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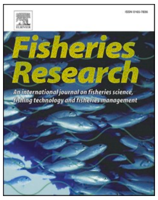

Best practices for defining spatial boundaries and spatial structure in stock assessment

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ABSTRACT

The ‘stock concept’ in fisheries science conforms to theoretical assumptions of stock assessment models, including negligible movement across stock boundaries, relatively homogeneous vital rates, and extensive mixing within stock areas. Best practices for representing population structure in stock assessment involve 1) interdisciplinary stock identification to delineate spatially discrete populations or more complex population structure; 2) stock boundaries that are aligned with the most plausible population structure; 3) spatially-explicit sampling, fleet structure or spatial structure in assessment models to account for heterogeneity, fishing patterns, and movement within stock areas; 4) routine stock composition sampling and analysis for spatially overlapping populations; and 5) simulation testing the performance of assessments with mis-specified or uncertain population structure. Practical assessment units that do not accurately represent population structure may not provide sufficient information to achieve fishery management objectives, so practical constraints should be addressed through iterative advances in routine stock identification, delineation of stocks to meet unit-stock assumptions, and stock assessment modeling.

1. Introduction

The unit stock concept has been recognized as a theoretical assumption of conventional stock assessment since the early stages of fisheries science (Cushing, 1968; Harden-Jones, 1968; Pauly, 1984; Hilborn and Walters, 1992; Sinclair and Smith, 2002). Russell’s (1931) initial derivations of sustainable yield and overfishing began with the assumption “*Let us simplify the problem down to its bare essentials by considering a completely self-contained stock of fish of one particular kind living in a large area which is systematically fished*”, and established the axiom of the stock concept (Cushing, 1983). The population and fishery processes assumed in most stock assessment models continue to imply 1) no movement of fish into or out of the stock area at any life stage, 2) vital rates (somatic growth, maturity, natural mortality, and fishing mortality with selectivity) are relatively homogeneous within the stock area, and 3) individual fish mix extensively throughout the stock area (Cadrin, 2020). Although these are collectively referred to as ‘unit stock assumptions’, the assumptions relate to fishing on biological population units rather than the practically defined ‘stock’.

A series of simulation experiments representing diverse fisheries and target species demonstrate that accurately accounting for population structure and fishing patterns in stock assessments can improve model performance, and case studies in fishery management demonstrate that ignoring such structure can lead to misperceptions of stock status (Punt, 2019; Cadrin, 2020; Bosley et al., 2022). Therefore, an important aspect of stock assessment is determining appropriate geographic boundaries to define the stock and patterns of spatial heterogeneity within the stock area. Stock identification infers spatial population structure to delineate stock boundaries that encompass discrete populations (e.g., Booke, 1981; Carvalho and Hauser, 1994). However, all biological populations have some spatial heterogeneity, many have connectivity with adjacent populations, some have geographic overlap with adjacent populations, and subpopulations in a metapopulation are more extensively connected at early or later life stages (Fig. 1). Population structure and major

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fishing patterns can be represented by fleet structure, spatial strata, or continuous gradients within the stock area, and stock composition analysis can be applied to mixed-population fisheries to support assessment of each population in the mixture (Punt et al., 2020).

Modeling approaches for representing population structure and fishing patterns vary widely among stock assessments, but most operational assessments that are used to support management advice assume a unit stock with no spatial structure within the stock area (Berger et al., 2017). Perspectives on the importance of stock identification for stock assessment and fishery management are diverse. At one extreme, which is unfortunately common, population structure is ignored, or violations of the unit stock assumption are casually dismissed because of practical constraints. At the other extreme, Link et al. (2020) list "*movement, migration and location*" as the first major mechanism impacting marine populations, followed by overfishing and other processes. The 2018 workshop on spatial stock assessment models convened by the Center for the Advancement of Population Assessment Methodology (CAPAM) suggested a practical order of priorities for stock assessment: "*accurate spatial modeling requires correct specification of all major features of population and fishery dynamics* (e.g., *natural mortality, growth, selectivity*), *because movement estimates are often confounded with estimates of recruitment or mortality*" (Cadrin et al., 2020). More recently, the 2019 CAPAM workshop on next generation stock assessment models concluded that "*a major challenge for any next-generation stock assessment package is the set of extensions needed to assess stocks that do not satisfy the 'well-mixed single-stock' paradigm*" (Punt et al., 2020). Punt (2023) listed the determination of stock structure hypotheses as the first step in good practices for conducting assessments. Although the importance of stock structure may vary among fisheries, and perceptions of its priority may differ among scientists, population structure and fleet structure are expected to be primary features of future stock assessment modeling.

Stock delineation has been notoriously political, because stock boundaries largely determine who has management authority and access to fishery resources. Therefore, best scientific practices for defining spatial boundaries, spatial structure, and fleet structure in stock assessment should consider biological reality, theoretical assumptions, and practical solutions for meeting fishery management objectives. As a contribution to the CAPAM workshop on stock assessment good practices, this review was invited to summarize relevant literature, common practice, best practice, and research recommendations for the related topics of stock identification, delineating stock boundaries, accounting for spatial structure within a stock area, and simulation testing misspecified population structure.

2. Background

Over the last two centuries, the theory and practice of stock assessment and stock identification co-evolved (Cadrin and Secor, 2009). Initial concepts of fishery production relied heavily on 'population thinking' to explain fluctuations in fisheries as the result of variable production of discrete fish populations (Sinclair and Smith, 2002). Cushing (1968) refined 'the idea of a unit stock' to describe dynamics of self-sustaining populations, and Harden-Jones (1968) summarized that "*management stocks are considered to respond largely independently to the effects of exploitation, because recruitment, growth and mortality within the stock are of more significance than emigration or immigration to the stock.*"

The importance of identifying and assessing self-sustaining stocks increased after claims of national and international fishery management jurisdictions. When the U.N. Convention on the Law of the Sea allowed for the establishment of exclusive economic zones (i.e., coastal nations claiming jurisdiction for fishery management) and the 'high seas' (i.e., outside of these jurisdictions), it provided for international agreements to cooperatively manage stocks that cross jurisdictional boundaries (UN, 1982). 'Transboundary stocks' inhabit the exclusive zones of two or

