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Space Oddity: the Mission for Spatial Integration

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Title: Space Oddity: the Mission for Spatial Integration

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Abstract

Fishery management decisions are commonly guided by stock assessment models that aggregate outputs across the spatial domain of the species. With refined understanding of spatial population structures, scientists have begun to address how spatiotemporal mismatches among the scale of ecological processes, data collection programs, and stock assessment methods (or assumptions) influence the reliability, and ultimately, appropriateness of regional fishery management (e.g., assigning regional quotas). Development and evaluation of spatial modeling techniques to improve fisheries assessment and management have increased rapidly in recent years. We overview the historical context of spatial models in fisheries science, highlight recent advances in spatial modeling, and discuss how spatial models have been incorporated into the management process. Despite limited examples where spatial assessment models are used as the basis for management advice, continued investment in fine-scale data collection and associated spatial analyses will improve integration of spatial dynamics and ecosystem-level interactions in stock assessment. In the near future, spatiotemporal fisheries management advice will increasingly rely on fine-scale outputs from spatial analyses.

Keywords: Spatial models, fisheries management, stock assessment, distributional modeling, tagging, population structure

Introduction

"Commencing Countdown, Engines On"

Understanding how and why organisms disperse can help identify species' response to environmental and anthropogenic perturbations, which is important for modeling population dynamics and for predicting spatial distributions (Bowler and Benton 2005). Many of the basic principles of connectivity modeling were first evaluated for terrestrial species for which empirical studies and causal relationships are typically more easily developed than for marine species (Kritzer and Sale 2004). Recognizing changes in spatial structure can be particularly important for exploited species (e.g., managed fish stocks), because localized depletion or distributional shifts across environmental gradients may impact population resilience and susceptibility to harvest (Kerr et al. 2010b; Ciannelli et al. 2013). The presence of non-random, spatially-varying species density is widely acknowledged for aquatic resources (Cadrin and Secor 2009; Cadrin et al. 2014). Despite having the conceptual models and empirical techniques to delineate spatial population structure, the ability to incorporate complex spatial processes into aquatic population dynamics models, especially to guide fine-scale management decisions, has often lagged (Goethel et al. 2011, 2016; Kritzer and Liu 2014).

A unique quandary in applied fisheries population dynamics research is the need to balance broad-scale population models (to maintain tractability) against fine-scale spatial management policies that intend to avoid localized depletion and erosion of population structure. Ultimately, species biocomplexity results from among-individual variation in relative fitness to local conditions (e.g., due to habitat variability, community interactions, and localized adaptation), but any number of biotic or abiotic factors can influence population-level dispersal dynamics

(Bowler and Beton 2005; Berger et al. 2012; Kerr and Goethel 2014). Assumptions of a closed, dynamic pool of individuals with fishing mortality homogenously spread across all individuals underlie the tractable stock assessment modeling approaches that have conventionally been applied to determine harvest levels at typically broad spatial scales (Orensanz and Jamieson 1998). However, this classic approach is inappropriate for many aquatic species, because management boundaries rarely line-up accurately with biological and demographic spatial structure (Smedbol and Stephenson 2001; Berger et al. 2012). Spatial management policies are often enacted at a finer scale than the management unit in order to protect components of the population (e.g., spawning contingents; La Valley and Feeney 2013; Kerr et al. 2014). Although well-intentioned, management advice can then become essentially *ad hoc*, because outputs from the stock assessment model do not match the scale of management (Goethel et al. 2016; Kerr et al. 2016). In many cases, it may be preferable to define spatial boundaries based on areas where individuals from a given stock exhibit similar local adaptation and harvest characteristics to better capture population-unit differences in demographic rates, fishing pressure, gear selectivity, and management regulations.

There has been a long history of researchers acknowledging the importance of spatial considerations and the potential pitfalls of ignoring connectivity dynamics in assessment methods (e.g., Beverton and Holt 1957; Aldenburg 1975; Quinn et al. 1990; Cadrin and Secor 2009; Goethel et al. 2011; Ciannelli et al. 2013). However, previous generations lacked the computational and statistical tools to implement spatial models, and had far less options for acquiring the explicit spatial information often needed to develop data-driven population dynamics models that match the scale of hypothesized spatial processes (Goethel et al. 2011).

As a result, for much of the 20th century, fishery management and assessment methods most often ignored the spatial-structure of marine species (Orensanz and Jamieson 1998). A revival of spatial modeling practices in the 1990s, along with improved understanding of spatial population structure led to an increased focus on the importance of defining population responses to spatiotemporal fishing and environmental pressures (e.g., localized depletion; Quinn 2003). Despite this increased awareness and the availability of new modeling techniques, spatial analyses remain underutilized (Kerr et al. 2014; Kritzer and Liu 2014). Orensanz and Jamieson (1998) noted that spatial considerations were often deemed necessary only for species with "strong and persistent spatial structure" (e.g., sessile invertebrates), as opposed to those with transient spatial structure such as most mobile fish species. Further, it can be unclear how outputs from theoretical spatial models, such as those describing metapopulation dynamics, could be directly incorporated into management decisions (Orensanz and Jamieson 1998).

Although tremendous strides over the last decade have been made in accounting for spatial processes in modeling and managing marine species, largely due to technological advances that have allowed real-time and fine-scale data collection (e.g., oceanographic and fishing vessel monitoring via satellite and electronic tagging) and improved computing power, there almost always remains a disconnect in the assumed spatial scales at which stock assessments are conducted and the resulting fine-scale policy actions (Cope and Punt 2011; Goethel et al. 2016). In many cases, causes for these mismatches are either due to political interference inhibiting the redefinition of spatial boundaries, despite analyses indicating improperly defined units (i.e., due to refined stock identification techniques suggesting differences in biology or harvest; La Valley and Feeney 2013), a lack of model outputs at the scale of spatial management regulations (e.g., to inform spatial quota allocation; McBride 2014) or a lack of genetic information to define population structure (Kerr et al. 2016). When spatial scales do not match at the realm of interaction between scientific advice used as the basis for management actions and resultant policy decisions (i.e., the assessment-management interface; Figure 1) there can be significant negative consequences (Goethel et al. 2016). From a social perspective, stakeholder confidence in the management system can erode when there is a lack of transparency in how scientific analyses contributed to management decisions or when the analyses do not align with observed ecology (e.g., spatial structure and connectivity dynamics). Further, the resulting management actions can be overly aggressive or overly conservative, creating biological implications that range from localized depletion or forgone yield to reduced ability to withstand ecosystem perturbations (Reiss et al. 2009; La Valley and Feeney 2013; Kerr et al. 2014; Kerr et al. 2016).

The motivation for this paper began with the symposium titled “Space Oddity[1]: Recent Advances Incorporating Spatial Processes in the Fishery Stock Assessment and Management Interface” at the 145th American Fisheries Society Annual Meeting, where research contributions collectively represented significant advancements in accounting for spatial processes in fisheries science (see Berger et al. 2017, this issue). Following upon this symposium was a New Zealand-United States Joint Commission Meeting (JCM) workshop on “Spatial Fish Population Dynamics and Stock Assessments”, which focused specifically on the spatial methods and management approaches being utilized by the respective countries. In this paper, we provide an overview of the historical

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[1] The theme of the session revolved around the David Bowie song “Space Oddity”, the lyrics of which are surprisingly prophetic when interpreted in the context of the schism between spatial modeling techniques and resulting spatial management advice. We use lyrical snippets as alternative section headers indicating the various stages of spatial modeling over the years.

context and evolution of spatial fisheries models, highlight recent spatial modeling approaches, and discuss the incorporation of spatial models into management (capturing salient points from the N.Z.-U.S. JCM workshop). We focus on demographically-structured modeling approaches (e.g., using spatially-explicit tagging, assessment, and simulation models) that aim to better understand the underlying population dynamics that cause observed spatial structure (e.g., connectivity), as well as species distribution modeling (SDM) approaches that aim to uncover and predict spatiotemporal resource distributions. Both approaches have demonstrated the consequences of failing to account for observed spatial complexity and have exposed new insight into how spatiotemporal distributions develop (Planque et al. 2011). We discuss how these spatial modeling techniques can be used synergistically to develop operational, spatially-explicit analyses that form the basis of management advice; why spatial models have not been widely used to set management advice; and what can be done to better integrate results from these approaches with policy decisions to bridge the gap that often exists across the assessment-management interface (Figure 1).

