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Steven X. Cadrin

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Steven X. Cadrin

University of Massachusetts Dartmouth, School for Marine Science and Technology, Department of Fisheries Oceanography, 836 South Rodney French Boulevard, New Bedford MA 02744 USA

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ABSTRACT

In principle, the spatial extent of fishery stock assessment should reflect the biological population, and major fishing patterns or population heterogeneity within the area should be represented. However, these theoretical requirements are commonly dismissed in practice, often when there is compelling evidence that spatial scope and structure is mis-specified and without testing if the mis-specified model performs well for informing fishery management. Population dynamics theory, case studies in fishery management as well as simulation tests demonstrate that accurately accounting for spatial structure in stock assessments can improve model performance, and ignoring spatial structure can lead to misperceptions of stock status and failures in fisheries management. Therefore, the development of stock assessment applications should include an evaluation of the most appropriate spatial scope and structure. Some common challenges in defining and modeling spatial structure can be addressed by adopting general best practices, but each species and its fisheries are unique. Accordingly, determining the most appropriate spatial structure involves 1) an interdisciplinary synthesis of all available information to determine the most plausible paradigms of population structure and fishing patterns, 2) the development of spatial operating models that are conditioned on these paradigms, and 3) testing the performance of estimation models and management strategies that are based on the current spatial management unit as well as alternative spatial scopes and structures that reflect population structure and fishing patterns.

1. Introduction

Many fishery management units are spatially defined by geographic jurisdiction or fishing grounds, but conventional stock assessment models assume that the fishery resource is a single, homogeneous population. Despite some successes in refining assessment and management units to match population structure (e.g., Kerr et al., 2017b), compelling evidence of mis-specified stock structure is often dismissed because of practicalities, perception that it is not important, or convenience (Orensanz et al., 1998; Schindler et al., 2010; Cadrin et al., 2014b). Appropriate spatial structure should be recognized as an important component of model development and as part of the process to advance assessments toward 'next generation' methods (e.g., Lynch et al., 2018; CAPAM, 2019), particularly when attempting a spatially-structured stock assessment (Kumar et al., 2019; Maunder et al., 2019).

In principle, identifying appropriate management units and persistent spatial patterns within them is essential for achieving fishery management objectives (e.g., Wilson et al., 1999; Martien et al., 2013). However, in practice, stock assessments are applied to a wide range of fishery management units, from species complexes to local harvest stocks (Fig. 1), usually assuming that each management unit can be adequately modeled as a single biological population. In such situations, the accuracy of stock assessment and effectiveness toward meeting fishery management objectives may be improved by better representation of the spatial scope and structure in the assessment model.

The complexities of marine populations present many challenges for defining population structure, but a variety of tools have been developed for stock identification, and a convention has developed for piecing the puzzle together to accurately represent major patterns of population structure in stock assessment models. This review of theoretical principles, example case studies in fishery management and simulation-estimation testing is intended to demonstrate that accurate representation of population structure and fishing patterns is important enough to warrant consideration in routine development of stock assessment applications. Stock identification methods are also reviewed, including best practices for determining the appropriate spatial extent and structure of stock assessment.

2. Terminology and theory

Spatial boundaries among and within populations can be difficult to define because biology is messy (Tawfik, 2010). The species concept is a theoretical foundation of biology, but identifying species in a biological community can be a ‘fuzzy art’ (Zachos, 2016; Milius, 2017). Similarly,

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E-mail address: scadrin@umassd.edu.

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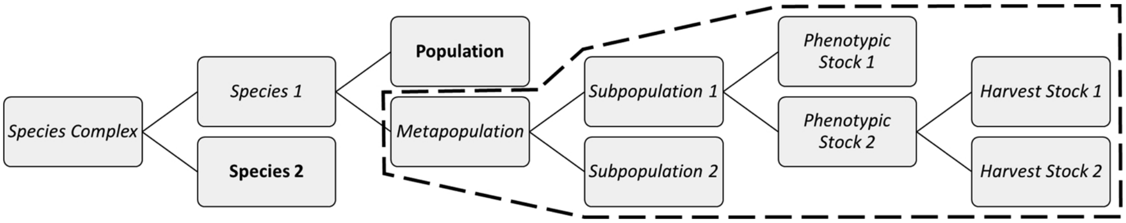

Fig. 1. The range of fishery management units (boxes), expressed as tiers of biological organization (adapted from Cadrin, 2006). In principle, the management units in bold are most suitable for conventional stock assessment applications, and those encompassed by the dashed polygon are suitable for spatially-structured assessments. Applications of stock assessment models to management units labeled in italics violate model assumptions and should be simulation tested to confirm that they adequately meet the needs of the management system.

Table 1
Common terms applied to spatial structure for stock assessment with precise definitions.

Term	Definition	Source
species	a group of individuals that actually or potentially interbreeds	Zachos, 2016; Milius, 2017
population	a group of interbreeding individuals that exist together in time and space	Hedrick, 2000; Waples and Gaggiotti, 2006
metapopulation	a system of interacting biological populations, termed subpopulations, that exhibit a degree of independence in local population dynamics as well as connectivity between subpopulations	Cadrin et al., 2014b
stock	biological population or metapopulation, a portion of a population, or multiple populations	Cadrin et al., 2014b
phenotypic stock	characteristics which are expressed in one or more ways depending on the type of environment	Booke, 1981
harvest stock	local group of fish that has an independent response to fishing, regardless of genetic or phenotypic similarities to adjacent resources	Gauldie, 1988

the stock concept is essential for fishery stock assessment, but defining stock structure can be difficult (Booke, 1981; Carvalho and Hauser, 1994). Unfortunately, the stock assessment literature is also somewhat messy, and terminology for population structure, stock identification, stock structure, mixed stocks, and spatial structure is inconsistent, perhaps as a reflection of the underlying complexity of spatial population structure. Consistent use of more precise and consistent terminology will help to confront the spatial complexity of populations for fishery stock assessment (e.g., Table 1).

The term ‘population’ can be defined from an evolutionary paradigm as “a group of interbreeding individuals that exist together in time and space” (Hedrick, 2000; Waples and Gaggiotti, 2006), and this definition is particularly appropriate for stock assessment or reference point models that assume a stock-recruit relationship. A metapopulation is defined as “a system of interacting biological populations, termed subpopulations, that exhibit a degree of independence in local population dynamics as well as connectivity between subpopulations” (Cadrin et al., 2014b).

The term ‘stock’ is used more loosely and can refer to a biological population or metapopulation, a portion of a population, or multiple populations (Cadrin et al., 2014b). Within a population, a ‘phenotypic stock’ maintains “characteristics which are expressed in one or more ways depending on the type of environment” (Booke, 1981). Alternatively, a ‘harvest stock,’ is a local group of fish that has an independent response to fishing, regardless of genetic or phenotypic similarities to adjacent resources (Gauldie, 1988).