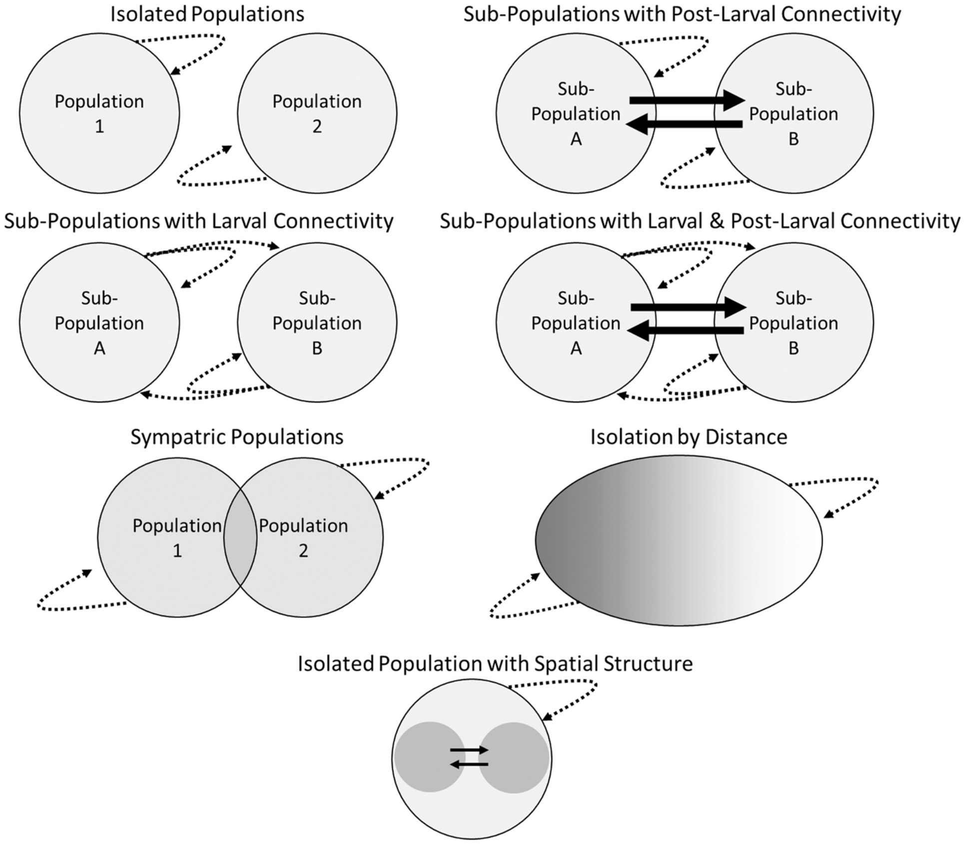

Fig. 1. Seven general population structure scenarios, including larval connectivity (dashed arrows) or post-larval connectivity (solid arrows) among subpopulations in a metapopulation.

more coastal states, ‘straddling stocks’ extend from an exclusive zone into the international high seas, and ‘highly migratory species’ move among multiple exclusive zones and the high seas. The determination of stocks that justify international fishery management agreements has been based on their biological characteristics, particularly their geographic range and degree of mixing between exclusive zones and the high seas, with recommendations to assess the entire range of transboundary stocks (Gulland, 1980; FAO, 1994). Guidance for international cooperation was provided by the Fish Stocks Agreement (UN, 1995), including the requirement to assess straddling or highly migratory stocks, implicitly as a unit stock. Even in situations where cooperative management may not be needed (e.g., transboundary stocks with low movement rates or low exploitation rates in each area), cooperative stock assessment has been recognized as a good practice (Gulland, 1980; Hilborn and Sibert, 1988; Caddy, 1997).

More recent technological advances led to the identification of complex population structure for many species (Kerr et al., 2017). These findings, as well as increased spatial resolution of fishery data and the development of spatial methods for stock assessment, revived the consideration of population structure in fisheries science. The revival of stock identification as a major feature of stock assessment is demonstrated by its inclusion in the topics considered for improving methods used in stock assessment and development of a good practices guide (Punt, 2023).

2.1. Stock identification

The identification of self-sustaining fishery stocks transitioned through several stages of development. Traditional approaches included conventional tagging, phenotypic variation, parasites as natural tags, and spatiotemporal fishing patterns (Marr, 1957). The study of polymorphic genetic markers revolutionized the ‘stock concept’ with an emphasis on reproductive isolation (Booke, 1981). The next stage involved a more holistic multi-disciplinary approach based on congruence among methods (Pawson and Jennings, 1996; Coyle, 1997; Begg and Waldman, 1999). The development of genomics, electronic telemetry, otolith chemistry, and otolith microstructure have supplemented traditional approaches for more informative stock identification. Traditional approaches to stock identification focused on results from a single methodological approach, then multi-disciplinary evaluations considered weight-of-evidence from several studies, and recent reviews recognize the advantages of interdisciplinary inferences of spatial population structure (Cadrin et al., 2014). An inter-disciplinary approach to stock identification considers the complementarity of methods in which each method characterizes precise aspects of population structure. For example, homogeneity of neutral genetic characters may not be congruent with geographic patterns in phenotypic variation that result from environmental differences among areas, but both are important for stock identification, because persistent phenotypic differences can have strong influence on population dynamics.

Three interacting aspects of population structure are evaluated in interdisciplinary stock identification: distribution, dispersal, and geographic variation - but no single source of information can support inferences of all three. Information on geographic distribution (e.g., fishery monitoring, fishery-independent surveys) can define a species range, spatial continuity, areas of high abundance, spawning areas, nursery areas, and fishing grounds for each fleet. Connectivity is evaluated from information on dispersal of early life history stages (e.g., plankton surveys, bio-physical models) and movement of juveniles, adolescents and adults from conventional tags, electronic telemetry or ‘natural tags’ (e.g., parasites, otolith chemistry). Geographic variation in phenotypic characters, neutral genetic characters or those subject to selection can inform patterns of population heterogeneity, lack of mixing, reproductive isolation, or local adaptation. Spatial patterns in neutral genetic characters indicate reproductive isolation among areas, and differences in selected characters or phenotypic characters reflect both genetic and environmental differences. Some phenotypic traits (e.g., growth rate, age at maturity) affect population dynamics more directly than others (e.g., morphology), but any persistent geographic variation in genetic or phenotypic characters should be considered in stock identification because it indicates limited mixing among areas. These complementary sources of information can be geographically integrated to form inferences of plausible population structure, including the identification of discrete populations for delineating stock boundaries, identification of subpopulations to account for spatial structure within stock areas, and identification of finer scale structure that may be relevant to productivity, fishery management and conservation (e.g., behavioral contingents, spawning aggregations; Kerr et al., 2010b).

2.2. Stock boundaries

Most stock assessments assume that the stock is a single discrete population (Hilborn and Walters, 1992), but most assessment units were delineated to encompass major fishing grounds or jurisdiction, which may not align with the spatial extent of biological populations that are being fished. Therefore, stock identification is needed to confirm that the entire biological population is within the stock area, there are not multiple populations or sub-populations of the species in the stock area, and there is negligible dispersal across boundaries or connectivity with adjacent areas (Cadrin et al., 2014).