Evolution of Spatial Population Models

"You've really made the grade"

The evolution of spatial population dynamics modeling for aquatic species can be traced in two branches: (1) estimation of movement parameters and (2) spatially-referenced stock assessment models. As noted by Seber (1982), interest in movement parameter estimation commenced in the 1950's with articles by Schaefer (1951), Chapman and Junge (1956), Beverton and Holt (1957), Darroch (1961), and Overton and Davis (1969). These articles had a common basis of a population stratified into discrete areas and two time periods, the first for marking in all areas, the second for recapture sampling in all areas. This approach is often referred to as the stratified Petersen method. Darroch's work is the best known and makes extensive use of maximum likelihood theory. Interest in estimating movement piqued again in the 1990s with the emergence of a variety of novel tagging approaches. Hilborn (1990) provided a generic approach for simultaneous maximum likelihood estimation of movement and other population parameters. The approach consisted of four components: (1) a population dynamics model containing fundamental elements of movement and mortality, (2) an observation model for the tag recovery process, (3) a probability distribution for the tag recaptures, such as Poisson or multinomial, and (4) a method for nonlinear maximization of the likelihood. The method is based on the assumption of Markovian movement and was illustrated by application to tropical tuna populations. Brownie et al. (1993) developed a non-Markovian model for movement to estimate migration rates, while Dupuis (1995) developed a Bayesian approach for estimating movement. A variety of approaches have been developed for estimating migration rates for bird and wildlife populations [see Hestbeck et al. (1991), Nichols (1996), and Schwarz and Seber (1999)], many of which have been adapted for marine populations.

The second branch of spatial population dynamics modeling originated with the book "On the Dynamics of Exploited Fish Populations" by Beverton and Holt (1957; Section 10 being devoted to spatial modeling and fisheries considerations). Spatial differential equation models are developed for the cases of random dispersion, box-transfer among subareas using transport coefficients, dispersion as a function of food abundance, and oriented dispersion such as a spawning migration. In this branch, a range of spatial considerations have been entertained, including the use of closed areas in fisheries management, the effects of spatial differences on fishery catch rates when using those rates to estimate trends in stock abundance, the influence of spatial patterns when interpreting the total magnitude of fishing induced mortality, the consequences of spatial differences among fishing vessels and fish, and the ability to achieve optimum harvest levels.

The increased availability of spatial information from large-scale tagging programs has been a key driver in advancing spatial population dynamics models for marine fishes. The Inter-American Tropical Tuna Commission established such a tagging program in the Pacific Ocean, because the migrations of tuna were a major factor in stock assessment and fisheries management (e.g., Bayliff 1979). A Markovian diffusion model developed by Deriso et al. (1991) confirmed that mixing rates of yellowfin tuna differed substantially among geographic areas, which translated to area-specific impacts of fisheries management measures in the exclusive economic zones (EEZ) of different countries. Spatial models used by the International Pacific Halibut Commission (IPHC) were developed using large tagging studies over many years because, like tuna, halibut also migrate substantial distances. Deriso and Quinn (1983) conducted a scientific study that estimated halibut migration rates and developed an assessment model they termed migratory cohort analysis to provide abundance information for sub-population areas. Migratory cohort analysis is an extension of Pope's cohort analysis (see Quinn and Deriso 1999), which models fish movement among areas using a migration matrix. Their study also led to a further extension of migratory cohort analysis and catch-age analysis (Deriso et al. 1985), known as migratory catch-age analysis (Quinn et al. 1990). The development of spatial assessment models that directly utilized tagging information demonstrated that the two branches of spatial dynamics models had connected by the early to mid-1990s.

In retrospect, these efforts to estimate movement and to understand its effects on population dynamics from the 1950s to the 1990s provided a theoretical foundation for advancing contemporary spatial stock assessment. As noted in Quinn (2003), "Spatial considerations have occurred throughout the history fisheries science [e.g., Beverton and Holt (1957)], but it has really only been in the last twenty years that spatial models have emerged." The review paper by Goethel et al. (2011) and the remaining sections of this paper describe recent advances related to spatial considerations in stock assessment and management.

Recent Advances in Spatial Modeling

"The Stars Look Very Different Today"

The progression of previous fisheries symposiums focusing on spatial issues supports the view that there is a coevolution of data collection methods and modeling techniques, but incorporating the results of these efforts into management advice often lags. For instance, the "North Pacific Symposium on Stock Assessment and Management of Invertebrates" was one of the first fisheries symposiums (known to the authors), which dedicated a large portion of the meeting to spatial modeling techniques (Orensanz and Jamieson 1998). The study of invertebrates provided an opportunity to expand spatial models because collecting and analyzing spatial data is more straightforward for sessile species as compared with many motile living marine resources. Important modeling directions highlighted by this symposium included the increased use of geostatistical techniques that included environmental correlates; metapopulation models as tools for assessing spatially structured abundance and interactions among sub-populations; and incorporation of spatial fleet dynamics (i.e., incorporating effort mapping and allocation into reference point models; Orensanze and Jamieson 1998). An important theme from this conference was that, despite better recognition and incorporation of spatial processes into fisheries models, it was still unclear how to effectively use these models in the provision of management advice (Oresanz and Jamieson 1998).

No single factor can explain why spatial analyses have proliferated so rapidly since the invertebrate symposium. In 2003, Quinn noted that in order to avoid “devolution” of fisheries modeling, a critical research need would be continued advances in spatial assessment modeling. A portion of his “clouds on the horizon” outlook revolved around the belief that data collection programs would not be able to keep pace with the data needs of more complex models, particularly the requirement for spatially-explicit data. However, unforeseen technological improvements have greatly enhanced the ability to collect new information on landings locations, time spent fishing, and migration patterns, which have improved sample sizes at finer spatial scales. Similarly, enhanced computing power and advances in statistical computing software (e.g., AD Model Builder, Fournier et al. 2012; and Template Model Builder, Kristensen et al. 2016) have allowed a rapid increase in the ability of integrated stock assessment models to include non-traditional and unprocessed data, while modeling both fine- and broad-scales, which was not possible a decade previously (Maunder and Punt 2013). The field of stock identification has also matured greatly, allowing improved understanding of biocomplexity through analysis of genetics, otolith microchemistry, habitat mapping, and environmental conditions (among others; Cadrin et al. 2014). This groundswell of technical and scientific advances was an important factor in the proliferation of spatial fisheries models by providing new, spatially-explicit data sets and better understanding of the ecology underlying biocomplexity. Although the importance of preserving spatial population structure has been widely recognized, the ability to provide fine-scale scientific advice informed by observations is relatively new.

Understanding biocomplexity of fish has lagged that of other aquatic resources such as sessile invertebrates, because the complex connectivity dynamics have hindered the ability to discern population structure and to collect data at the scale necessary to model spatial dynamics appropriately (Orensanz and Jamieson 1998; Reiss et al. 2009; Goethel et al. 2016). However, due to technological advances and improvements in data availability noted previously, spatial modeling has continued to progress. Presentations at the 2015 AFS "Space Oddity" symposium highlighted that we now have data and modeling techniques to provide spatially-explicit management advice (Berger et al. 2017, this issue). Although many of the underlying methods have not changed drastically from those available during the 1998 symposium on invertebrate dynamics, the tools have been refined, are more thoroughly tested, are easier to implement, and are more flexible, including the capacity to incorporate alternate population structures (e.g., natal homing) and more rigorous statistical frameworks (e.g., the use of random effects) with increased computing power.

An interesting dichotomy arose during the AFS symposium, where it has appeared that spatial modeling research has taken diverging, yet not opposing tactics (see Figure 1 in Berger et al. 2017, this issue). The first approach emphasizes a relatively more empirical methodology by teasing out spatial information directly from the observed data. These species distribution modeling (SDM) approaches represent powerful tools in fisheries science by addressing changes in spatiotemporal distributions over time. While these statistical analyses allow implicit deduction of movement patterns, the improvement in tagging technology and associated analyses has enabled further understanding of direct movement pathways and rates of exchange from individual tag tracks. The second approach (demographically-structured modeling) emphasizes the development of spatially-explicit assessment and simulation models to explain population structure through first principles of population dynamics and the explicit modeling of connectivity. By incorporating all available spatially-explicit data sources, assessment models can explore more sophisticated movement patterns and population structures (e.g., age-based and ontogenetic movement). Both SDM and demographically-structured modeling approaches to spatial modeling have been essential for improved understanding of marine population dynamics and can be used synergistically to better assist management (Planque et al. 2011). We briefly review advances in modeling spatial processes over the last 5-10 years with a focus on significant advancements in this special issue.