Conventional stock assessment models make three related assumptions about spatial scope and structure: the population is closed, homogeneous, and well-mixed. Russell’s (1931) conceptualization of sustainable yield as a function of biological productivity, and his definition of overfishing as yield greater than a biological population’s productivity, implicitly assume a closed population, because those definitions assumed no immigration or emigration. The ‘unit stock’ conceived by Russell (1931) is implicitly assumed to be a reproductively isolated population that is demographically independent from other populations of the same species, and young fish in the population are assumed to be entirely spawned from adults in the same population. Isolated populations are expected to exhibit demographic independence, with different trajectories of stock, recruitment, mortality, and age composition (i.e., the population parameters estimated by stock assessment). By extension, partially isolated populations have varying degrees of demographic independence.

An important aspect of the closed population assumption is the approach used to model recruitment for stock assessment and fishery management (e.g., Cadrin et al., 2019). Models that assume a stock-recruitment relationship (e.g., Beverton and Holt, 1957) imply that all recruits in a spatial management unit are produced by spawners in the same management unit (usually with some process error that could account for loses or subsidies to and from adjacent areas), and recruitment in any area within the unit is a function of the total adult population. Recruitment subsidies from outside the management unit are rarely identified and accounted for in stock assessment or fishery management (e.g., Fogarty, 1998). Some stock assessment models do not assume a stock-recruitment relationship and can effectively monitor post-recruit production. However, harvest control rules or management reference points that are based on conserving spawning potential (e.g., Gabriel et al., 1989) are justified by the implicit assumption that depleted spawning stocks will have negative recruitment consequences. Therefore, understanding the source of recruitment is essential for informative stock assessment and successful fishery management.

Stock assessment models also typically assume homogeneous vital rates for all members of an age, length, or sex class; forming a ‘dynamic pool’ (Beverton and Holt, 1957). For example, size at age is either modeled using a single growth function or empirically based on unimodal sample statistics. Mortality is modeled as the sum of constant natural mortality and fishing mortality rates that apply to all members of a demographic class during a time interval. If fishing effort is distributed relatively evenly across the population, it can produce similar age and size distributions throughout the stock, but spatial fishing patterns violate the assumed homogeneous fishing mortality rates (e.g., Hart, 2001). Reproductive potential is modeled as a single maturity or fecundity function. Therefore, the dynamic pool assumption is inconsistent with heterogeneous vital rates (growth, survival and reproduction) within the stock area.

Thirdly, the conventional estimation of abundance from a time series of fishery catch, indices of abundance, and size or age composition assumes a well-mixed population. Similar to many mark-recapture and tag-recovery models that assume complete mixing of newly tagged fish with previously tagged and untagged fish in the population within a time interval (Hoenig et al., 1998), many fishery stock assessment models implicitly assume that fishery removals from one area in a time interval affect the density of the entire population during the interval. For example, abundance indices sampled during the interval are assumed to reflect population-wide trends that are responsive to fishery removals. Spatial sampling strata or spatial standardization can limit the mixing assumption to within strata for some population processes if the entire population area is sampled (e.g., Walters, 2003; Campbell, 2004; Shelton et al., 2014; Cao et al., 2016; Thorson et al., 2017). Mixing tends to homogenize populations, so the homogeneity and mixing assumptions are related. However, many populations maintain homogenous vital rates even when there is negligible post-settlement mixing (e.g., shellfish). The distinction between mixing and homogeneity assumptions is important for defining population structure, because tagging or larval dispersal can inform mixing, and geographic variation tests the homogeneity assumption.

Based on these typical assumptions, the management unit that is ideally suited for conventional stock assessment models is an entire species distribution or an entire distinct and self-sustaining population with no connectivity to other populations, with no spatial heterogeneity, free mixing, and random mating (e.g., the bold boxes in Fig. 1). Contrary to those assumptions, all populations and all fisheries have some spatial structure with mixing patterns (Cope and Punt, 2011), and many populations have some connectivity with adjacent populations (Ciannelli et al., 2013). In the practice of stock assessment and fishery management, some single populations contribute to multiple management units, and some management units include multiple distinct populations (e.g., Smedbol and Stephenson, 2001; Reiss et al., 2009) or even multiple species (Fig. 1). Many fishery management units include multiple distinct spawning groups defined by spawning areas (e.g., Fromentin and Powers, 2005), spawning seasons (e.g., Zemeckis et al., 2014), or both (e.g., Clausen et al., 2007). Different populations can have spatially overlapping feeding areas or nursery areas (e.g., Saha et al., 2016). Some stocks are well defined by geographic features (e.g., estuaries, bathymetry, ocean basins), but others are more defined by three-dimensional habitat (e.g., Cadrin et al., 2010). The trend toward changing thermal environments and shifting distributions complicates the determination of boundaries between biological populations (e.g., Perry et al., 2005; Link et al., 2010).

Another complication for representing spatial scope and structure in a stock assessment is that the most appropriate structure may be different for meeting each of these theoretical assumptions for some species and fisheries. For example, a reproductively isolated population assumed for stock-recruit modeling may inhabit a large area, but spatial components of that population may have different vital rates or fishing patterns. Therefore, conventional stock assessment assumes that the stock assessment area encompasses a biological population, and fishing patterns or population heterogeneity within the area are represented in the assessment. Although these assumptions of stock assessment models are often dismissed, the exploitation and management histories of several fisheries as well as simulation studies demonstrate their importance.

3. Fishery case studies

Several case studies demonstrate that recognizing and conserving spatial population structure can support productive fisheries (e.g., Hilborn et al., 2003). Conversely, ignoring population structure in stock assessment and fishery management can unintentionally allow overfishing and severe depletion of spatial components, stock collapse, or failure to rebuild (e.g., Berkeley et al., 2004; Ciannelli et al., 2013). When the management unit is not aligned with the population's distribution, perceptions of stock trends can be misleading, often failing to detect declines in some populations (Link et al., 2010). Many fisheries examples demonstrate the importance of defining spatial structure and reflecting that structure in stock assessment.