The amount of movement across a stock boundary that violates the unit stock assumption cannot be generalized (Aldenberg, 1975), because sensitivity to movement rate depends on the movement pattern, relative population sizes, degree of reproductive mixing, and conservation status. More precise definitions of ‘negligible movement’ across stock boundaries requires stock-specific simulation to determine if observed cross-boundary movements impact the performance of stock assessment and fishery management in the context of other vital rates and relative abundance. For example, the larger eastern population of Atlantic bluefin tuna is less sensitive to movement and stock mixing than the smaller western population (Morse et al., 2020). Caddy (1997) suggested a threshold for cross-boundary dispersal as enough to produce a +/− 10% error in perception of local biomass, but in some cases the threshold may be smaller.

Movement patterns that involve post-spawning dispersal and natal homing can produce a seasonal mixture of populations on feeding grounds and in fisheries (i.e., ‘overlap’, Porch et al., 2001). This movement pattern adds some seasonal immigrants to catches or excludes some emigrants that are caught outside the stock area, thereby adding noise to time series signals of year class strength, mortality, or selectivity. For example, assessing mixed New Zealand snapper populations as single unit stock could not account for spatial patterns in age composition and growth, resulting in catch advice that was unsustainable for a depleted population in the mixture of populations being harvested (Francis and McKenzie, 2015; Berger et al., 2017). Movement patterns that result in reproductive mixing across a stock boundary (i.e., ‘random movements or dispersions’ Gulland, 1980; ‘diffusion’, Porch et al., 2001) also add noise to year-class signals and the stock-recruit relationship.

A common feature of marine fishes and other animals is the rare occurrence of much further-than-average movements (Secor, 2015), which may draw attention to the extreme movements despite a relatively low average movement rate. A few diffusive movements among subpopulations over a generation can produce enough reproductive mixing to homogenize genetic composition but may not disrupt demographic independence for stock assessment (e.g., Haugen et al., 2022). By contrast, movement of a few individuals may be more impactful for identification of spatial units for threatened species (Eagle et al., 2008).

Some populations can be effectively delineated by geography because they are strongly associated with benthic habitat or stable oceanographic features and have discontinuous distributions among populations. However, other populations are more spatially dynamic, have less discrete boundaries with adjacent populations, or may have some connectivity with other populations. Another challenge for representing spatial population structure is the resolution and accuracy of spatially explicit data used for stock assessment. Despite these challenges, stock boundaries should be based on stock identification and approximately encompass populations to meet conventional stock assessment model assumptions.

2.3. Spatial structure within stock areas

Population structure is a continuum in which the isolating mechanisms that form separate populations within a species, and potentially separate species over geological time, also form subpopulations within a population in ecological time. Spatial structure within populations can be discrete, with well-defined boundaries, or more continuous, resulting in clinal variation and isolation by distance (Fig. 1). Although stock boundaries should be based on biological population structure, spatial patterns within a stock area can also be influenced by fishing. If mixing is limited within a population, geographic fishing patterns can create differences in survival among areas (e.g., marine protected areas impose strong spatial heterogeneity in fishing mortality and potentially other vital rates). Heterogeneity within stock areas violates dynamic pool assumptions and complicates parameter estimation or management reference points (Goethel and Berger, 2017). For example, heterogeneous habitats and spawning behaviors can influence stock-recruit relationships (Skoglund et al., 2022).

Geographic patterns within a stock can be represented by spatially explicit samples, fleet structure, or spatially structured assessment models, but the impact of spatial patterns on stock assessment modeling depends on the source of heterogeneity (e.g., fishing patterns vs. biological patterns) and the movement rate among areas. Spatially explicit sampling (e.g., stratified random or systematic designs) can characterize fisheries or stocks that have spatial patterns so that the contribution of each area is appropriately weighted for a representative sample. However, population estimates based on weighted averages may not accurately reflect the combined results of local dynamics (Hart, 2001).

If spatial heterogeneity primarily results from fishing patterns and limited movement, fleet structured sampling and modeling can help account for spatial structure. Many integrated stock assessment models assume constant selectivity, often within multi-year periods (Methot, 2023, this issue). Constant selectivity assumptions within periods may be valid for fleets that use the same fishing gear but may not be valid for fisheries that use multiple fishing gears. Therefore, fleet stratification is commonly applied to monitor landings, discards, size- or age-composition, catch rate indices, and economic information to support fleet-based management (e.g., Lennert-Cody et al., 2010, 2013; Ulrich et al., 2012; Frawley et al., 2022). Fleet structure within an integrated stock assessment can greatly improve estimates of selectivity (Punt et al., 2014). Fleets are largely identified by fishing location, so fleet structure in a stock assessment can account for spatiotemporal fishing patterns as well as some spatial heterogeneity in the fish population (Berger et al., 2012; Waterhouse et al., 2014; Hurtado-Ferro et al., 2015). However, substantial movement or heterogeneity may require spatially structured assessment models (Goethel et al., 2023, this issue).

If spatial structure involves reproductively isolated populations or partially isolated subpopulations, information on stock composition is needed to estimate their relative contributions to the mixed-population fishery and stock over time (Utter and Ryman, 1993). Unfortunately, the term ‘sub-stock’ has various definitions in the fisheries literature, with different implications for stock assessment models. For example, Punt (2019) used the term to describe stock components that have extensive reproductive mixing with other stock components, but others use the term to describe reproductively isolated populations within a stock area (e.g., Frank and Brickman, 2000; Sterner, 2007; Lindegren et al., 2013). In this paper, we attempt to distinguish terminology for biological units (species, populations, metapopulations, subpopulations, behavioral contingents, spawning aggregations) from practical units (jurisdiction, stock, fishing ground, statistical reporting area, sampling strata, model strata) to avoid the common implication that practical units accurately represent biological reality.

2.4. Simulation testing

Simulation analyses were initially applied to spatially complex fisheries to understand the implications of population structure (e.g., Beverton and Holt, 1957; Ricker, 1958; MacCall, 1990; Kerr et al., 2010a). These heuristic simulations provided the framework for simulation-estimation studies that evaluate the performance of relatively simple estimation models for accurately representing complex populations and fishing patterns (e.g., Aldenberg, 1975; Porch et al., 1998; Berger et al., 2017). Simulation has also emerged as an integrative tool for interdisciplinary stock identification by conditioning operating models on information from several methodological approaches (e.g., Kerr and Goethel, 2014).