Species Distribution Modeling Approaches

One of the rapidly expanding and potentially powerful fields of study in fisheries science over the last decade has been the development and application of various modeling techniques adapted to analyze the type and amount of spatially-referenced data that is being collected. These include kriging, general additive models, state-space time-series models, hierarchical models, and the use and interpretation of random effects in mixed-effect models. These approaches have aided management decision-making by improving understanding of spatiotemporal distributions, determining how such distributions relate to biotic and abiotic factors, and predicting where high incidences of bycatch are likely to occur.

In particular, the parameterization of ecological and population models with random effects has been conducive for advancing the bounds of statistical inference, distinguishing sources of error variation, and establishing a framework for continued emerging spatial research. One area of development is the multivariate extension of random effects models to account for unobserved random stochastic processes across continuous space, such as those arising from the collective influence of environmental and biological variation/covariation across a landscape. In this context, recent advances in the application of Gaussian Markov random fields (Cressie 1993; Lewy and Kristensen 2009; Haran 2011) for estimating parameters in geostatistical models have shown promise for improving survey abundance indices used in stock assessment (Thorson et al. 2015b; Cao et al. 2017, this issue); decomposing covariation between spatial distributions of species and variation due to fishing behavior in multispecies catch rates (Thorson et al. 2017b, this issue); incorporating size-specific spatiotemporal variation in species distributions (Kai et al. 2017, this issue); and detecting shifts in species distributions in response to environmental gradients (Thorson et al. 2016). In addition to providing inference about spatial dynamics, many of these geostatistical modeling techniques facilitate the proper statistical treatment of typical fisheries data that tends to exhibit strong spatial correlation.

A species' distribution, and how it changes through time and space, can be particularly informative about how a population responds to fishing, prevailing environmental conditions, multi-species interactions, and/or management regulations. Contemporary analyses of distribution (or range) shifts have moved away from point-wise descriptive statistics to the use of model-based inferences that account for the underlying correlation structure in the spatial data (e.g., geostatistics; Rivoirard et al. 2000). For example, output from geostatistical models can include location-based quantities such as the center of gravity (center of population distribution), population boundary (spatial extent), area occupied, or density hot spots (Reuchlin-Hugenholtz et al. 2015; Thorson et al. 2016), which can be used to evaluate range shifts and hypothesized factors underlying distribution changes (e.g., environmental gradients). Kai et al. (2017, this issue) applied a geostatistical framework to fishery-dependent spatiotemporal catch rate data for shortfin mako shark (*Isurus oxyrinchus*) and demonstrated, using the covariation structure among fishing locations off of Japan, that shark hotspots were not stationary through time and spatial patterns were based on shark ontogeny and length (e.g., immature individuals were more concentrated in coastal waters, while hotspots for adults were offshore and coastal). Cao et al. (2017, this issue) used a similar framework to improve survey indices of abundance for northern shrimp (*Pandalus borealis*) in the Gulf of Maine by accounting for spatial structure in the catch data and including location-specific habitat information. By directly incorporating the covariance structure in location-based data, less biased and more precise indices of abundance were developed compared to traditional design-based indices.

One relatively new area of research in distribution modeling is joint modeling of the distribution of multiple species (Clark et al. 2013; Pollock et al. 2014). Several novel approaches have been proposed to extend single species distribution models into a multi-species context by using species interaction matrices (Kissling et al. 2012). Thorson et al. (2015c) applied spatial factor analysis to jointly estimate the distribution of 20 Pacific rockfishes, and showed that in many cases it improved predictive accuracy (i.e., survey density estimates) over a single-species geostatistical approach. A further advancement has been the application of multi-species geostatistical models to fishery catch rate data that explicitly accounts for spatiotemporal variation in fishing location and timing, while also accounting for the covariance structure among species (Thorson et al. 2017b, this issue).

There are many advantages to collecting spatially-referenced data, including improved ability to evaluate broad ecosystem-based considerations under altered environmental states (e.g., climate change or other large-scale oceanographic anomalies). Changes in sea temperature, as predicted by many global circulation or ocean forecast models under increased atmospheric warming, can have a profound effect on species distribution (Walther et al. 2002; Perry et al. 2005; Hollowed et al. 2013). Much research over the last decade has been devoted to how changing oceanographic conditions leads to population redistribution through range expansion/contraction (e.g., Nye et al. 2009; Lynch et al. 2015; Thorson et al. 2016; Adams 2016), latitudinal/longitudinal range shift (e.g., Perry et al. 2005; Nye et al. 2009; Thorson et al. 2016), or shifting depth preferences (e.g., Perry et al. 2005; Engelhard et al. 2014). For example, Turner et al. (2017, this issue) used a general additive model (GAM) to show that observed and forecasted oceanographic conditions could be used to predict species distributions to reduce incidental catch of pelagic non-target species. Ecosystem-level spatial considerations can also help better determine parameters that are notoriously difficult to estimate directly (e.g., natural mortality). For instance, Sagarese et al. (2015) explored the overlap of reef fish distributions in the Gulf of Mexico with areas of high red tide incidence rates to develop an index (i.e., temporal deviates) related to time-varying natural mortality. However, such models are often validated through statistical means only with further field-based validation rarely being attempted, or with dissimilar results. For example, Anderson et al. (2016) discovered that field validation data suggested that their distribution models were invalid for sessile invertebrate species, even though those models had adequate statistical goodness of fits. Reasons suggested for the apparent model misspecification included the paucity of data available, particularly the recording of absences, the low precision of environmental variables used, and the lack of data on substrate at the resolution of the model.

Recent developments in spatial modeling have facilitated new insights into fisheries science and management, yet many of the analytical techniques underlying these models rely on extensive and accurate spatial data. Thus, there is an increasing need for data collection programs to accurately capture spatial catch, effort, and ecosystem data, particularly for programs that collect fishery-dependent data. The automation of collecting vessel location information (e.g., vessel monitoring systems or VMS data) has permitted real-time management and an improved understanding of fleet dynamics (Vermard et al. 2010; Walker et al. 2015). For example, Ducharme-Barth and Ahrens (2017, this issue) used VMS data to characterize the spatial distribution of fishing effort, including uncertainty associated with processed fishing location data, to evaluate changes in fishing behavior in response to the Deepwater Horizon oil spill. Fine-scale spatiotemporal catch and effort information (CPUE) for the snow crab fishery in the southern Gulf of St. Lawrence was used by Cadigan et al. (2017, this issue) to show strong density dependence as well as spatial variation in catchability, which if not properly addressed in the model would lead to biased stock assessment estimates (Harley et al. 2001; Wilberg et al. 2010). In general, spatial heterogeneity in population densities can result in density dependence in catch rates, which have the possibility of being diagnosed and addressed with the use of spatial models (Thorson et al. 2014). In addition to advancing new technologies for spatial data collection (e.g., satellite imagery), reconstructions of historical fishery data using contemporary techniques is still needed, because these set the context for evaluating how ecosystem services (e.g., the spatial valuation of catch; Miller et al. 2017, this issue) have changed over time.

Demographically-structured Modeling Approaches

Spatially-explicit population dynamics models incorporate assumptions of demographic processes (e.g., survival, movement, maturity, and individual growth) in an attempt to translate observed and theorized behavior into a rigorous mathematical construct (Quinn and Deriso 1999). A benefit of the explicit modeling of connectivity and spatial population structure is that hypotheses can be directly tested and compared with observed data (e.g., observed spatial distributions) to estimate the value of demographic parameters that best matches observed distributions. A better understanding of the ecological principles driving population distributions can help ascertain population resilience and allows developing predictions of potential future responses to fishing pressure and environmental change. Of course, model frameworks are simply hypotheses and fitting observed data does not guarantee accurate assumptions or predictions. However, demographically-structured modeling approaches, which explicitly model movement and spatial structure, help researchers incrementally improve understanding of how individual behavior leads to population responses and, ultimately, helps to determine levels of harvest that may or may not be appropriate (Kerr and Goethel 2014). Three alternative, though not mutually exclusive, approaches (tagging, spatial stock assessment, and simulation analysis) are often used to develop and evaluate demographically-structured spatial models that attempt to capture population structure.

