2015a,b for an example application to yellowtail flounder off of New England and Aires-da Silva *et al.*, 2009 for an example application to blue shark in the North Atlantic).

Mixed stock composition analysis (e.g. the use of otolith shape or structure to assign survey and catch data to its natal origin) is a solution to mixed stock fisheries that does not require explicitly accounting for movement dynamics in the stock assessment. By parsing data back to the stock of origin, assessment inputs are adjusted to strictly account for removals from the natal population (e.g. eastern and western Baltic cod, case study IV), which often provides a more accurate view of stock biomass than assessments based simply on total removals within a stock area. In some cases, limitations in data and resources and the discrimination capacity of stock identification techniques may prohibit partitioning of data back to the natal population (e.g. herring west of the British Isles; ICES, 2015b). In these cases, it may still be possible to use abundance index time series to monitor individual population trajectories if the survey is specifically designed to sample the population component (e.g. surveys conducted on the spawning grounds).

Management can construct harvest rules to operate at any given spatial and temporal scale; however, fine-scale spatial management is simpler for species with local distributions or that exhibit limited migration (Kritzer and Liu, 2014). Spatially explicit management tools (e.g. closures of spawning habitat) can be effective even if the data do not support development of sub-stock or spawning component quotas (Kritzer and Liu, 2014). The example of Gulf of Maine Atlantic cod (case study III) demonstrates that this approach alone is not always sufficient to prevent declines in biomass, but it also illustrates the importance of a holistic analysis of population structure (i.e., accounting for both broad-scale and fine-scale dynamics). Without accounting for spatial population structure in the assessment and management of the entire stock complex, sub-stock closures alone cannot sufficiently limit fishing effort or rebuild stock biomass. Likewise "weakest link" management (e.g. case study II, North Sea herring) may protect minority spawning components, but without an assessment of the size of the component, overexploitation or foregone yield can result. When uncertainty in stock delineation exists and is not reconciled, imposing precautionary buffers within catch limits may be required to further guard against adverse effects from spatial mismatches (Kritzer and Liu, 2014).

In some cases, both the scale of assessment and management can be re-defined to reflect biological population structure. In scenarios where biological units are effectively fished independently (i.e. harvest stocks) and historical data can be parsed to the appropriate unit, a revision of the existing stock boundaries may be the most appropriate and practical approach (e.g. redfish, case study Vb). However, many populations or fisheries may be too complex to be spatially delineated at the population-scale (e.g. fisheries targeting mixed stocks). In these instances, monitoring of the spatial and temporal population structure is recommended (Smedbol and Stephenson, 2001).

Practical considerations

Practical limits to the scale of assessment and management should be considered in scoping alternative approaches to address biological structure of fishery resources. Before incorporating additional complexity into the fisheries management system, the practical costs and anticipated benefits must be evaluated. For instance, does incorporating additional layers of complexity reduce uncertainty and increase sustainability (Cochrane, 1999)? Inclusion of stakeholders input at this stage can be extremely useful in identifying practical management solutions based on their knowledge of the fishery and the needs of management and industry (Trenkel *et al.*, 2015).

Limitations to the scale of stock assessment are typically determined by the spatiotemporal scale at which data are collected. However, there are also fundamental limitations to the dynamics that can be represented by models (e.g. transitory dynamics may not be predictable). Thus, the answer to the question of what scale of biocomplexity should be preserved depends on characteristics of the species (including the spatial and temporal aspects of spawning components, populations, and metapopulations), consideration of the scale at which we can practically assess and manage the species, and the socioeconomic considerations identified by various stakeholders (McBride, 2014). Ultimately, MSE can be a valuable tool to inform the optimal scale of biocomplexity preservation, while also weighing social and economic goals.

Management of migratory populations that cross or straddle several management units adds another dimension of complexity to resolving the appropriate scale of fisheries management (Kritzer and Liu, 2014). Monitoring migratory species is a difficult, and oftentimes costly, task that may require internationally coordinated efforts, while the identification of population structure for these species is often at the limit of fisheries science. Due to uncertainty about the structure and movement of pelagic fish, such as blue whiting *Micromesistius poutassou* or mackerel *Scomber scombrus*, changes in distribution patterns are sometimes seen by fishermen and 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; Nye *et al.*, 2009; Pointin and Payne, 2014).