Operating models for simulation testing were initially conditioned on generic ‘fish-like’ population parameters with simple biological structure (e.g., two subpopulations of equal size) with uniform movement rates (e.g., Aldenberg, 1975). These relatively simple simulations were designed to make general inferences about the effect of population structure on stock assessment. More recently, simulation-estimation studies and management strategy evaluation have been more precisely conditioned to represent specific fisheries (e.g., Deroba et al., 2015; Punt et al., 2016). Simulation of spatially complex populations can evaluate the robustness of stock assessments in the context of uncertain population structure and demonstrate the risks of violating unit stock assumptions for specific fisheries (e.g., Punt, 2019; Berger et al., 2021; Bosley et al., 2022).

3. Common practice

3.1. Stock identification

Stock assessment reports describe stock boundaries, and most provide a justification for the stock area delineation and spatial strata, often with a summary of the available information on spatial population structure. The scientific process for providing this information varies among regional fishery management organizations. When population structure is identified as a major source of uncertainty in a stock assessment, or the assessment model exhibits diagnostic problems suggesting mis-specified stock structure, some organizations host a workshop to review the available information on stock identity and form recommendations for spatial assessment units (e.g., ICCAT, 2001; ICES, 2009, 2020, 2022b; Quinn et al., 2011; WPFMC, 2014; Moore et al., 2020a). Some organizations have standing expert groups to review and update information on population structure of specific stocks and to recommend revised stock definitions to assessment working groups (e.g., ICES, 2022a). Other organizations recently added routine stock identification workshops into their stock assessment process in advance of data and model workshops to define the most plausible stock boundaries based on the available information to meet the needs of the fishery management system (e.g., SEDAR, 2018, 2020, 2021; Fig. 2). Finally, some stock assessments have specific terms of reference to investigate spatial population structure (e.g., NEFSC, 2012, 2020; Punt et al., 2019). These standing committees, workshops or terms of reference within a stock assessment require broader expertise than typical stock assessment working groups or peer reviews.

Many stock assessment documents report that little information is available on stock identity. However, basic information on the species (e.g., geographic range, distribution patterns, early life history; www.fishbase.org), the fishery (e.g., fishing grounds, seasonality), and data

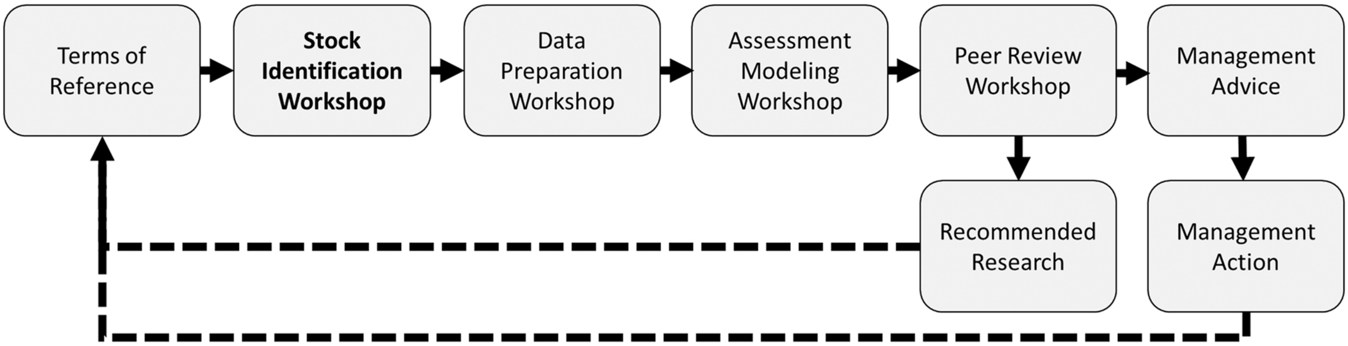

Fig. 2. Iterative stock assessment process with sequential stock identification, data preparation, modeling, and peer review workshops, producing management advice and research recommendations that can be addressed in a subsequent iteration. The stock identification workshop reviews available information to infer plausible scenarios of population structure (including the most plausible scenario if possible) and potentially recommend revised stock definition for assessment and fishery management. The data preparation workshop should support the recommended stock definitions so the assessment workshop can develop models for the recommended stock, sensitivity to plausible alternatives, and potentially performance testing. Peer review can be integrated into each workshop, and additional science-management interactions early in the process are needed if revised stock definitions are recommended.

collected for stock assessment (e.g., spatial patterns in size or age composition, size-at-age, maturity-at-age) can be used to investigate putative stock structure (e.g., Begg and Waldman, 1999; Lennert-Cody et al., 2010, 2013). Therefore, every routine stock assessment offers an opportunity to review the information available and recommend future research to support iterative improvements.

3.2. Stock boundaries

The most common sequence of events defining stock boundaries is an initial claim of management jurisdiction for fisheries in an area, the collection of data for fisheries in the jurisdiction, and the development of stock assessments for target species in the area or discrete fishing grounds within the area. As a result, spatial boundaries of many stock assessments do not adequately represent population structure, because there was no consideration of population structure in the initial stock definition. Stock identification can either confirm that the management unit is a population or that stock boundaries do not conform to unit stock assumptions. Defining or re-defining the spatial extent of stock assessment is needed in advance of data compilation or model development. Unfortunately, limited spatial resolution of historical fishery data often constrains the definition of stock boundaries and strata (e.g., ICES, 2020, 2022b). Stock definition is often a practical compromise between scientists and fishery managers so that the spatial unit of assessment is consistent with the management unit.

Some stock boundaries have been revised based on new perspectives of population structure, but many more stock boundaries are maintained despite their known misspecification (e.g., Reiss et al., 2009; Kerr et al., 2017; Ommer and Perry, 2022). Common practice is to assess the management unit and ignore model assumptions that are violated when spatial data are not available to support the assessment of a discrete population, management jurisdiction precludes the management of a unit stock, or population structure is too complex to meet unit-stock assumptions. As a result, many assessment units include portions of a larger population, multiple discrete populations, subpopulations of the same species, or even multiple species (Cadrin, 2020). Considering the large number of potentially mis-specified stock boundaries, poor performance of spatially mis-specified assessment models, and fishery failures resulting from mis-specified population structure, it is reasonable to conclude that many stock assessments can be improved by revising the stock boundary to meet unit stock assumptions.