1. Tagging

For exploited aquatic resources, a common goal of modeling population dynamics is to determine appropriate catch levels based on the observed and assumed dynamics. Stock assessment models have evolved to make use of new data sets to provide insights on spatiotemporal population structure (Goethel et al., 2011). In some cases, the assumption of closed population dynamics may no longer be reasonable, because assessment models can provide estimates of movement among regions by incorporating mark-recapture or satellite tagging information when available. Therefore, one of the most important uses of tagging data and the information garnered from tag analyses is to improve stock assessment models (Goethel et al. 2011). Information from tag data can be utilized in spatially-explicit assessment models in many ways (Goethel et al. 2011) including: to qualitatively evaluate assumptions regarding population structure or movement pathways; to quantitatively fix movement rates at the estimated value from the tag analysis (e.g., Quinn et al. 1990); and as an unprocessed data source within a tag-integrated assessment model (e.g., Maunder 1998; Goethel et al. 2015a).

Tagging experiments are often used to estimate movement between areas (or dispersion from a release point) and mortality over time based on tag recaptures. A population dynamics observation model of the released cohort is utilized to predict spatiotemporal recaptures, and model parameters are estimated by fitting observed to predicted recaptures through a statistical framework (e.g., Hilborn 1990). Many tagging studies still rely on the traditional mark-recapture framework to analyze tag returns, which involves discrete time steps and ignores the potential for complex spatiotemporal movement and migration pathways. Studies have shown that when the simple assumptions inherent in many tag analyses (e.g., the Brownie tag-return model) are violated, the models' ability to accurately estimate population parameters can be severely impacted (Hestbeck 1995; Hearn et al. 1998). Lauretta and Goethel (2017, this issue) developed a spatiotemporal tagging simulator to demonstrate the pitfalls of ignoring both the complex temporal and spatial dynamics of fishery processes and fish connectivity when applying Brownie tagging models. Although results indicated that reliable parameter estimates could be obtained from relatively simple tagging models, it was necessary to adjust estimation model mortality calculations for the temporal fleet structure and tag release timing and to account for connectivity dynamics.

Advances in tagging technology (i.e., the development of electronic tags) has led to the ability to better define migration pathways and uncover complex spatial population structure (e.g., natal homing) which, in turn, has required refinements in tag analysis methods (Sippel et al. 2015). For instance, traditional analyses often ignore the underlying population structure of the system (e.g., movement is treated as a Markovian process that occurs once during the time step). Herbst et al. (2015) incorporated both spawning and feeding migrations to account for complex natal homing population dynamics in a Bayesian tag analysis model. Not surprisingly, expanding electronic tag technology and methods have brought new data streams, which have introduced analytical challenges, dependent on the type of technology utilized. For instance, archival data storage tags require that geolocation methods be used to infer movement based on recorded environmental factors (e.g., temperature, depth, and, in particular, light). Liu et al. (2017, this issue) provide a novel geolocation method for demersal fish that cannot rely on light-based inference by improving geolocation likelihoods to better account for land deterrence and responses to varying tidal events. Results provided new insight into the management of Atlantic cod that traditional mark-recapture analysis could not have provided (i.e., movement across stock boundaries despite release and recapture in a single stock unit). Additionally, given that experimental designs of tag experiments are often tailored to answer ecological questions, the structure of tag release and returns is not always amenable to stock assessment applications, particularly for electronic tags (Eveson et al. 2012; Sippel et al. 2015). Galuardi et al. (2014) demonstrated how individual-based estimates of advection and diffusion from satellite tagging data could be scaled to the population level and, thereby, be directly applicable for use within spatially-explicit stock assessments.

The continuous movement exhibited by many aquatic species also warrants careful consideration. For instance, the discrete movement assumptions that are often utilized in many studies (e.g., box-transfer) may be violated, given that fish may move in and out of different mortality regimes within a given model time-step (Hestbeck 1995). Miller and Andersen (2008) provided a potential solution to the discrete movement dilemma by developing a tag estimation framework that was able to estimate a continuous time movement parameter, analogous to the way a continuous time fishing mortality parameter is estimated in most fisheries applications, which could incorporate both conventional mark-recapture and electronic tag returns into the likelihood function.

A unique alternative approach to using mark-recapture data to estimate movement is the use of natural tags (e.g., parasites; de Moor and Butterworth 2015). Bio-tagging data can refine movement hypotheses, while improving the precision in movement estimates when incorporated directly into the likelihood function of a tag-integrated assessment (e.g., South African sardine; de Moor and Butterworth 2017, this issue). Larval individual-based models (IBMs) also represent a potential alternate information source that can be utilized similar to tagging data to determine connectivity dynamics of egg and larval stages. A critical limitation for many IBM approaches, however, has been the ability to validate results with real world data (Kerr and Goethel 2014; Lowerre-Barbieri et al. 2016). Methods for evaluating simulated larval dispersal through geostatistical comparisons with larval surveys has shown promise (e.g., Hinckley et al. 2016), but unique mark-recapture experiments, implemented by chemically marking larval otoliths, provides the most direct validation tool for larval dispersal models (Secor et al. 2017). IBM results can be particularly useful to help refine estimates of productivity and population mixing within integrated life cycle frameworks (e.g., Rochette et al. 2013; Archambault et al. 2016).

2. Spatial Stock Assessment

With the ability to incorporate almost any type of quantitative data, integrated stock assessments are uniquely equipped to evolve with advances in spatially-explicit data collection techniques whether it is electronic tagging, mark-recapture, bio-tagging, genetic, otolith microchemistry or larval dispersal information (Maunder and Punt 2013). The degree of complexity of spatial assessments varies widely depending on assumed population structure and available data sources. For instance, Berger et al. (2012) developed a spatially-implicit fleets-as-areas model of Lake Erie walleye that explicitly modeled spatially-distinct fishing fleets (through different selectivity patterns) that acted on different components of the population that were assumed to have different catchability. Fleets-as-areas models (e.g., Sampson and Scott 2011; Waterhouse et al. 2014; Stewart and Martell 2014) apply separate selectivity patterns for fleets in different areas in an attempt to account for spatial differences in availability of fish as result of population structure, while still assuming a single homogenous population. On the other hand, the MULTIFAN-CL software program (Fournier et al. 1998; Hampton and Fournier 2001) explicitly models connectivity, which can be estimated from mark-recapture information (e.g., the application to Pacific yellowfin tuna), while assuming a single interbreeding population with high dimensionality in the number of regions over which individuals can be distributed. Maunder (1998) and Goethel et al. (2015a) used metapopulation dynamics to model snapper (stock SNA1) in New Zealand and yellowtail flounder in New England, respectively, allowing connectivity between sub-populations. A similar approach has also been developed for natal homing situations, which requires the additional complexity of accounting for the spatial overlap of individuals from multiple spawning populations [e.g., Atlantic bluefin tuna, Porch et al. (2001), and New Zealand snapper, Francis and McKenzie (2015)].

Although spatial models can be implemented in almost any assessment framework [e.g., virtual population analysis, Porch et al. (2001), or surplus production, Shibata et al. (2015)], integrated statistical catch-at-age modeling (Maunder and Punt 2013) is now the most commonly used approach for conducting spatial assessments of data-rich stocks because of its flexibility and statistical rigor. For example, Taylor et al. (2011) developed a tag-integrated, spatially-explicit stock assessment model for bluefin tuna that was able to incorporate information from conventional, archival, and satellite tags along with information on stock compositions of catch based on otolith microchemistry. The Taylor et al. (2011) model currently represents one of the most holistic spatially-explicit, tag-integrated assessment approaches developed due to the inclusion of varying tagging data sources, age-based movement, five geographic areas, and the incorporation of natal homing. However, the Taylor et al. (2011) model has not been implemented as the basis for providing management advice. Indeed, limited applications of spatial assessment models to real-world data exist (particularly outside of the tuna literature) and barriers that develop within the management process often prevent their use as management tools (see 'Common Pitfalls' section below and Table 1). Therefore, many recent spatial stock assessment frameworks are still undergoing simulation testing to evaluate robustness and determine reliability.