Mis-specification of spatial structure played an important role in the decline of crab and shrimp fisheries in the Gulf of Alaska. Orensanz et al. (1998) concluded that these crab and shrimp resources were overfished because fisheries sequentially expanded to new areas and produced serial depletions, leading to an overestimation of productivity by conventional stock assessments. For example, recruitment of Kodiak red king crab appeared to be strong in the 1960s, but that perspective was an artefact of the spatial expansion of fishing facilitated by larger vessels (Rothschild et al., 1970). A similar pattern of spatially expanding fisheries and local depletion was observed for Dungeness crab in southeast Alaska (Koeneman, 1985). Orensanz et al. (1998) warned that mis-matches between the geographic scale of the population and the assessment, spatial patterns in fishing, and assuming a dynamic pool for a spatially heterogeneous resource can lead to a myopic view of productivity. Although these patterns were observed for relatively immobile invertebrates, similar changes in the spatial distribution of fishing on patchy distributions of highly migratory fish was a challenge for assessment of the southern bluefin tuna (e.g., Campbell, 2004).

The collapse of the 'northern cod' fishery in the early 1990s offers an example in which recruitment overfishing occurred despite a productive resource with superlative fecundity, a relatively data-rich stock assessment, and a relatively comprehensive fishery management system (Walters and Maguire, 1996). Although several factors contributed to the collapse of the northern cod fishery, the mismatch between the spatial management unit and population structure played a central role in the unintentional overfishing in the 1980s (Hutchings, 1996; Smedbol and Stephenson, 2001; Lilly, 2008). The Atlantic cod resource off Newfoundland and Labrador (NAFO divisions 2 J, 3 K and 3 L) is a single management unit, but there are separate inshore and offshore populations, as evidenced by egg and larval distributions, spawning times, dispersal patterns, genetics, growth rates, number of vertebrae and parasites (Ruzzante et al., 1996). In the 1980's, increasing catch rates from the inshore fishery provided a misleading index of abundance for the entire management unit, because the offshore population declined, and the winter distribution of cod shifted southward in response to changing environmental conditions (Rose and Kulka, 1999). The assumption of homogeneous rates of growth and reproduction throughout the management unit also contributed to overestimating productivity of the resource (Morgan and Brattey, 2005). Similar patterns of population structure, misperceptions of stock status, and depletion of spatial components have been observed for Atlantic cod fisheries in the North Sea (e.g., Hutchinson, 2008), on Scotian Shelf (Smedbol and Stephenson, 2001), and off New England (Zemeckis et al., 2014).

Atlantic herring is a population rich species (i.e., there are many populations within the species; Sinclair, 1988), but several fisheries collapsed from the depletion of local spawning areas (Smedbol and Stephenson, 2001). For example, relatively small spawning components in the Gulf of Maine, Bay of Fundy and off southwest Nova Scotia were 'progressively eroded', because they were initially considered too small to be explicitly accounted for in stock assessments (Stephenson et al., 2001). A similar scenario occurred for North Sea herring (Dickey-Collas et al., 2010). Based on these lessons, some spawning components of Atlantic herring are now monitored and catch is allocated by relative abundance (Stephenson et al., 2001; Dickey-Collas et al., 2010), and conservation of spawning groups helped to rebuild Norwegian spring spawning herring (Ciannelli et al., 2013).

In a review of Pacific groundfish, Berkeley et al. (2004) concluded that conventional stock assessments of spatially-structured populations could not detect overfishing and depletion of reproductively isolated populations within the management unit. Such spatial complexity is a challenge for stock assessment, but if spatial structure is recognized and conserved it can also confer resilience and productivity (Smedbol and Stephenson, 2001; Hilborn et al., 2003; Schindler et al., 2010). For example, conserving complex population structure played an important role in managing the sustained productivity of Bristol Bay sockeye fisheries (Hilborn et al., 2003), and such sustained production contrasts with many depleted salmon fisheries that did not effectively conserve populations (Schindler et al., 2010). Therefore, reflecting spatial population structure in stock assessments promotes conservation of spatial population components and management of sustainable and productive fisheries.

4. Simulation case studies

Fishery case studies are instructive, but successes and failures in assessment and management usually result from several factors. Population simulation is a valuable tool for understanding population dynamics and for testing outcomes of controlled scenarios. For example, similar to the lessons demonstrated by Bristol Bay sockeye salmon, Kerr et al. (2010) found that population structure conferred stability, resilience, and productivity from simulations conditioned on white perch. Guan et al. (2013) also concluded that population structure and connectivity increased the productivity and stability from simulations conditioned on Atlantic cod.

Simulations have been used to evaluate the performance of stock assessment models for recovering population trends from a spatially-structured operating model (e.g., Kerr and Goethel, 2014; Berger et al., 2017; Punt, 2017). In some cases, spatially-simple stock assessments performed relatively well for scenarios conditioned to represent Atlantic bluefin tuna (Porch et al., 1998), Atlantic cod (Cao et al., 2014; Jardim et al., 2018), yellowtail flounder (Goethel et al., 2015), Pacific herring (Benson et al., 2015), and sardine (Jardim et al., 2018). However, in other simulated scenarios of spatial heterogeneity or metapopulations, conventional stock assessment models (i.e., with no spatial structure) could not reliably estimate abundance or mortality of spatially-complex populations, and accuracy of spatially-structured assessments depended on accurate specification of spatial structure. Several simulation studies evaluated the effect of spatial heterogeneity on stock assessment models. Cope and Punt (2011) found that conventional stock assessments performed poorly when applied to a Cabezon-like population with spatial patterns in exploitation history. Similarly, Fay et al. (2011) showed that mortality estimates from catch curves were sensitive to spatial fishing patterns from an operating model conditioned on blue eye trevalla. Fisheries managed by area closures impose spatial heterogeneity in fishing mortality, and simulations from generic operating models suggest that the accuracy of conventional stock assessments depends on the size of area closures (Pincin and Wilberg, 2012) and movement rates (McGilliard et al., 2015). Conventional stock assessments produced significantly biased estimates when applied to an operating model of pink ling fisheries with spatial heterogeneity in fishing mortality, growth, and recruitment (Punt et al., 2015). Truesdell et al. (2017) reported that conventional reference point models produced biased estimates based on an operating model of Atlantic sea scallop with spatial fishing patterns.