Some stock assessments account for movement of fish across stock boundaries by adjusting the value of assumed natural mortality, *M* (ICES, 2021), or as process error in total survival or natural mortality (Frisk et al., 2008; Aldrin et al., 2019; Nielsen and Berg, 2023, this issue). Emigration may have similar effects as mortality on changes in abundance over time, and immigration can have a similar result as a lower mortality rate, but aliasing movement as mortality ignores the form of movement (e.g., fish that leave the stock area but return to spawn). Although an assumption of increased natural mortality may account for emigration in survival predictions, the two processes have different effects on management reference points and catch projections (Goethel and Berger, 2017). The history of stock assessment has trended toward more accurate model specification, but the '*M*-agic' of aliasing movement as mortality deliberately mis-specifies one process (natural mortality) to account for misspecification of another process (movement) or represents a nonrandom process (movement) with random process error. Therefore, given the management implications of these implicit assumptions regarding connectivity, it is not recommended as an appropriate tool for addressing spatial processes.

3.3. Spatial structure within stock areas

The majority of stock assessments assume no spatial structure within the stock area. For example, a survey of U.S. stock assessment scientists indicated that most (83%) assessments assumed no spatial structure, but there was evidence of spatial structure for most of those stocks (Berger et al., 2017). In common with other structural features of assessment models (e.g., age, sex, fleet), spatial structure requires spatially explicit data. Fortunately, data from fishery monitoring or fishery-independent surveys are spatially explicit or stratified to represent the stock or fishery through stratified estimates or spatiotemporal analysis (e.g., Currie et al., 2019). For multispecies fisheries and surveys, sample stratification often considers ecosystem boundaries (e.g., geographic, bathymetric or oceanographic features) that may be putative spatial structure for multiple stocks. Punt (2023) explained that spatial strata are often defined by jurisdiction, and jurisdictional strata can account for national fleets or management regimes.

Most fisheries are sampled by fleet, in which vessel-based fleets or trip-based métiers are defined primarily by fishing gear, target species and fishing locations (e.g., Ulrich et al., 2012; Lennert-Cody et al., 2013; Frawley et al., 2022). Fleet structure in stock assessment models helps to estimate selectivity and can account for some spatial heterogeneity, often imposing time-varying selectivity on the oldest or largest fish (Methot, 2023, this issue). Many assessments model the fishery as a single fleet, assuming constant selectivity within periods of similar fleet composition, regulations, or fishing behavior. Information on fishing mortality for each fleet can be derived from their partial catch-at-age or -at-length in aggregate-fleet assessments (e.g., Porch et al., 2001), and state-space models can estimate annual process errors in aggregate-fleet selectivity to allow for varying contributions of fleets to total catch (e.g., Nielsen and Berg, 2014). However, these single-fleet approaches cannot account for the spatial heterogeneity imposed by different fishing patterns among fleets.

Spatial structure resulting from a mixture of multiple sympatric populations within a stock area can be accounted for with stock composition analyses. Routine stock composition sampling and analyses have been successfully applied to assessment of many mixed-stock salmonid fisheries for decades (Utter and Ryman, 1993), and genetic stock identification for Pacific salmon has been refined over time to be cost-effective (e.g., Beacham et al., 2020). Stock composition sampling and analysis has also been applied to some non-salmonid fisheries (e.g., Kerr et al., 2022). Many other fisheries catch a mixture of intraspecific populations, but the mixture is assessed as a single stock, with no monitoring of stock components, risks of depleting components, or potential failure to achieve optimal yield (Ricker, 1958).

Spatially structured stock assessment models have been developed, but few are applied as the basis for fishery management because of model complexity, data requirements, difficulty estimating movement rates, policy implications, or institutional inertia (Berger et al., 2017; Punt, 2019). Similar to the constraints of data resolution on stock definition, strata definition is also commonly constrained by the resolution of fishery data (e.g., Cope and Punt, 2011; Gertseva and Cope, 2017, Thorson and Wetzel, 2016). Although many fishery systems now collect spatially explicit data with high-resolution, historical data typically has lower resolution (Goethel et al., In press).

Some management strategies require information on spatial structure. For example, some spatially aggregated assessments include spatially disaggregated forecasts to support spatial catch allocation (Kapur et al., 2021). Bosley et al. (2019) evaluated performance of spatial forecasts and found that those based on local stock indices performed best for achieving nearly maximum system yield, but all approaches frequently led to local depletion when spatial structure was ignored or specified incorrectly. Spatial stock assessment information can also help to evaluate effectiveness of other spatial management actions (e.g., marine protected areas, spawning closures).

3.4. *Simulation testing*

Despite several recommendations for routine simulation testing to evaluate the consequences of model misspecification (Hilborn and Walters, 1992; Deroba et al., 2015), few stock assessments include simulation to evaluate performance of the estimation model, and almost all of those assume a unit stock in the operating model. Most simulation-estimation testing occurs in research projects that are somewhat independent from the stock assessment process, and results are not always considered in the assessment. Similar to other model misspecifications that receive more attention, stock assessments with mis-specified stock boundaries or spatial structure can be misleading. Therefore, simulation testing is needed in which operating models represent plausible population structure (Cadrin, 2020).

4. Suggested good practices

4.1. *Stock identification*

Regardless of assessment or management constraints, plausible population structure should be inferred from an interdisciplinary synthesis of all information available, including perspectives from the fishery. If possible, the most plausible scenario of population structure should be identified to simplify data compilation for a single stock assessment model. However, even the most data-rich fisheries will have some uncertainty for inferring population structure, which can be expressed as multiple plausible scenarios of population structure. For well-informed inferences, plausible scenarios may have a common archetype of population structure (Fig. 1), with alternative scenarios of boundary locations or movement rates. More uncertain inferences of stock identity may be represented as alternative plausible archetypes. Plausible scenarios can be depicted as conceptual models (e.g., ICES, 2009, 2020; Quinn et al., 2011; Zemeckis et al., 2014; Minte-Vera et al., 2023, this issue).

Revising stock assessments to more accurately reflect population structure can improve model performance, but reviewing information on stock identification should be routine and not limited to problematic assessments. A summary of stock identification and how well it matches the current assessment or management unit should be updated in every stock assessment report (e.g., an updated summary of information should be a generic term of reference for all assessments). These summaries can be supported by stock identification workshops, ideally within the stock assessment process and before data compilation so that data can be subsequently compiled to support the recommended spatial boundaries and strata (Fig. 2). An inclusive process for comprehensively reviewing, integrating, and updating the information available on population structure was developed by ICES (2009) for deep-sea redfish and subsequently applied to some cod fisheries (e.g., ICES, 2020, 2022b), offering a methodology for wider application of stock identification workshops. Coordinating processes for stock identification and stock assessment (e.g., Fig. 2) facilitates the transition from conceptual models of population structure (e.g., data maps, workflows) to observation models in integrated stock assessments (Minte-Vera et al., 2023, this issue). Coordinated processes also promote the incorporation of stock identification information as data in spatially structured assessments (e.g., tagging, population-of-origin indicators).