3. Simulation Analysis

Simulation analysis remains an important tool for understanding marine spatial processes (Kerr et al. 2010a), and is particularly useful for testing the robustness of spatially-explicit assessment models to various hypothesized spatial structures (Kerr and Goethel 2014). One particular complexity of developing a spatial simulation is determining realistic parameter values within and among spatial units. An approach that has been utilized is to apply a spatial assessment model to observed data in order to estimate the population parameters of interest (e.g., productivity and movement), and using those values as the basis of the operating model (Goethel et al. 2016). By using the best fit parameter estimates, the operating model is being informed by observed data and the results can be used to narrow down potential connectivity scenarios (among other important parameter gaps), while sensitivity runs can be carried out to investigate potential uncertainty in estimates or to explore alternate population states. Kerr et al. (2017, this issue) utilize this approach for Atlantic bluefin tuna by mixing expert knowledge and best fit spatial assessment parameter estimates (e.g., from the spatial assessment model of Taylor et al. 2011) to develop a seven area, two population spatial operating model incorporating natal homing. They investigate the impact of varying assumptions regarding recruitment, movement, and biology on spatial distributions, catch compositions, and population sizes. Spatial distributions and population size estimates differed substantially across the assumptions tested. Several simulation scenarios indicated that a large fraction of the smaller western population were being harvested in areas associated with the eastern population, which may be unaccounted for mortality in current closed population, single area assessment models.

Spatially-explicit simulations have provided insight into the performance of various assessment frameworks when confronted with spatial structure by exploring three common themes: the robustness of multiple independent stock assessments (i.e., no connectivity) or spatially-aggregated approaches (Cope and Punt 2011; Ying et al. 2011; Guan et al. 2013; Cao et al. 2014; Goethel et al. 2015b; Li et al. 2015; Punt et al. 2015); the performance of spatially-explicit models (particularly in regards to estimating movement and the level of correlation among movement and recruitment parameters; Maunder 1998; Carruthers et al. 2011; Hulson et al. 2011; Goethel et al. 2015b); and the expected improvement in spatial models that can be gained from including tagging data (Maunder 1998; Carruthers et al. 2011; Hulson et al. 2011; Goethel et al. 2015b). In general, spatially-explicit methods have been found to perform well, particularly when incorporating tagging information, but simpler approaches that ignore movement or are spatially-aggregated may be more robust in cases where population structure or movement mechanisms are not well understood (Hulson et al. 2011; Goethel et al. 2015b; Li et al. 2015; Punt et al. 2015). Langseth and Schueller (2017, this issue) make an important note that care must be taken in analyzing bias among spatial and non-spatial models in simulation analyses. Using a variety of methods to calculate area-specific and spatially-aggregated fishing mortality, it was demonstrated that true total fishing mortality could differ by as much as twofold depending on the method utilized, and that the relative size of areas (in relation to the fraction of fishing mortality within each area) influenced resulting calculations.

Performance of spatial models is context specific and depends strongly on the assessment model type (e.g., statistical catch-at-age or surplus production), the simulated spatial structure of the population (i.e., the combination of population structure, connectivity dynamics, and spatiotemporal variation in vital rates and recruitment), and data quality and availability. For instance, Benson et al. (2015) demonstrate that, in certain instances, spatially-aggregated assessment models can be used to develop robust management advice, but performance was critically dependent on the interactions among population structure, fleet dynamics, and management uncertainty. However, using a fine-scale simulation of a sessile scallop resource, Truesdell et al. (2017, this issue) demonstrated that spatiotemporal variation in fishing mortality led to overestimation of mortality and underestimation of biomass when the assumption of homogenous fishing pressure (i.e., equal capture probability) was not met. Similarly, Porch et al. (1998) compared a two region virtual population analysis model with and without mixing using a spatial operating model and demonstrated that, because movement was inherently misspecified (i.e., the estimation model with mixing assumed annual box-transfer movement, while the operating model utilized advection-diffusion movement with monthly time-steps), the model without movement often performed as well as that with movement (unless movement levels were extremely high). On the other hand, Ying et al. (2011) and Carruthers et al. (2011) illustrated that ignoring movement or spatial structure could be risk-prone (i.e., cause localized depletion), and that spatial surplus production models performed well for species with limited age or tagging data.

When a single population with spatial structuring exists, but limited spatially-explicit data is available, the fleets-as-areas approach is often utilized where multiple fleets, each with uniquely estimated selectivity, are used to implicitly account for spatial variation without directly modeling movement. Cope and Punt (2011) demonstrated that when catch history varied by region, aggregate and fleets-as-areas (assuming only logistic selectivity) assessments performed poorly and individual assessments of each area had low bias despite low sample sizes. Hurtado-Ferro et al. (2014) supported these findings with a spatial operating model of Pacific sardine, illustrating that in the presence of complex movement and spatial recruitment dynamics the fleets-as-areas approach can reduce bias in population parameter estimates by adjusting fleet selectivity estimates; however, large sources of bias remained. Waterhouse et al. (2014) and O'Boyle et al. (2016) demonstrated that dependable selectivity parameter priors are needed to reliably apply fleets-as-areas models, because the form or level of movement and the magnitude of differences in fishing pressure between regions will lead to estimated selectivity patterns that differ from the true selectivity patterns. For example, domed-shaped selectivity may arise from spatial heterogeneity in fishing and incomplete mixing even though true selectivity is asymptotic (Sampson and Scott 2012).

Punt et al. (2015) developed an operating model that allowed spatial variation in recruitment, growth, and mortality and found that most assessment methods (e.g., spatially-aggregated, fleets-as-areas, and spatially-explicit) resulted in biased parameters, and only spatially-explicit models that correctly identified spatial processes were unbiased. Lee et al. (2017, this issue) tested a wider variety of alternate fleets-as-areas approaches and investigated the impact of age-based movement on assessment model performance. Once again, all methods were highly biased with only the correctly specified spatially-explicit model demonstrating unbiased estimates. Notably, the spatial model that did not account for time-varying movement performed poorly, whereas a fleets-as-areas model with increased observation error (to implicitly account for process error by down-weighting length compositions) performed moderately well.

A growing concern for spatially-aggregated models has been the increased implementation of marine protected areas (MPAs), which create inherent spatial structure in the distribution of fishing effort (Punt and Methot 2004; Field et al. 2006). Because no fishing occurs inside the MPA, the fleets-as-areas approach is often ill-suited to account for MPA impacts and spatially-explicit approaches are often needed. However, Punt et al. (2017, this issue) use spatial MPA simulations to show that although a fleets-as-areas assessment for pink ling in Australia remained biased in terms of spawning stock biomass (though less biased than the spatially-aggregated assessment), this assessment approach was still able to achieve management targets provided adequate management frameworks were in place. Most studies that investigate the performance of assessment models in the presence of MPAs have generally agreed that applying spatially-explicit models that account for movement are the only way to obtain unbiased parameter estimates (Pincin and Wilberg 2012; McGilliard et al. 2015; Punt et al. 2016). Little et al. (2017, this issue) utilized a two region operating model of coral trout on the Great Barrier Reef, where the two regions were connected by larval dispersal and one area was closed to fishing (i.e., representing an MPA), to investigate the performance of a spatially-explicit assessment model ignorant of larval dispersal and the complex protogynous life history trait of the simulated population. The results support findings from previous MPA simulations that ignorance of the spatial connectivity dynamics led to bias, and the degree of bias was dependent on the level of spillover between the MPA and open areas. This bias also holds true for spatially-aggregated models, but it can be exacerbated by spatial variation in growth and exploitation (e.g., Garrison et al. 2011; Punt et al. 2016). The collection of data within the MPA (i.e., monitoring abundance through surveys) can greatly enhance model performance, and has been shown to be particularly helpful for the estimation of natural mortality (Garrison et al. 2011; Pincin and Wilberg 2012). In general, better accounting of the spatial characteristics of fisheries data (e.g., by addressing the synoptic nature of its collection, particularly in regards to the spatiotemporal synchronicity of survey data) can greatly enhance estimation of population parameters whether or not an MPA is implemented (Jiao et al. 2016).

Another form of spatial population structure that has become increasingly recognized in fish populations is natal homing. Because fish from multiple populations that do not reproductively mix overlap at various life stages and are caught as part of mixed stock fisheries, natal homing behavior has unique potential to negatively impact naïve assessment models due to ignorance of spatially varying vital rates, reproductive dynamics, and population-specific (compared to stock- or fleet-specific) fishing mortality rates (Porch et al. 2001; Guan et al. 2013). The reliability and necessity of applying natal homing models relies heavily on the situational context. For instance, Guan et al. (2013) demonstrated that if fishing is homogenously spread across the regions that the populations inhabit, then ignorance of natal homing is not detrimental. However, spatial heterogeneity in fishing practices is common, and accounting for natal homing often improves assessment and management unless movement among areas is limited (Guan et al. 2013; Li et al. 2015). Vincent et al. (2017, this issue) provided one of the most thorough investigations of the performance of assessment models that account for natal homing by simulating the dynamics of Lake Erie walleye that intermix during harvest seasons, but separate by natal population for spawning. Results illustrated that natal homing models can be reliably applied for a variety of connectivity scenarios when tagging data is available, and that both natural mortality and tag reporting rate can be accurately estimated simultaneously with movement rates. However, similar to Li et al. (2015), results indicated that natal homing models can have estimation difficulty at low inter-stock movement rates. Additionally, large discrepancies in productivity among the populations may hinder the performance of models that account for natal homing.