Changes in fish distributions due to climate change can pose problems for designing short and long-term management frameworks and sampling programs (Nye *et al.*, 2009; Pinsky *et al.*, 2013; Kleisner *et al.*, 2016), because spatial habitat utilization may eventually extend outside the jurisdiction of the managing authority (e.g., northeast Atlantic mackerel; ICES, 2011). The potential for concurrent changes in the distribution and quality of habitats due to directional environmental changes can also influence fish distributions and potentially impact population structure (Shackell *et al.*, 2014; Kritzer *et al.*, 2016). A shift in population distribution may also result in a change in fishery dynamics (e.g. components of the stock may be harvested by new or different fishing fleets), complicating the stock assessment along with the determination of management targets. Furthermore, the environment fish encounter in new areas may affect life-history parameters, resulting in different population dynamics all together.

Quantitative evaluation of alternative assessment and management approaches

Developing spatially-explicit operating models that incorporate population structure and movement can provide a basis for determining how ignoring spatial structure may detrimentally impact the entire resource and fishery (e.g. by comparing assessment and management frameworks that utilize different assumptions about population structure and mixing; Kerr and Goethel, 2014; Goethel *et al.*, 2016). Thus, the output provided by simulation models can be an invaluable tool for management bodies, providing additional information regarding the short-term and long-term consequences of their choices on the resource. Key steps in the development of MSE for evaluating the implications of mismatches between biological and stock structure include (Kerr and Goethel, 2014):

(i) Development of operating models that represent the leading hypotheses of population structure of the fishery resource
(ii) Simulation of alternative management strategies
    (a) Generation of data from operating models and application of stock assessment methods
    (b) Application of alternate management strategies that integrate information on population structure
    (c) Projection of the operating model given the advice from management strategies on allowable catch
    (d) Repeat steps (i)–(iii) for a fixed projection period
(iii) Evaluation of performance of alternative management strategies against performance criteria (including biological, economic, and social objectives).

MSE is a powerful tool for developing fishery policy and strategic advice, but can be time consuming to develop and validate (Bunnefeld *et al.*, 2011). Ideally, all decisions would be tested using MSE to determine the best alternative. However, most management decisions must be made on short-term time horizons, especially in cases of conserving minority components of a stock complex. Therefore, interim measures (e.g. localized spatial management) may be required when MSE cannot be developed in a timely fashion.

Conclusions: synthesis of lessons learned

Our synthesis of the six case studies from the North Atlantic indicates that management bodies are becoming more aware of the importance of spatial structure and connectivity, and that proactive solutions are critical for the preservation of the natural stability and resilience of fish species. Ultimately, when spatial structure is identified, stock identification methods should be applied to help understand the existing biocomplexity (Cadrin *et al.*, 2014b). Management should take a proactive role in synthesizing the best available stock identification information and apply this knowledge to determine potential mismatches between biological and management structure. The degree of spatial isolation or overlap between populations and harvest stocks are important determinants of the appropriate strategy. Ideally, alternative approaches to resolve this mismatch should be identified and evaluated through MSE with biological, economic, and social trade-offs examined with stakeholders.

The prevalence of incongruities between biological and management units can be attributed in part to strong institutional inertia to maintain *status quo* management. However, given the importance of preserving biocomplexity, *status quo* management can range from sub-optimal to detrimental with respect to the impact on the resource. In the past, legal mandate or political pressure was often required to adjust stock boundaries. Our review indicates that recognition of the need for proactive rather than reactive management is becoming more widespread, especially when it involves the protection of unique spawning populations. However, regardless of the amount of monitoring that is undertaken, it is not possible to develop perfect stock boundaries, especially given the impacts of climate change on species distribution.

In the marine realm, most species exhibit some level of complex spatial structure, but not all aspects of population structure are necessary to incorporate into assessment and management (e.g. movement among stock units did not greatly alter perception of stock status for a metapopulation of yellowtail flounder; Goethel *et al.*, 2015a). However, our review suggests that in order to maintain sustainable fisheries, it is necessary for management agencies to be able to rapidly develop and apply adaptive spatial management, which can account for population structure to the extent practicable. Although impossible to develop generalized and prescriptive adaptive management guidelines, the critical element is for management bodies to remain flexible in order to protect biocomplexity (e.g. spawning components) when new information becomes available, and, ultimately, to not be limited by the comparatively slow refinement of stock boundaries and quantitative assessment techniques.

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