New information from advanced methods (e.g., genomics, electronic tagging, otolith chemistry) should be reconciled with previous information from traditional approaches (fishery perspectives, tagging, parasites), recognizing their relative sensitivities, and which aspect of population structure each source of information represents. Genomics is emerging as a powerful and cost-effective tool (Rodriguez-Rodriguez et al., 2022), and broad genome coverage is considered best practice for detecting reproductively isolated or locally adapted populations (Valenzuela-Quinonez, 2016). Genetic variation can also be used to estimate effective dispersal in some situations (e.g., Broquet and Petit, 2009). However, persistent patterns of phenotypic variation that reflect environmental differences also influence population dynamics. Therefore, complementary information on life history, distribution, dispersal, and phenotypic variation adds interpretive value to genomics for determining the most plausible population structure.

Similar to other population processes, stationarity is often assumed for stock delineation and fleet definition, but the persistence of spatial patterns should be regularly tested to detect possible changes (e.g., shifting geographic distributions in response to climate change). Fishery and survey data should be routinely mapped to explore patterns and detect changes in distribution as well as the persistence in patterns of size and age composition, size at age and maturity at age (Hilborn and Walters, 1992). Analyses of spatial shifts require sampling throughout the population's range, including its boundaries (Karp et al., 2019). Spatial shifts complicate the determination of stock boundaries, fleets, and strata, but better representation of spatial structure can help to identify the mechanism of shift and how to appropriately account for the shift (Currie et al., 2019). If individual fish are moving from unsuitable to suitable habitats or the population's range is expanding as a result of changes in effective dispersal (Hare and Able, 2007), then revised spatial strata may be needed, or stock boundaries may need to be extended. If the shift involves a demographic pattern associated with depletion or rebuilding (Bell et al., 2015), then the stock area should represent the distribution of a rebuilt population. If the apparent shift in distribution results from divergent trends of independent allopatric populations (Link et al., 2010), separate stock areas should be defined or maintained for each population.

Recommended best practice for stock identification is to include a description of the spatial assessment unit and a summary of available information on stock identity in every stock assessment report. Each assessment should also examine evidence for spatial shifts. Finally, stock assessments should provide research recommendations to fill gaps or investigate emerging patterns. Moore et al. (2020b) offer an excellent example of research recommendations developed through an interdisciplinary review of stock identification. Implementing an iterative process of updating information on stock identity, recognizing research needs, and investing in research (Fig. 2) can help advance all stock assessments, including those for data-limited fisheries, toward an appropriate geographic scope and structure for meeting the management needs of each fishery.

4.2. Stock boundaries

Stock boundaries should be delineated to represent a biological population as closely as possible with the data available. Isolated populations can be assessed as unit stocks and stock status can appropriately be based on stock-recruit reference points when all life stages of a population are contained within the stock area, including those that demonstrate ontogenetic movement patterns. The entirety of sympatric populations should be accounted for in stock assessments by assigning all data (e.g., fishery catch, index catch, size or age composition) to each population in the mixed stock. If population structure is more complex, stock boundaries should encompass a complete metapopulation while monitoring subpopulation trends. For example, each population or metapopulation depicted in Fig. 1 should be assessed as a stock unit, and subpopulations within metapopulations should be accounted for with spatial structure within the stock area. There may be tradeoffs between 1) mis-specified stock boundaries that allow a longer time series of historical information with coarse spatial resolution and 2) correctly specified stock boundaries with a more restricted time series of recent spatially explicit data.

If changes to stock definitions or boundaries are needed to improve the representation of population structure, fishery managers should be consulted early in the stock assessment process so they can communicate any additional practical constraints and consider adapting to new assessment units (e.g., support management actions with information from new assessment units, revise management units to match assessment units). Ideally, management units should also represent biological populations, because management models (e.g., optimum yield, overfishing, rebuilding plans) imply the same assumptions as stock assessment models. Accordingly, a common standard for managing U.S. marine fisheries is to manage a stock as a unit (e.g., USA, 2007). Therefore, stock definition should be based on the best scientific information available to meet management objectives while considering practical constraints, similar to other stock assessment assumptions that have management implications (e.g., stock-recruitment, natural mortality, selectivity, data weighting).

If practical challenges preclude the assessment of entire metapopulations with subpopulation structure, subpopulations that have some larval connectivity with other subpopulations, but negligible post-settlement connectivity, can be effectively assessed with separate assessments and stock status can be appropriately based on per-recruit reference points. However, reproductive capacity of the entire metapopulation requires conservation. For example, source-sink dynamics and increased vulnerability of source subpopulations should be considered in stock assessment and fishery management.

If spatial management units include multiple discrete populations, each population should be separately assessed. Consistent productivity assumptions and model settings can help to provide comparable abundance and mortality estimates for management of the combined unit (PFMC, 2021). Separate stock assessments with consistent assumptions provide estimates of stock size, mortality and projected catch that are more comparable and potentially additive for aggregate catch advice (e.g., Jardim et al., 2018). Such consistency in assessment methods can help to avoid misleading inferences of spatial distribution and associated management conflicts. For example, Georges Bank cod and haddock assessments demonstrate how lack of consistency between assessments can create challenges for fishery management. U.S.-Canada transboundary management units are nested within larger U.S. management units (Pudden and VanderZwaag, 2007), but separate assessments with different methods and assumptions (e.g., natural mortality) produce estimates of stock size that are not comparable and catch advice that is not even approximately additive. As a result of these inconsistent methods and assumptions, subtracting total allowable catch for the smaller area from allowable catch for the larger area currently leaves little cod catch for U.S. fisheries (NEFMC, 2022).

4.3. Spatial structure within stock areas

If population structure is too complex to define distinct spatial stocks, stock assessment may require spatial stratification, spatiotemporal analysis, or stock composition analysis to account for heterogeneity. For example, assessment of metapopulations needs to account for each subpopulation (Fig. 1). Populations with discrete spatial structure require stratification of samples or models, depending on the degree of connectivity. Complex populations with isolation by distance within the stock area require spatially explicit data and assessment models.

Routine stock composition sampling is needed to account for sympatric populations. Stock composition (i.e., population-of-origin for individuals in a mixed stock) can be representatively sampled with other compositional samples (e.g., size, age, sex), and archived samples can be used to derive historical stock composition (e.g., genetics, otolith chemistry and microstructure; e.g., Smith and Campana, 2010). Stock composition sampling and analyses have been successfully applied to some fisheries, but they are typically applied to data preparation (e.g., catch by population).