Regardless of the mechanism underlying population structure, the functional form of movement assumed within the spatial operating model and the associated parametrization of movement in the estimation model can strongly impact expected performance. For instance, when density-dependent movement was simulated for three stocks of yellowtail flounder off New England, Goethel et al. (2015b) illustrated that estimating time-invariant movement led to a bias similar to ignoring connectivity altogether. However, Cao et al. (2014) demonstrated that, although ignoring mixing for a metapopulation of cod off New England did cause assessment bias, the assessment model performed relatively well in terms of providing management advice, but results were heavily dependent on the timing and level of seasonal mixing.

The promising addition of linking environmental forcing variables (e.g., imposed by climate change) to spatiotemporal movement and recruitment dynamics in simulation models has been attempted in recent years. Hulson et al. (2013) investigated potential climate change impacts by simulating a northward shift in distribution and declining mean recruitment over time for Bering

Sea Pollock. Although spatially-aggregated assessment models performed well when no climate-induced impacts were simulated (i.e., movement was random), only spatially-explicit models that directly estimated year-specific movement and recruitment apportionment could accurately estimate population parameters under climate scenarios. Denson et al. (2017, this issue) simulated dynamics for a population distribution over two regions with varying fishing mortality patterns and differential recruitment apportionment determined by an environmental factor (i.e., constant, regime shift, and cyclical). The results indicated that a spatial assessment that accounted for the environmental forcing through a covariate in the recruitment function only provided more accurate parameter estimates compared to models without the environmental index if mortality differed substantially among regions. Additionally, high quality regional surveys were of more value than environmental covariates, because, in this case, surveys were able to better inform overall recruitment to the population. Although ignoring connectivity or environmental forcing in stock assessment models can be detrimental to management advice, the added complexity does not guarantee improved model performance. For instance, incorrect specification of movement dynamics (e.g., assuming time-invariant movement) may lead to biased advice, particularly in regards to estimates of productivity (i.e., due to the resulting correlation in movement and recruitment parameters; Hulson et al. 2011, 2013; Goethel et al. 2015b).

Projecting sustainable catches is, in many ways, as important as developing an accurate stock assessment model. However, the incorporation of spatial processes into simulation techniques used to develop future catch scenarios has often been overlooked, despite the increase in spatial assessment models. Ying et al. (2011) developed spatially-explicit biological reference points for a metapopulation and demonstrated that misidentifying the population structure (i.e., assuming a single population or three independent populations) led to inappropriate harvest strategies and localized depletion. Similarly, Kerr et al. (2014) demonstrated that when the complex spawning structure and connectivity dynamics of natal homing for Atlantic cod were modeled, resulting reference points (i.e., F_{MSY}) decreased substantially in comparison to results that used current management unit boundaries that ignored sub-stock structure. A spatial operating model was developed by Goethel and Berger (2017, this issue) in order to provide a holistic demonstration of how population structure and connectivity interact to determine appropriate harvest levels and evaluate the consequences of misdiagnosing population structure when setting exploitation targets. Results indicated that biological reference points substantially differed across population structures, and incorrectly specifying spatial dynamics when setting harvest levels could be as detrimental as assuming a single aggregated population. However, if fishing effort was not homogenously distributed, ignoring spatial structure became more detrimental (as the fishery aggregated on more productive units of the population). The latter result was supported by Truesdell et al. (2016), who illustrated that the spatial distribution of effort can be as important as the total fishing mortality when attempting to optimize yield- or spawning biomass-per-recruit, particularly for sessile species. The latter results highlight the importance of exploring the expected outcomes of different spatial management policies (e.g., MPA designs) and whether they will be able to meet conservation goals (e.g., Colloca et al., 2015; Edwards and Plagányi, 2011; Metcalfe et al., 2015), because most will act to redistribute fishing effort. For example, Mormede et al. (2017) applied a fine-scale operating model for Antarctic toothfish (*Dissostichus mawsoni*) incorporating connectivity between regions to determine the likely impact of various closed areas and MPA designs on future catch given a predefined management target (i.e., 50% of virgin spawning biomass; see the Antarctic toothfish case study for further discussion).

The development of spatial multispecies models is an important next step to test various single-species and multispecies management actions. Kapur and Franklin (2017, this issue) used a spatially-explicit, biophysical functional group multispecies simulation model, wherein various animal and plant groups with similar ecosystem roles were modeled as a single unit, to investigate ecosystem responses to environmental change and fishery closures. By taking a multispecies approach they found that, despite a simulated decline in coral cover, fish biomass and catches were unlikely to be impacted to the extent previously envisioned. However, catch composition would likely change from predominantly piscivores to herbivores (as coral was replaced with algae) and the use of MPAs would unlikely mitigate coral declines or ecosystem reorganization. Multispecies versions of SDMs are also becoming increasingly available for exploring the impact of species interactions on ecosystem dynamics (Thorson et al. in press). Ultimately, better understanding of spatial processes will aid in the development of ecosystem management, which requires knowing how individual species utilize various spatially-defined habitat niches and how spatial interactions within and across species impact management performance.

Incorporating Spatial Models into the Management Process

"Now It's Time To Leave The Capsule If You Dare"

There is little indication that spatial modeling techniques have been fully utilized in providing scientific advice for fishery management, despite increasing use of these methods. A prominent sentiment from the AFS "Space Oddity" symposium was that many managers do not fully understand how to translate spatially-explicit scientific results into spatial policies, which mimics a point of emphasis from the 1998 invertebrate symposium (Orensanz and Jamieson 1998). For example, spatial management measures (e.g., closed areas) are often based on scientific evidence (e.g., observed distributions of spawning), but seldom are models used directly to provide quantitative support for the placement of MPAs or the setting of regional quotas (La Valley and Feeney 2013). Distributional modeling has quickly become a powerful tool that allows for near real-time spatial management based on model predictions of habitat utilization or species co-occurrence, often to prevent bycatch of a particular species (e.g., Hobday et al. 2010; Cosandey-Godin et al. 2014, Ward et al. 2015, Turner et al. 2017, this issue). Yet, these approaches have rarely been applied as direct tools to inform spatiotemporal quota determinations. Without the ability to advise management with stock assessment outputs that match the scale of desired regional or sub-stock catch limits, many management decisions remain essentially *ad hoc* and informed by qualitative observations (Orensanz and Jamieson 1998; Goethel et al. 2016) or historical fishing measures (e.g., catch and effort). In order to develop fully integrated spatial management, fisheries policy needs to be shaped by both model outputs at appropriate spatial scales and observed data at all stages of implementation.

There is common acknowledgement that spatial processes are important and that spatial structure should be maintained, yet a disconnect remains preventing the flow of information needed to address spatial considerations in fisheries resources (Figure 1). Ideally, spatial heterogeneity in resource distribution and demographics should be accounted for in the assessment, which can then provide outputs at the scale of spatial management actions, with distributional models reflecting real-time data then applied to implement dynamic spatial management (e.g., bycatch avoidance). These methods have been used infrequently as the base-case model that supports management (e.g., Thorson and Wetzel 2015). So why have these methods not been more thoroughly implemented and fully utilized for quota management? We believe that many of the impediments are due to data (quality and quantity) or institutional limitations (Table 1). Either the lack of spatial data prevents implementation of the various types of spatial modeling techniques, or institutional inertia is preventing the uptake of results from more complicated approaches, such as spatial models, by managers. Limited understanding, perceived deficiencies, or assumed lack of fully vetted methods may lead to inadequate trust in new models and delay the peer review process leading to a continuation of status quo management. Thus, communication among scientists, managers, fishermen, and other stakeholders is likely to remain a major impediment to using spatial models as the basis of management advice.