Simulation has also been used to evaluate the effect of metapopulations and mixing patterns on stock assessment. Porch et al. (1998) simulated eastern and western Atlantic bluefin tuna with separate spawning populations and found that spatially-structured stock assessment models performed better for estimating abundance than two separate stock assessments of eastern and western Atlantic fisheries when movement rates among areas were assumed to be relatively high. Carruthers et al. (2011) found that population estimates from conventional assessment models are biased and lead to overexploitation of some areas using an operating model conditioned on Atlantic tunas and billfish. Ying et al. (2011) tested the performance of stock assessments using an operating model to represent three connected subpopulations of small yellow croaker and observed that assessing and managing each subpopulation as a unit led to overfishing and managing the metapopulation as a unit stock often led to local depletion. Carruthers et al. (2015) found that conventional stock assessment produced biased estimates of maximum sustainable yield from an operating model conditioned on spatially-structured populations of red and gag grouper. Three separate-area stock assessments did not perform well for estimating a dominant year class when applied to pseudo-data from a yellowtail flounder metapopulation, with unique stock-recruitment relationships and post-recruit movement among subpopulations (Goethel et al., 2015). A conventional assessment model did not perform well for estimating abundance from an operating model of black sea bass that had a single stock-recruitment relationship, but spatial structure of post-recruits (Fay and Cadrin, 2016). Jardim et al. (2018) found that when heterogeneity and connectivity among sub-populations is high, separate assessment of subpopulations are not accurate. Punt et al. (2018) developed an operating model to represent Pacific herring with a single stock-recruitment relationship and post-recruitment dispersal to ten areas and found that conventional single-stock assessments produced biased stock estimates. These simulation studies demonstrate that accurate representation of spatial scope and structure is needed in many situations, and the performance of conventional stock assessment models can be simulation tested using spatially-structured operating models.

5. Best practices for considering spatial structure in stock assessment

Some common challenges in defining spatial structure for stock assessment can be addressed by adopting general best practices (Table 2), but some of these practices are not feasible for some fisheries, and more specific guidance depends on features of the resource and the fishery. Best practices refer to the spatial extent of stock assessment to sufficiently represent a closed population (i.e., the bold boxes in Fig. 1) and spatial structure of an assessment that reflects major patterns of biological heterogeneity or fishing patterns (e.g., the boxes encompassed by the dashed polygon in Fig. 1). Best practices also include diagnostics for testing assumptions and options for stock assessment when spatial assumptions are violated (Table 2).

Exploratory stock identification can detect patterns of spatial heterogeneity, and spatial patterns that are significant and persistent should be considered in stock assessment. For some discriminating features (e.g., morphometrics, otolith chemistry, parasites), extrinsic classification accuracy of known groups significantly greater than random assignment may be more meaningful than significantly different means. Temporal stability of spatial differences should be tested over multiple years and ideally over the entire assessment time period.

Sampling designs for fishery data and fishery-independent data should be spatially explicit to explore spatial patterns in data, support a spatially-structured stock assessment, or spatially-stratified estimation of catch, size or age composition, and relative abundance indices. Including all fished and unfished resource areas in sampling designs

Table 2
General best practices for defining spatial structure in stock assessment.

- Spatial Extent of Stock Assessment
  - Include the entire species range
  - Include the entire habitat area of a discrete portion of the species range
- Spatial Structure in Stock Assessment
  - Include all areas in standardization of stock indices
  - Consider geographic, bathymetric or oceanographic boundaries for spatial strata
  - Consider ecological boundaries for spatial strata
  - Consider discrete fishing grounds for spatial strata
  - Consider areas with significantly different vital rates for spatial strata
- Diagnostics
  - Examine synchrony of resource and fishery trends in the assessment area with those from adjacent areas
  - Monitor spatial population components within the assessment area
- Violated Assumptions
  - Identify and communicate violation of model assumptions
  - Adopt spatially-explicit sampling designs and stratified estimates for inputs to assessment models
  - Account for spatial fishing patterns with flexible fishery selectivity assumptions
  - Test performance of mis-specified assessment model
  - Describe stock and fishery trends for each spatial population component
  - Recommend consideration of precautionary management targets
  - Recommend consideration of management strategies to conserve population components

and post-hoc standardization of stock indices helps to account for some spatial heterogeneities (e.g., Walters, 2003; Campbell, 2004; Shelton et al., 2014; Cao et al., 2016; Thorson et al., 2017), but cannot account for complex interactions between heterogeneous vital rates, fishing patterns and movement. Stock index standardizations are sensitive to the spatial extent and strata used (e.g., Tian et al., 2009), so information on stock structure is also important for that aspect of stock assessment.

When general best practices are not feasible, violations of the unit stock, dynamic pool and well-mixed population assumptions should be recognized, and the implications of violated assumptions should be evaluated. For example, resource and population trends within the assessment area should be compared to those in adjacent areas to test for synchronous trends and mixing. Violated assumptions should be identified as a source of uncertainty to be considered in fishery management. For example, Ying et al. (2011) suggest that precautionary management targets should be considered to avoid depletion of components. If stock assessments are not spatially-structured, they should allow for the dome-shaped fishery selectivity (i.e., the oldest or largest fish are not fully vulnerable to the fishery) that is expected from spatial fishing patterns (Sampson and Scott, 2011; Sampson, 2014). Conventional stock assessments can also be supplemented by monitoring population components (e.g., Stephenson et al., 2001; Dickey-Collas et al., 2010), using stock composition sampling for mixed-population fisheries (e.g., Kerr et al., 2019), and fishery management can include procedures to conserve population components, such as spatial catch allocation (e.g., Bosley et al., 2019), reproductive refugia (e.g., Orensanz et al., 1998) or spawning closures (e.g., Zemeckis et al., 2014).

Beyond these general practices, determining the most appropriate spatial extent and structure of stock assessment for each fishery involves 1) an interdisciplinary synthesis of all available information to determine the most plausible paradigms of population structure and fishing patterns, 2) the development of spatial operating models that are conditioned on these paradigms, and 3) testing performance of estimation models and management strategies that are based on the current management unit as well as alternative spatial structures that reflect population structure and fishing patterns.

5.1. Stock identification methods

Spatial patterns are often complex and difficult to define, but a wide range of methods are available for stock identification, from spatial analysis of conventional fishery data to sampling for genetic stock composition. Information from multiple approaches provides a more holistic perspective (Begg and Waldman, 1999), and multi-disciplinary analyses have been developed to simultaneously analyze data from different disciplines (e.g., Brodziak, 2005). However, common challenges for stock identification include apparent contradictions of information from different disciplines and politicized debates about trans-jurisdictional stock delineation. Therefore, recognizing the complementary perspective offered from each discipline is needed to reconcile apparent contradictions (Table 3). Applying best practices in each discipline helps to minimize sampling error or estimation bias, and interdisciplinary synthesis is essential for objective determination of spatial structure for stock assessment. Best practices within disciplines and for interdisciplinary analysis have been developed (e.g., Cadrin et al., 2005, 2014a) and are routinely updated and refined by the International Council for the Exploration of the Seas, Stock Identification Methods Working Group (e.g., ICES, 2018).

5.1.1. Spatial distribution

A species' spatial extent can reveal discontinuities or natural barriers that define putative stocks. Spatial distributions are often density-dependent (MacCall, 1990; Reuchlin-Hugenholtz et al., 2015), so historical distributions can be informative for stock identification of depleted populations. Even if the resource of interest is a discrete portion of the species range, recognizing spatial patterns and processes in other areas can provide valuable context for identifying spatial structure within the area of interest. For example, the local inshore and offshore populations found for 'northern cod' (Ruzzante et al., 1996) are also observed throughout their geographic range (Pampoulie et al., 2006, 2011; Westgaard and Fevolden, 2007; Hutchinson, 2008; Ciannelli et al., 2013; Zemeckis et al., 2014).