Stratified sampling and fleet structure can account for some fishing patterns and heterogeneous vital rates (e.g., Berger et al., 2012; Waterhouse et al., 2014; Hurtado-Ferro et al., 2015). Fleet definition involves the recognition of heterogeneous fishing patterns, so that fishing behavior and selectivity are relatively homogenous within fleets. Good practice for fleet definition involves hierarchical classification using information on fishing effort (e.g., location, season, fishing gear, mesh size, horsepower), a priori target species (e.g., fisher interviews), or catch (e.g., species composition, size composition; e.g., Marchal, 2008; Lennert-Cody et al., 2010, 2013; Ulrich et al., 2012; Frawley et al., 2022).

Spatially structured population models are generally preferred over the fleets-as areas approach (Methot, 2023, this issue) and spatial model structure may be needed for stronger patterns of heterogeneity (Berger et al., 2017; Punt, 2019). Sub-annual time intervals are needed in spatially structured models to represent seasonal movement patterns and the sequence of movement with other events (e.g., spawning, fishing, surveys; Bentley et al., 2004; Taylor et al., 2011). Low spatial resolution of some data may not be an obstacle for spatial structure in assessment models, because integrated models can fit directly to spatially aggregated data (e.g., historical fishery data) as well as spatially disaggregated data (e.g., recent fishery data and survey data) to represent spatial structure and include all available information (Fig. 3). Many sex-structured models demonstrated how integrated models can fit to aggregated and disaggregated data (Maunder and Punt, 2013; Wilberg et al., 2023, this issue). If data are not sufficient to support a complex estimation model, sensitivity analyses can help to evaluate the consequences of simplification. For example, Thorson and Wetzel (2016) found that their two-area model assuming no post-settlement movement produced similar results as sensitivity runs that assumed a single area or a range of assumed movement rates among areas.

Spatial structure within a stock area can also be represented by spatiotemporal analyses (e.g., Cao et al., 2020). Spatiotemporal models are particularly well suited to population structures and geographic pattens that are less discrete (e.g., isolation by distance, geographic clines) because they account for spatial correlation. Spatiotemporal models are promising but may need further development for application

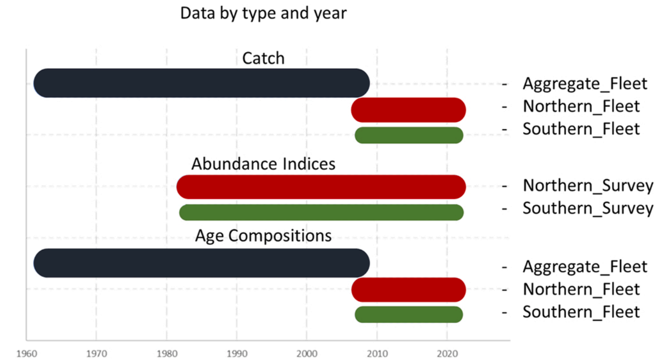

Fig. 3. Data inventory for an integrated stock assessment with spatial structure (two areas: north and south) fit to spatially aggregated historical data and spatially disaggregated recent data, showing that poor spatial resolution of historical fishery data may not be an impediment to spatially structured stock assessment.

to complex population structures (Goethel et al., 2023, this issue).

4.4. Simulation testing

If stock identification is routinely reviewed in the stock assessment process, some assessments will be recognized as mis-specified for representing the most plausible population structure. 'Cross-test' simulations should be conducted for any suspected misspecification (Deroba et al., 2015; Punt et al., 2020), so assessments that cannot conform to unit stock assumptions are simulation-tested to evaluate performance (e.g., Goethel et al., 2016). Simulation-estimation testing would be most appropriately done within the stock assessment process so that results can be considered in determining best practice for each assessment (e.g., Jacobsen et al., 2022). However, if simulation testing is beyond the scope of operational assessments, it should be developed as a research project in coordination with the assessment process.

If the information available supports multiple plausible stock structures, they can be represented as multiple operating models, and simulation testing can evaluate the robustness of estimation models to the range of plausible scenarios (e.g., Porch et al., 1998, Jardim et al., 2018, Punt et al., 2018). If assessment of the current stock area does not perform well, alternatives (e.g., redefined stock boundaries, spatial structure) should be tested that use currently available data. Alternative assessment methods that require new data investments may also be required, and the cost-benefit of data collection can be quantified within the simulation framework.

Ideally, results from spatially complex estimation models that fit the available data can be used to condition operating models (i.e., conditioning on data; e.g., Goethel et al., 2015). When the available data cannot support such complex estimation models, spatial operating models can be conditioned on results from exploratory estimation models or a combination of estimated parameters and expert judgment (i.e., conditioning on models). For example, alternative approaches to simulation testing Atlantic bluefin tuna assessments and management procedures used spatial models with a range of relative population abundance from separate-area assessments (Carruthers and Butterworth, 2018) or results from separate-area assessments combined with connectivity information from fishery-independent telemetry (Morse et al., 2020). These challenges in conditioning spatial operating models demonstrate the need to continue investments and advances in spatially structured estimation models (Goethel et al., 2023, this issue), so that operating models can be conditioned on data rather than on disparate model results that have inconsistent assumptions about population structure.

If spatially mis-specified assessment models do not perform well for providing accurate stock status and more appropriate specification is not possible within jurisdictional or data constraints, management strategy evaluation is needed to confirm that the current management strategy can meet management objectives (Punt et al., 2016, 2017). Precautionary harvest control rules account for some uncertainty, but assessments that produce substantial bias in parameter estimates and their variances may not perform well for providing the information needed by the control rule. If the current management strategy does not perform well, additional management features can be considered for testing alternative options (e.g., marine protected areas, spawning closures, escapement thresholds for spawning groups, spatial catch allocation; Bosley et al., 2019). Spatial operating models that represent multiple populations, mixing and fleet structure can be used to test empirical management procedures (e.g., Carruthers and Butterworth, 2018) or relatively simple model-based procedures (e.g., Morse et al., 2019; Weston et al., 2019). Management strategy evaluation may be needed before revising management units to justify the costs of transition.

5. Required research

Investments are needed to regularly update stock identification information (e.g., Fig. 2), to fill critical information gaps, and to address uncertainties. Although inter-disciplinary stock identification remains best practice, genomics is emerging as a cost-effective approach that can be applied to many more species. As applications of close-kin mark recapture increase, genetic data can provide information for stock identification (e.g., Trenkel et al., 2022; Bravington, 2023, this issue). These investments involve commitments to 1) consider the new information in the context of other available information, 2) potentially revise perceptions of population structure, 3) evaluate the consequences of any mismatches between the current assessment unit with the new perception of population structure, and 4) revise stock boundaries, spatial structure, or management procedures if needed.