Common Pitfalls Associated with Spatial Models

Historically, implementation of spatial modeling techniques was hindered by the ability to definitively prove when spatial processes were important and thus explicit modeling of them was necessary. However, given the current state of knowledge regarding the importance of spatial dynamics in defining population structure and optimizing resource utilization, the issue has shifted to defining when spatial structure can safely be ignored, understanding the implications of ignoring it, and identifying specific data gaps that hinder further spatial model development (Table 1). Accounting for spatial processes requires first knowing what type of spatial structure exists. Stock identification techniques and the collection of spatially-explicit data have been useful to identify population components and resource distributions, but this type of information is simply not available for all species or population components. Additionally, connectivity among population components remains difficult to identify and parametrize, and no clear guidance is available on what type or levels of movement require explicit incorporation in spatial models. When complex spatial structure exists (with or without connectivity among population components), value judgements are often needed to determine conservation goals (Kerr et al. 2016). For instance, at what spatial scales do population components require protection? Simulation modeling can be a useful tool to explore implications of different conservation strategies, but clear communication of management objectives is needed to guide model development (e.g., spatial scales of management importance) as is the conveyance of data and model limitations on output used for management (Figure 1).

Spatial assessment models can be more data intensive than non-spatial counterparts, but in some cases the data required are available but are not utilized, underutilized, or aggregated (Ultang 1998; Cope and Punt 2011). Compared to non-spatial models, spatial models need to be more explicit about the assumptions that underlie the population dynamics, and therefore analysts are often forced into using more data to justify these explicit assumptions that otherwise would be left unexamined. In some cases (e.g., as with distribution models), utilizing data at the scale it was collected can provide more direct information or allows it to be spatially linked to other spatial attributes (e.g., satellite oceanographic imagery). Similarly, integrated assessment models are able to incorporate alternate data sources (e.g., tagging information) that might otherwise be overlooked. Although spatial models may be difficult to implement in some data-limited situations, spatial techniques are often able to utilize the same data as spatially-aggregated models, while providing more information content (e.g., Thorson et al. 2017a). To optimize the value of data for spatiotemporal modeling, data collection protocols should consistently include spatial attributes (whenever possible) that can be used to cross-reference or supplement standard data series.

Overcoming the difficulty of conveying the multidimensional aspect of spatial models to stakeholders can complicate implementation, and more resources and improved communication are required to promote understanding and comfort with model results. Spatial models are often perceived as more complex than spatially-aggregated models, which has often led to criticism that they are over-parametrized or unstable models requiring more thorough validation. There are typically more data weighting issues (e.g., how to internally weight tagging data versus traditional assessment data) and other complexities that need to be resolved when performing spatial assessments. For instance, recruitment and movement parameters are often highly correlated (i.e., without high quality tagging data, movement can be interpreted as recruitment and vice versa in spatial assessment models), which can impact the ability to accurately estimate population productivity and biomass (e.g., Goethel et al. 2015b; Vincent et al. 2017, this issue). However, similar complexities need to be dealt with when using statistical spatially-aggregated models as well (e.g., recruitment parameters are often highly correlated and not well estimated). In addition, spatial models have the potential for increased variance of parameter estimates when limited data are split into spatial units. However, simulation testing of distribution models and spatial assessments has shown that accuracy can be improved (or similarly bias removed) by accounting for spatial processes (e.g., Goethel et al. 2015b).

Development of spatially-explicit stock status indicators (i.e., biological reference points) has lagged spatial assessments mainly because uncertainty exists in how to deal with assumptions regarding future connectivity dynamics and at what spatial scale reference points should be applied. Without well-defined reference points, it is difficult to implement a spatially-explict assessment as the basis of management advice. Although there is uncertainty in spatial reference points models, there is also inherent uncertainty when predicting future recruitment and when attempting to spatially partition regional quotas from non-spatial models (e.g., as is done with Bering Sea and Gulf of Alaska sablefish; Hanselman et al. 2015). Eventually, alternate metrics could be used as spatial stock status indicators, which could avoid the need to project uncertain population dynamics (Reuchlin-Hugenholtz et al. 2015, 2016).

Given the multitude of spatial models and spatially-explicit data sets, we argue that a spatial technique exists for many fisheries applications. Although spatial techniques have a number of limitations compared to spatially-aggregated counterparts, they have the potential to provide more robust management advice at desired spatiotemporal scales. Spatial models can provide more realistic frameworks that better match the population distribution and heterogeneity in spatial processes. However, spatial applications may not be necessary or appropriate in some situations, especially when limited data exist or little is understood regarding population structure. Yet, as the push for spatiotemporal adaptive management advice moves forward, it is important to realize that methods exist to evaluate spatial processes across the assessment-management interface.

Operationalizing spatial models for use in management

In a recent survey of United States stock assessments, around 60% of assessed stocks were identified as exhibiting spatial structure, but only 16% of the assessments actually accounted for the observed spatial processes (Figure 2). The mismatch between observed or hypothesized spatial dynamics and spatial assumptions in the corresponding assessments is concerning, especially considering the mounting evidence that ignoring spatial population structure and connectivity can bias assessment outputs (Cope and Punt 2011; Hulson et al. 2011; Goethel et al. 2015b). As discussed, there are a variety of valid and perceived reasons that spatial modeling techniques have not been more widely incorporated into the stock assessment process (Table 1). The question is then, how can these obstacles be overcome in order to better utilize spatial models and incorporate the information garnered from them into management advice? We suggest that a synergistic use of both spatial distribution and demographically-structured models along with aggregated, non-spatial models can help provide the most robust advice to fisheries managers. Continued fine-scale data collection and better communication with stakeholders and managers is also needed to increase the implementation of spatial methods (Table 1).

Distributional modeling and integrated assessment models should not be viewed as opposing paradigms for dealing with spatial structure. Both approaches can be applied to provide improved management advice that incorporates spatial processes (Figure 3). For instance, Thorson et al. (2017, this issues), Cao et al. (2017, this issue), and Kai et al. (2017, this issue) demonstrate how distributional models can be used to provide refined abundance indices that account for spatiotemporal variability. The results of these approaches can then be easily incorporated into spatially-explicit integrated assessment models to account for connectivity and spatial processes within the population dynamics. The flexibility of distributional models can also help guide management post-assessment by informing real-time adaptive spatial management (e.g., bycatch avoidance; Turner et al. 2017, this issue).

Although there is strong evidence to suggest that spatial models should become *de facto* tools for many assessed fish stocks around the world, we do not suggest the abandonment of non-spatial approaches. When spatial structure is observed, it should become routine practice to simulation test the robustness of both non-spatial and spatially-explicit methods. Ideally, full management strategy evaluation (MSE) would be applied to determine whether simplistic non-spatial or trend-based (e.g., Geromont and Butterworth 2015) assessment methods could be robustly implemented in conjunction with adaptive spatial management when spatial processes exist (Punt et al. 2017, this issue). However, as Goethel and Berger (2017, this issue) illustrate, when full assessments are utilized it is also important to use MSE to test the robustness of the potential harvest control rules (including the spatial assumptions of the models used to develop stock status indicators), because the reliability of the associated biological reference points can be as important as the robustness of the assessment model itself.

Communication breakdown is a major hindrance to the implementation of properly specified spatial management (Table 1). Although it is now widely understood by scientists, managers, and stakeholders that spatial processes are important for the persistence and resilience of aquatic resources, there remains a communication gap in terms of what spatiotemporal scales can be reliably monitored, what data might be needed to provide model outputs at the scale of desired management actions, whether it is necessary to have model outputs at that scale, and whether spatial processes are important enough to even require consideration. It is possible that with increased implementation of MSEs, which by definition includes stakeholders directly in the development of management procedures, communication may be improved. Ultimately, a flow of information is necessary among stakeholders, managers, data collectors and assessment scientists to develop and refine the framework upon which management is based (Figure 1). Through simulation analysis and resulting decision support tools (e.g., MSE), scientists can examine the importance of spatial processes and the implications of ignoring them under alternative management frameworks, while also illustrating the cost and benefits of new data collection schemes or the addition of new types of data (e.g., tagging or ecosystem data). Using MSE to examine the entire assessment-management framework (i.e., data collection, stock assessment, stock status determination, and harvest policy) is a rigorous approach to evaluate numerous aspects of the management process and promotes understanding of the implications of various management decisions.

We illustrate problems encountered when attempting to implement spatial models as the basis of management advice through the examination of case studies (Figures 4-6). Each case study highlights lessons learned and practical guidance for the process of providing advice on spatially-structured populations for fisheries management.

Conclusion

"Can you hear me, Major Tom?"