Fishing grounds and spatiotemporal patterns in fishery data can suggest putative stocks. Carl Walters contended that long-term fisheries successes result from a 'spatial accident' in which the spatial management unit serendipitously matched the population unit (Orensanz et al., 1998). However, considering that fisheries target persistent resource densities or aggregations, and many management units are defined by fishing grounds, frequent matches may not be entirely accidental. Many fisheries now have high-resolution catch reporting, but the spatial resolution of historical fishery data often constrains the resolution for defining stocks and spatial structure in stock assessment. At the lowest resolution, ocean basins and major fishing areas can be used to define stocks (FAO, 2004). Fishery reporting areas within regional fishery management organizations offer intermediate spatial resolution, and geographic strata for national catch reporting offer greater resolution for defining fishing grounds or putative stocks (e.g., Halliday and Pinhorn, 1990). Defining fleets by area and season can be helpful for understanding which spatial components of the population are vulnerable to which fleets and if fleet monitoring data can represent discrete population components. Fishermen's Ecological Knowledge can be valuable for mapping spatial distributions. For example, historical and current spawning grounds of Atlantic cod have been delineated through fishermen interviews (Ames, 2004; DeCelles et al., 2017)

Fishery-independent data can provide high-resolution spatial information on spatial distribution that is not constrained by fishing patterns or fishery regulations. Mapping the seasonal distributions of early life stages (e.g., eggs and larvae from ichthyoplankton surveys), juveniles (e.g., from recruitment surveys) and spawning or non-spawning adults (from fishery monitoring or fishery-independent surveys) can reveal aspects of stock structure such as seasonal movement patterns, spawning grounds, nursery grounds, and feeding grounds (e.g., Pawson and Jennings, 1996; Begg, 2005; Planque et al., 2013). Similar to the utility of defining fishing fleets by area and season, documenting the seasonality and spatial extent of resource surveys helps to identify which population components they represent. Spatial density of survey observations is much less than that from fishery data, and some species are rarely caught in surveys, so pooling observations by time periods (e.g., decades) is often needed to infer temporally stable spatial distributions. Spatial interpolation based on habitat factors can improve inferences of distributions by filling gaps in fishery data or survey data (e.g., Shackell et al., 2016), and cross-validation suggests that such approaches can be informative. By extension, spatial population structure often reflects ecosystem boundaries. For example, the spatial structure of yellowfin tuna in the Indian Ocean reflects Longhurst biogeographical regions (Langley, 2015; Langley, 2019). Although distributional information is not definitive for identifying spatial structure of populations or fisheries, and some interpolation may be needed in data-limited situations (e.g., multi-year data pooling, habitat-based predictions), investigating all available information on spatial distribution provides valuable context for stock identification.

5.1.2. Dispersal patterns

Connectivity is the exchange of individuals among populations (Cowen and Sponaugle, 2009), and dispersal among populations can occur at any life stage. Connectivity can involve reproductive mixing, in which adults spawned in one area contribute to reproduction in another area (termed 'diffusion', Porch et al., 2001; or genetic interchange, Hawkins et al., 2016), or seasonal mixing of reproductive isolated populations (e.g., termed 'overlap' or ecological connectivity, often involving spawning site fidelity or natal homing). The degree and nature of connectivity among discontinuous distributions determines

Table 3
Information available for stock identification and relationships to spatial population structure.

	Information	Population Inference
Distribution	fishery data	spatial and seasonal fishing patterns by fleet; spawning, feeding and nursery areas
	fishery-independent surveys	distribution at early, juvenile and adult life stages
Dispersal	early life stage dispersal	connectivity of spawning and nursery areas
	conventional tags	movement patterns or rates
	archival tags	individual movement trajectories
	active telemetry	individual movement trajectories
	passive telemetry	movement patterns and spawning dynamics
Geographic Variation	selected genetic characters	reproductive isolation or local adaptation
	neutral genetic characters	reproductive isolation
	life history traits	limited mixing and possibly reproductive isolation or local adaptation
	morphology	limited mixing and possibly reproductive isolation or local adaptation
	meristics	limited mixing at early life stages and possibly reproductive isolation or local adaptation
	natural tags	limited mixing and environmental history
	abundance trends	demographic independence
	size or age composition	demographic independence or fishery selectivity

demographic independence and reproductive isolation among areas (Hawkins et al., 2016).

Early life history dispersal patterns can determine self-sustaining areas or link spawning grounds to distant nursery areas (i.e., contranatant advection; Harden Jones, 1968). Sinclair (1988) hypothesized that the number of larval retention areas determines the number of populations within a species. Effective dispersal of pelagic eggs and larvae is a complex process involving hatching, larval feeding, growth and survival through successive developmental stages to settlement or recruitment to suitable nursery habitats (Hare and Richardson, 2014). Individual-based bio-physical models can suggest patterns of retention or effective dispersal as a function of oceanographic patterns, but many of the assumed behaviors, growth rates and survival rates are highly uncertain, so empirical validation and consideration of other information is needed for confirmation.

Dispersal of later life history stages can be informed from conventional tagging or telemetry. Patterns of release and recovery of fish with conventional tags can document major movement patterns, suggest relative magnitude of movement rates, and inform movement rates among areas through independent analysis of tagging data (e.g., Schwarz, 2014; Hanselman et al., 2015) or tag-integrated stock assessment modeling (e.g., Goethel et al., 2011, this volume; Maunder et al., 2019). The estimation of movement rates requires representative tag-recapture designs and ancillary studies to account for fishing patterns, tag shedding and reporting rates.

Conventional and electronic tags provide complementary information on dispersal. Information from electronic tags provides greater spatial resolution and less reliance on fishery recaptures, typically from fewer tag deployments because of cost, and often over a shorter period because of battery life. Active telemetry or geolocation of archival tag data can provide trajectories of individual fish (Galuardi and Lam, 2014). Passive acoustic or radio telemetry can be used to infer movement patterns, spawning site fidelity, residency in spawning areas, and connectivity among areas (DeCelles and Zemeckis, 2014). A synthesis of the available tagging information can be used to map ontogenetic movement patterns.