Further development of spatial assessment models is needed so that estimation models can better represent complex populations and fisheries (Goethel et al., 2023, this issue). If spatial models are too complex to be supported by the information available for a specific fishery, exploratory spatial models may help to condition operating models for simulation testing. For example, if the data cannot inform the estimation of some model parameters, multiple operating models can be conditioned on a plausible range of assumed values (e.g., Carruthers and Butterworth, 2018). Considering the recommendations for routine simulation testing of stock assessments (Hilborn and Walters, 1992; Deroba et al., 2015), the next generation of stock assessment models should support efficient simulation testing of spatially structured or multi-population models (Punt et al., 2020).

The geographic integration of stock identification information from multiple disciplines remains somewhat qualitative (e.g., the conceptual models described by Minte-Vera et al., 2023, this issue). More quantitative integration and appropriate consideration of uncertainty would require the development of spatially explicit population genetics models to evaluate differences within and between populations. Conventional population genetics models (e.g., Rousset, 2007) would need to be extended to fit data on genetic variability, phenotypic variability, movement, and effective dispersal at ecological time scales. More accurate information on heritability of phenotypic traits and rates of early-life history dispersal and post-larval movement would be needed to support such integrated population genetics. Population genetics models may develop in parallel with the next generation of spatial stock assessment models.

6. Discussion

There are two main challenges for defining stock boundaries and strata within stock areas: 1) delineation of a stock that represents a discrete population, and 2) representing more complex population structure. Failing to address either challenge (i.e., violating unit stock assumptions or mis-specifying population structure) may corrupt stock assessments and mislead fishery management. Therefore, unit stock assumptions cannot be dismissed without simulation testing to confirm that mis-specified assessments perform well enough to meet objectives.

When stock identification suggests distinct populations, it may be cost-effective to revise stock boundaries, so they encompass each population. Inter-jurisdictional assessments may be needed to resolve boundary constraints (Gulland, 1980; Hilborn and Sibert, 1988; Caddy, 1997; FAO, 1994; UN, 1995). Data limitations can be confronted by improved monitoring systems that provide the required spatial data, and recovery of spatially explicit data from archives. The costs of these investments may be considerably less than the costs of misleading stock assessments for fishery management.

The scientific challenge is greater when stock identification suggests more complicated population structure. There have been advances toward accurately representing complex population structure in stock assessment for some data-rich fisheries, but many fisheries do not have the information to support such complex estimation models. This situation appears to present a 'Catch-22' conundrum, because spatial data are insufficient to correctly specify the estimation model, but spatial information is needed to condition operating models for simulation testing the performance of simpler estimation models. There are two alternative solutions to this challenge. Operating models can be loosely conditioned on the information developed by iterative stock identification to represent multiple plausible scenarios. Alternatively, operating models can be more precisely conditioned on results from exploratory spatial estimation models that are fit to the available data. Exploratory spatial models may not be reliable enough for precise status determination or catch advice, but the range of results may adequately represent the system for simulation testing. Advances in spatial estimation models should help to resolve this conundrum (Goethel et al., 2023, this issue).

Assessment of data-limited fisheries usually involves some form of model simplification, including bold assumptions that may not be valid (e.g., Cope, 2023, this issue). The data and model requirements for spatial assessment or testing are a particular challenge for data-limited fisheries, but model assumptions and consequences for violating them apply to all stocks. For example, in his manual of methods for stock assessment of tropical fisheries, Pauly (1984) began by explaining Russell's (1931) axiom of a unit stock and its assumptions. The iterative approach of routine stock identification, delineation of stocks to meet unit-stock assumptions, operational assessment, and research to fill information gaps (Fig. 2) can be applied to data-limited fisheries. The data collected for assessment can be explored for information on stock identity (Begg and Waldman, 1999), and the population richness of a species (Sinclair, 1988) can be considered for forming putative scenarios of population structure. The trend toward simulation testing data-limited assessments using the information available (Carruthers et al., 2014) can be expanded to spatial simulations with multiple operating models to represent plausible scenarios of population structure.

State-space models might offer a solution to account for relatively low rates of movement across stock boundaries as process error in survival (Frisk et al., 2008; Aldrin et al., 2019; Nielsen and Berg, 2023, this issue). However, the degree of structural misspecification that can be accounted for as stochastic process error needs to be determined. Similar to other potential approaches, the performance of state-space models that include process error in survival to account for immigration or emigration should be simulation tested.

The common terminology of 'stock' and 'unit stock assumption' may contribute to the common misspecification of population structure in stock assessments. It may seem like an obvious tautology, but simply calling a management unit or assessment unit a 'stock' does not imply that it meets unit stock assumptions. Viewing biological population structure through the human constructs of jurisdictions, fishing grounds, reporting areas, or geographic sampling strata often produces a distorted perspective, like the people in Plato's cave inferring reality from shadows on the wall. Furthermore, through the iterative process of stock assessment and fishery management, the management unit and stock appear to become biological realities themselves that conform to unit stock assumptions, like Pygmalion eventually believing his sculpture is a real person (Schnute and Richards, 2001). These human tendencies can be countered by routine stock identification to remind us that assessment models are simplifications and may not represent the reality of population structure. Iterative improvements to stock boundaries and model specifications will help to conform to unit stock assumptions.

7. Conclusion

Complying with the unit stock assumption may be the most important structural decision in stock assessment modeling, and many stock assessments can be improved by revising the stock boundary to encompass a discrete biological population. Stock boundaries and strata definitions should be routinely evaluated, informed by stock identification, and based on the most plausible stock structure. Iterative application of these practices for stock identification and stock assessments can advance assessment frameworks towards an appropriate geographic scope and structure for meeting the management needs of each fishery (e.g., Fig. 2).

Spatially complex populations present challenges associated with data limitations or jurisdictional constraints. Spatially mis-specified stock assessment models may not accurately represent complex populations. Therefore, simulation testing is needed to confirm acceptable performance for informing fishery management. The technical challenge for assessing spatially complex populations is the conditioning of operating models for simulation testing that adequately represent plausible scenarios of population structure informed by stock identification.

CRediT authorship contribution statement

Steven Cadrin: Conceptualization, Writing – original draft preparation, Writing – review & editing preparation, Visualization. **Daniel Goethel**: Writing – original draft preparation, Writing – review & editing preparation. **Aaron Berger**: Writing – original draft preparation, Writing – review & editing preparation. **Aaron Berger**: Writing – review & editing preparation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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