5.1.3. *Geographic variation*

Spatial patterns of demographic, genetic or phenotypic variability can indicate mixing or isolation of fish in different areas, because a well-mixed stock should be spatially homogeneous. Accordingly, the magnitude of geographic differences and their temporal stability reflect the degree of isolation or connectivity. Many measurable characters are available for analysis of geographic variation, from routine fishery sampling or ancillary studies, with the basis of variability ranging from purely environmental to entirely genetic (i.e., a heritability range of 0 to 100%). Therefore, each character informs a different aspect of connectivity and population structure.

5.1.3.1. Genetic variation. Genetic information provides the most definitive inference of reproductive isolation, but mutation rates and the vulnerability to natural selection vary widely among genetic characters. Therefore, the relative sensitivity and neutrality of each type of genetic marker needs to be considered to reconcile apparent contradictions among studies. Geographic variation in neutral genetic characters (i.e., those not subject to selection) indicate reproductive isolation, whereas geographic variation in functional genetic characters (i.e., those subject to selection) can indicate both isolation and adaptation to local environments (Mariani and Bekkevold, 2014). However, significant differences in neutral genetic characters indicate that the populations have been reproductively isolated for many generations, which is far longer than the ecological time scales that are relevant to stock assessment or fishery management (Waples and Gaggiotti, 2006). Therefore, populations that have been recently isolated on an evolutionary time scale may not exhibit genetic differences but may have demographic independence on ecological time scales.

Geographic variation in allozyme frequency formed the initial basis for the genetic stock concept in fisheries science (Berst and Simon, 1981), but they have been largely replaced by other genetic characters for stock identification. Allozymes are alternative forms of enzymes that are coded by different alleles at a genetic locus (Koljonen and Wilmot, 2005). The enzymes measured by allozymes are essential for cellular functions, so their frequency is subject to selective forces (e.g., many mutations are lethal), and allozyme variation is typically less than other genetic markers.

The earliest direct analysis of DNA for fishery stock identification involved mitochondrial DNA (mtDNA) because of its relatively simple molecular structure and size. Mitochondrial DNA is involved in cellular energy conversion, so it is subject to selection and has a low mutation rate (Antoniou and Magoulas, 2014). The simplicity of the mtDNA molecule confers a relatively constant mutation rate that can be used to approximate the recency of reproductive isolation. For example, mtDNA information suggests that the four Atlantic redfish species are relatively young on an evolutionary time scale, formed from North Pacific *Sebastes* ancestors that moved to the North Atlantic when Arctic waters warmed (Love et al., 2002), which explains their morphological similarities and frequent hybridization. Genetic divergence within Atlantic redfish species is even more recent (Cadrin et al., 2010). mtDNA is maternally inherited, so differences in mtDNA allelic frequency reflect reproductive isolation and selective forces in the female life cycle (including movement patterns, site fidelity, etc.), which can be different than male life cycles (e.g., Natoli et al., 2005).

Nuclear DNA (nDNA) is much more complex than mtDNA and provides a wide array of genetic markers for stock identification (Wirgin and Waldman, 2005; Mariani and Bekkevold, 2014). Microsatellites are small segments of repetitive DNA that are noncoding. All mutations in noncoding DNA survive, so variability in allelic frequencies and sensitivity for detecting genetic differences among groups of individuals is greater than for coding genetic characters. Single nucleotide polymorphisms (SNPs) provide a much larger set of characters, some with high variability (Wirgin and Waldman, 2005). The advancement of genomics, which involves hundreds to thousands of molecular markers to represent a large portion of the genome, has greatly expanded the number of characters available for stock identification (Mariani and Bekkevold, 2014). Genetic stock identification for some species has progressed from using a few markers to using thousands. Genomics has also improved the understanding of geographic variation in genetics. For example, some characters initially thought to be neutral (e.g., non-coding microsatellites) may be linked to coding regions, as detected by diagnostic statistical tests. As molecular methods have advanced and more variable genetic markers are developed with much greater sensitivity for detecting genetic differences among groups, genetic differences are being found within many coastal and oceanic species that were initially considered to be genetically homogeneous (Wirgin and Waldman, 2005).

5.1.3.2. Phenotypic variation. Life history and morphology are determined by both genetics and the environment, but temporally stable patterns of geographic variation in these phenotypic characters can be valuable for stock identification. For example, persistent patterns of geographic variation in size and maturity at age can delineate groups with limited mixing, regardless of the degree of heritability in those traits (e.g., Cadrin, 2010). Temporally stable patterns of life history variation are particularly relevant to determining spatial structure for stock assessment, because population dynamics models need to accurately represent these vital rates (Begg, 2005).

Geographic variation in morphology can be associated with differences in life histories. Circuli spacing patterns of fish otoliths or mollusk shells provide direct measures of growth patterns and can effectively detect differences in spawning seasons or growth rates (Brophy, 2014). General body morphology is often an indicator of growth rate, ontogenetic transition (e.g., maturation, diadromy), or eco-type (e.g., benthic vs. pelagic, resident vs. dispersive). Investigation of morphometric characters has advanced from multivariate analysis of traditional linear distances to geometric analysis of landmarks (e.g., truss networks or thin-plate splines of body shape) or outlines (e.g., mollusk shells or fish otoliths; Cadrin, 2000). Variation in meristics (i.e., morphological features that can be counted, like vertebrae, fin rays, gill rakers) are typically influenced by early-life history environments when the meristic features are developing. For example, vertebrae number is determined in the larval period and is inversely related to temperature for many fishes (Lindsey, 1988).

Other valuable features for stock identification such as parasites, otolith chemistry, and fatty acids are largely environmental covariates used as ‘natural tags’. Patterns of parasite infestations can indicate residence in areas of infection or spatial overlap with intermediate hosts (MacKenzie and Abaunza, 2014). Otolith chemistry (including major elements, minor elements, trace elements and isotopes) can indicate chemical environments for the entire lifespan from analysis of whole otoliths, from early life stages by analysis of the otolith core, or specific ontogenetic stages from material in each annulus (Kerr and Campana, 2014; Tanner et al., 2016). Differences in fatty acid profiles indicate different trophic patterns among groups and have been effective stock discriminators for several fishes and marine mammals (Grahl-Nielsen, 2014).

Heritability varies among and within these types of phenotypic traits. Heritability estimates are often greater than 30% for life history traits, range from 10% to 80% for morphometric traits, and range 40% to 90% for meristic characters (Swain et al., 2005). There is also some heritability of other natural markers, such as parasite resistance, chemical uptake into otoliths, and metabolism of fatty acids. Therefore, geographic variation in phenotypic characters can be interpreted as an indicator of incomplete mixing and possibly reproductive isolation or local adaptation.

5.1.3.3. Demographic variation. Similar trends in abundance among areas can reflect mixing, and different trends among areas may indicate isolation. Spatial structure has been defined by fishery landings (Campbell and Mohn, 1983), fishery catch rates (Lennert-Cody et al., 2013), fishery-independent surveys (Cadrin, 2010), or results from stock assessments of adjacent areas (Rothschild, 2007). For example, spatiotemporal patterns in surveys reflected recruitment synchrony of rockfish among areas (e.g., Field and Ralston, 2005).

Begg (2005) recognized that information on relative abundance and size/age composition are routinely collected to support stock assessment and are available for many fisheries for the investigation of stock structure. Differences in age or size composition can indicate geographic variation in recruitment or mortality. For example, Lennert-Cody et al. (2013) investigated spatial patterns in size of bigeye tuna to infer patterns of demographic independence or fishery selectivity among areas, both of which are informative for defining spatial structure for stock assessment.

5.1.4. Interdisciplinary stock identification

Information on distribution, dispersal and geographic variation from newly developed methods can be reconciled with previous information from more traditional methods to define spatial structure for stock assessment. Stock identification is an iterative process, in which each stage has different sampling designs and analytical approaches, and successive stages consider information from multiple disciplines (Table 4). The exploratory stage of stock identification should develop a synthetic population structure hypothesis that is consistent with all available multi-disciplinary information (Table 3).

Confirmatory analysis of geographic variation involves estimating the significance of differences among areas and recognizing the relative effect size of each approach (Abaunza et al., 2014). The most informative variables among the multiple disciplines in Table 3 are used for the latter stages of stock discrimination, delineation, and composition analyses. The integration of information can be facilitated by multidisciplinary sampling, in which data for each disciplinary analysis is sampled using the same spatiotemporal design (Abaunza et al., 2014).

Considering how different stock identification approaches inform complementary aspects of spatial population structure (Table 3), the synthesis of multidisciplinary information is usually conceptual and

Table 4
The successive stages of interdisciplinary stock identification (modified from Cadrin, 2000).

Stage	Objective	Sampling Design	Analytic Method
Exploratory Stock Identification	identify putative groups	all areas and seasons (multiple years)	ordination and cluster analysis of many variables for each discipline
Stock Discrimination	develop and test classification function	known-group (spawning) samples in each putative group, with sufficient replication (regularly updated)	discriminant analysis of baseline samples (and cross-validation) to identify discriminating variables and functions for each discipline
Stock Delineation	define stock boundaries	boundary areas (all seasons, multiple years)	classification analysis of selected variables from mixed-group samples for geographic analysis of scores
Stock Composition	estimate mixture	all mixed-stock areas and seasons, regularly	mixture analysis of selected variables from mixed-group samples

supported by geographic integration (e.g., Pita et al., 2016). In their chapter on Observing Fish Populations, Hilborn and Walters (1992) conclude that "Probably the most important rule is *know your data*… The second general rule when considering abundance is *spatial mapping*. If you don't do it, you only have yourself to blame when things go wrong." Booth (2000) offers tools to visualize spatial and demographic patterns of fishery monitoring and survey data for stock assessment. The same general practice applies to stock identification. Mapping the species' geographic range is an appropriate starting point for a stock identification investigation. Understanding where and when samples were collected for each investigation of stock structure and overlaying all spatial information on the map is a useful tool for integrating information on distribution, dispersal and geographic variation. The most plausible hypothesis of spatial structure (or multiple plausible scenarios) can be depicted geographically to design the latter stages of stock delineation and stock composition sampling.

The spatiotemporal overlap of populations in some mixed-stock fisheries requires routine stock composition sampling (Kerr et al., 2019). Sampling for stock composition can be integrated into fishery monitoring programs to estimate the catch of each component population in the mixture, using the same principles as sampling for species composition in data-limited species complexes or for sampling size and age composition. For example, North Pacific salmon fisheries are routinely sampled to determine catch of each salmon species and each intraspecific population in each fleet based on source population characteristics (e.g., Pella and Masuda, 2005; Ianelli and Stram, 2015; Beacham et al., 2016; Kang et al., 2016; McKinney et al., 2017).

Best practices within disciplines, appropriate interpretations, and integration among methods are most effectively achieved through a collaborative process, including experts in each discipline (Kerr et al., 2017b). Experts can review all available information within their discipline, and information can be conceptually integrated in a workshop or working group process. Interdisciplinary integration of information requires consideration of the unique perspective on population inferences from each methodological approach (Table 3), as well as the specific objectives, sampling designs and analyses of each contributing study. Such approaches have successfully met the challenging objectives of interdisciplinary stock identification for several fisheries (reviewed in Cadrin et al., 2014a; Kerr et al., 2017b) and are routinely being applied in several fishery management organizations (e.g., ICES, 2018; SEDAR, 2018).

5.2. Spatial simulation testing

Stock identification can delineate discrete populations, connectivity among areas, and patterns of spatial heterogeneity, but it cannot determine whether a stock assessment model is an adequate simplification of the complex reality to meet the needs of the fishery management system. Simulation-estimation testing is considered best practice for determining optimal model structure for stock assessment (e.g., Restrepo, 1998; Deroba et al., 2015), and determining the appropriate spatial scale and structure for stock assessment requires simulation testing with a relatively complex spatial operating model (Kerr and Goethel, 2014). Spatial operating models are used to generate pseudo-data that represent the quantity and quality of available data, and stock assessment models with different spatial structures are applied to the pseudo-data to determine which alternative model performs best for recovering true values from the operating model. For example, Martien et al. (2013) simulated a variety of population structure scenarios to determine the degree of reproductive isolation that justifies separate management units for meeting conservation goals of the International Whaling Commission.

Developing spatially-complex operating models that represent plausible scenarios of population and fisheries structure is a challenge. However, the objective for conditioning spatial operating models for simulation-estimation is to accurately represent stock dynamics and productivity (Kerr and Goethel, 2014), which is somewhat different than the objective of stock assessment: to precisely and accurately estimate current stock status and projections for informing fishery management. Models conditioned on generic populations and fisheries to represent typical features and dynamics can inform general best practices. For example, Jardim et al. (2018) simulated 'cod-like' and 'sardine-like' metapopulations with 'trawl-like' and 'purse seine-like' fisheries with hypothetical exploitation histories to test the performance of stock assessment models. However, the results of such 'fish-like' operating models may not represent a specific fishery. Spatially-structured operating models can also be conditioned on results from estimation models that reflect the most plausible population and fishery structure and are fit to the available data for a specific fishery (e.g., Goethel et al., 2016; Kerr et al., 2017a; Carruthers and Butterworth, 2018). However, spatial estimation models are often overparameterized and cannot always produce stable solutions (Punt, 2017, 2019).

A common alternative to conditioning on results from spatial estimation models is to condition on results from simpler models with modifications to reflect the most plausible spatial structure. A Frankenstein model (i.e., a composite of model parameters from different sources) can be conditioned on 1) results from a spatially-aggregated assessment model; 2) the population can be spatially distributed according to relative abundance data; and 3) movement among areas can be based on an ancillary study. For example, Kerr et al. (2010, 2014) developed a spatial operating model for Atlantic cod that was conditioned on aggregate abundance estimates from stock assessment models, spatially distributed abundance to subpopulations based on relative survey indices, and connectivity among subpopulations was derived from genetic differences among them. Similarly, Lee et al. (2017) conditioned a spatial operating model to represent Pacific Bluefin Tuna by conditioning on results from a spatially-aggregate Pacific-wide stock assessment model, distributing recruits in the spawning area of the western Pacific, and simulating ontogentic movement as a function of environmental conditions. A spatial operating model was also developed for Atlantic bluefin tuna by conditioning on separate eastern and western stock assessment results, as well as fishery-independent estimates of movement among areas from telemetry analysis (Morse et al., 2018; Cadrin et al., 2019). Bosley et al. (2019) conditioned spatial operating models on parameter values from sablefish and hake estimation models, as well as some hypothesized parameter values. The Frankenstein approach to conditioning produces spatial operating models that reflect perceived stock development and exploitation histories, but the combined set of parameter values from different models with different spatial assumptions may not optimally fit the available data, and the results can be scary.

Considering uncertainties in spatial scope, persistent patterns of spatial heterogeneity and movement rates, multiple spatial operating models are typically needed to reflect alternative plausible scenarios. A series of alternative stock assessment models with different spatial structures can be simulation tested. The spatial structures of alternative estimation models should include a range from simple to complex, including a unit stock (e.g., the spatial extent of the current management unit with no spatial structure), intermediate structure (e.g., modeling 'areas-as-fleets', Waterhouse et al., 2014), and complexity that approaches the structure in the operating models. For some fisheries, spatially-simple stock assessments performed well in simulation tests (e.g., Porch et al., 1998; Cao et al., 2014; Benson et al., 2015; Goethel et al., 2015), but in other situations of spatial structure and mixing, spatially-structured assessment models are needed for accurate population estimates (Carruthers et al., 2011; Cope and Punt, 2011; Ying et al., 2011; Punt et al., 2015, 2018; Cadrin et al., 2019). The performance of spatially-structured assessments also depends on correct spatial specification. For example, performance of spatial models was no better than conventional models when they had mis-specified movement (e.g., Goethel et al., 2015; Lee et al., 2017), mis-specified spatial strata (e.g., Punt et al., 2015, 2018) or insufficient tagging data (e.g., Vincent et al., 2017). Therefore, the optimal spatial scope and structure depend on the nature of spatial structure, as well as the information available for stock assessment.

6. Discussion

The theoretical assumptions of typical stock assessment models are that the spatial extent and structure of stock assessments should be fair approximations of spatial population structure. However, perceptions of population structure for most fisheries have only recently come into focus, long after management units were defined, fishery and resource sampling programs were designed, stock assessments were developed, and spatial catch allocations were negotiated. Therefore, revising management units and stock assessment methods may not be a viable option for responding to new or revised stock structure paradigms. Accordingly, Kerr et al. (2017a,b) present a range of approaches to consider for improving assessment and fishery management when there are mismatches between the scale of biological populations and management units, including status quo management (i.e., assuming that the stock assessment adequately represents the system, which should be simulation tested), "weakest link" management (constraining the fishery to conserve the most vulnerable population component, which requires monitoring each component), spatial and temporal closures to conserve population components, stock composition analysis to support assessment of each component in a mixed-population fishery, and finally re-definition of management units and the spatial extent of stock assessments.

Cadrin and Secor (2009) predicted that spatially-structured stock assessments would proliferate because of the trend towards spatially explicit fishery data, integrated stock assessment modeling, and the advancement of stock identification methods. However, nearly a decade later, Berger et al. (2017) found few examples of spatially-structured assessment models that are the basis of fishery management advice. Punt (2017, 2019) attributes the slow progress toward spatially-structured stock assessments to limitations in data and software, the increased challenges of parameter estimation, and institutional inertia. Furthermore, spatially-structured assessments have challenging policy implications that need to be confronted (Goethel and Berger, 2017). Continued development and technical support of software that supports spatial stock assessment is needed. Although most fishery management systems are investing in spatially-explicit data, and routine monitoring data can be used to define spatial structure, these data may need to be supplemented with ancillary sampling for stock composition and tagging to inform spatial stock assessments. Institutional inertia often results from paradigm paralysis or confirmation bias in which information is interpreted through the lens of the current spatial management units. Resistance to considering alternative paradigms of population structure can be confronted by demonstrating the relative performance of status quo and alternative stock assessment methods for informing fishery management. Simulation-estimation studies can also be extended to management strategy evaluation to confront some of the tradeoffs of spatial management.

A developing consensus for spatial stock assessment modeling is that other important features of population and fishery dynamics (e.g., natural mortality, selectivity, recruitment, growth, …) should be resolved before attempting spatially-structured stock assessments, because mis-specification of other processes will be confounded with spatial structure (Maunder et al., 2019). For example, exploratory stock assessment modeling for Eastern Pacific bigeye tuna suggested that specification of natural mortality and growth are needed before spatial structure can be explored, despite evidence of spatial structure within the Eastern Pacific and substantial connectivity with the Central Pacific (Punt et al., 2019). Conversely, spatial structure can influence all those dynamics, and spatial structure may be more important than other aspects of population dynamics for some fisheries. Considering spatial structure to be a second-order dimension of complexity essentially reaffirms the 'unit stock' assumption and the need to align stock assessments with the spatial extent of a single population. Considering the challenges of developing and routinely updating a spatially-structured assessment model for fishery management advice, perhaps the most promising application for spatial models is for conditioning a spatially-complex operating model that represents most likely biological population structure for testing the performance of simpler models and management procedures (e.g., Kerr and Goethel, 2014; Kerr et al., 2017a; Goethel et al., 2016).

7. Conclusions

Interdisciplinary stock identification can determine the most likely paradigm of spatial extent and structure that is consistent with all information available. There are several general options for addressing representing spatial structure in stock assessment and fishery management. The most appropriate alternative for assessing and managing spatially complex populations should be determined from performance testing, including practical considerations, costs and benefits. In the context of limited data, capacity for complex model development, as well as the assessment and management processes, the primary role of spatially complex stock assessment models may be to condition operating models for simulation testing of spatially-simpler management procedures. As advances in stock identification methods are applied to more fisheries resources, the trend in detecting spatial complexities is expected to continue, so guidance on best practices in spatially-structured stock assessment models (Mander et al., 2019) is needed.

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