Spatial population complexity can influence assessment and management considerations at two different, though not mutually exclusive, biogeographic scales. Inter-stock (or population level) spatial complexity can manifest when spatially-distinct or spatially-overlapping populations or population components exist within a management unit and require independent monitoring. Relatively low spatiotemporal overlap or limited interchange (e.g., metapopulation dynamics) can result in population components that respond differentially to environmental perturbation or harvest, while overlapping populations may exist with distinct productivity and growth dynamics maintained through natal homing. In either case, inter-stock spatial complexity may warrant independent conservation of populations or population components whether or not genetic differences exist.

Intra-stock (or contingent level) spatial complexity is exhibited when there are temporal changes in spatial distributional patterns (e.g., due to seasonal migration) or management measures (e.g., harvest regulations); gradients in demographic rates or sex and age composition (e.g., due to ontogenetic movement); or localized variation in abundance (e.g., due to habitat suitability or sessile adult stages). When intra-stock spatial complexity exists, fine-scale management may be necessary to avoid localized depletion, especially when interchange rates between low and high density areas are limited.

Even though there are strong differences in assessment and management approaches for inter- compared to intra-stock spatial complexity, applying models that account for spatial structure at the appropriate scale is important for implementing well-informed management advice. The case studies exemplify these differences where spatial uncertainties are issues for management. New Zealand snapper demonstrates inter-stock complexity where the management area comprises two or more biological stocks, but there is uncertainty about the number of stocks, spatial stock boundaries, and levels of interchange among geographic areas (Figure 4). Pacific halibut (Figure

5) and Antarctic toothfish (Figure 6) illustrate intra-stock complexity wherein the spatial extent of the stock is reasonably well understood, but there is uncertainty in the spatiotemporal dynamics. It is important to delineate these types of spatial complexities while adequately estimating scientific uncertainty, because management considerations (e.g., catch limit buffer) and assessment requirements differ depending on the situation.

While detailed spatial analyses can provide unique insight into micro- and mesoscale population dynamics, many challenges inhibit their implementation and use as management tools. Applying spatial approaches tends to increase data requirements and complexity, which necessitates additional investments in research and monitoring, and may expand the scope of the stock assessment and peer-review process **(**Table 1**)**. Additionally, it can be difficult to explain model complexities to stakeholders, which may generate reluctance by stakeholders to embrace an alternative approach, and validation of new modeling techniques can be arduous when other well understood and generally accepted approaches have been utilized for decades (i.e., overcoming institutional inertia). However, spatial models can be configured to match the scale of data currently being collected and are more readily amenable to the complex population structures that are being uncovered for marine species. Additionally, better accounting of biocomplexity may lead to models that better reflect observed patterns by fishermen, which can help improve acceptance of scientific outputs and collaborations with stakeholders (La Valley and Feeney 2013).

Transitioning to spatially-explicit assessments is not always necessary (or even feasible), but when spatial structure is a critical component of a species' life history and spatially-explicit data exist, investigation of spatial approaches can be advantageous. Alternative hypotheses regarding spatial processes can be further evaluated in simulations, and the robustness of management advice provided through both spatial and non-spatial models can be explored. In some cases, spatially-aggregated models have proven more robust than spatially-explicit counterparts, especially when there is uncertainty in movement dynamics, but this needs to be tested as it is case-specific. Even after spatial assessment techniques have been thoroughly vetted and validated with simulated and observed data, there has often been reluctance to adopt them. Given the capability of spatial models to reflect the spatiotemporal dynamics of fleet behavior, catch and effort, population structure, management regulations, and spatial zoning, we conclude that spatial models should be more routinely considered. Additionally, when spatially-explicit stock assessment approaches have been rigorously tested, they should become more readily utilized as the basis for management advice. Ultimately, we envision that the next step in the development of holistic ecosystem-based management will be improved understanding of spatial processes and incorporating the spatial dimension (which often inherently includes ecosystem interactions) into current single species modeling and management advice. The articles in this special issue (see Berger et al. 2017, this issue) represent significant advances toward this goal.

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Table 1. Potential barriers to implementation of spatial models as the basis for fisheries management advice along with future solutions.

	Hindrance	Future Needs
Data	Lack of Spatially-Resolved Data	Continued Spatially-Explicit Data Collection
	Uncertain Population Structure	Genetic and Otolith Data/Analysis
	Unresolved Connectivity Dynamics	Improved Tagging Information
Models	Performance Uncertainty	Ongoing Simulation Testing
	Ability to Make Operational	Time to Apply within Assessment Cycles
	Limited Forecasting Ability	MSE[1] to Evaluate Robust Assessment-Management Frameworks
Management	Mismatch with Assessment Spatiotemporal Scale	Communication of Ideal Spatial Scales from Managers to Scientists
	Limited Understanding	Communication of Model Structures from Scientists to Stakeholders
	Institutional Inertia	Increased Exposure

[1] Management strategy evaluation

Figure 1. Conceptual diagram illustrating the flow of information necessary to eliminate discontinuities across the assessment-management interface (shaded dashed rectangle) when implementing spatial management. Various participants involved in the management process (top circle) should determine the desired spatiotemporal management scale, which must then be clearly communicated to data collectors and stock assessment scientists. Scientists involved in the development of resulting scientific advice (bottom circle) must then determine the feasibility of the desired management scales, and the implications of choosing a given spatiotemporal scale should be communicated back to managers. Through decision analysis tools, such as management strategy evaluation (MSE), scientists and managers should be continually interacting to refine harvest strategies and improve resulting management advice, thereby creating a holistic approach that bridges the assessment-management interface.

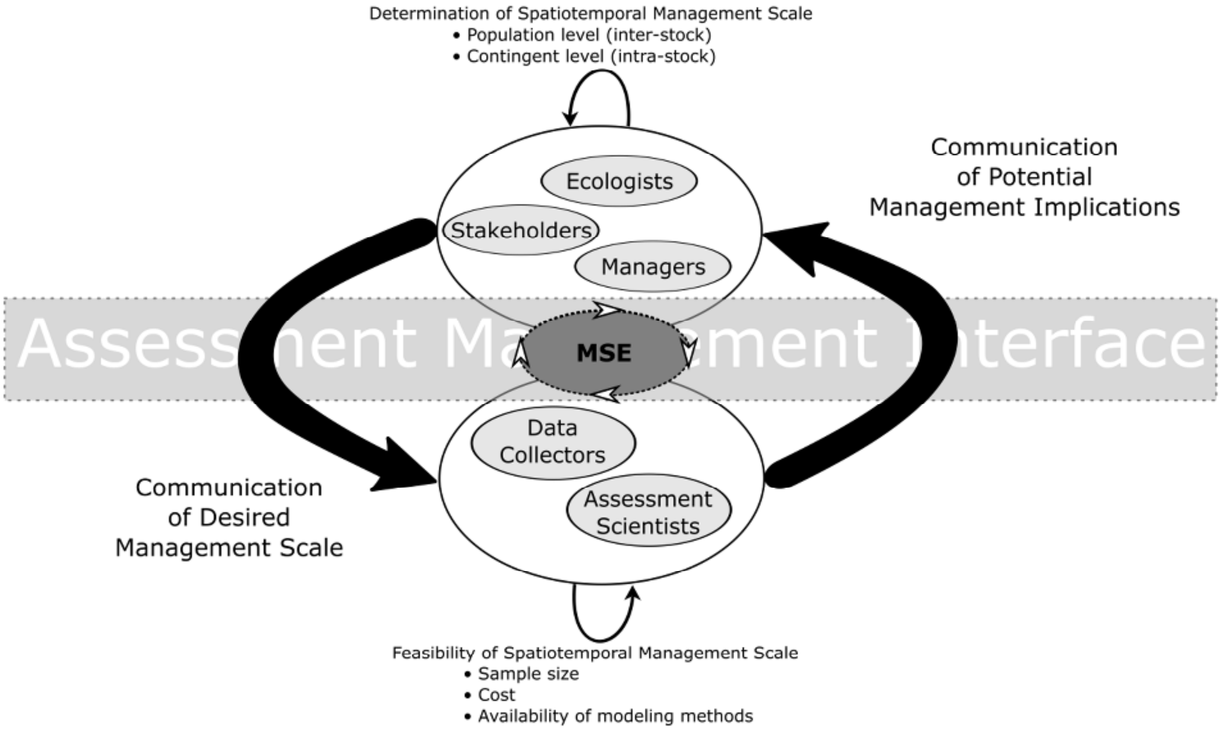


Figure 2. Summary of responses by National Marine Fisheries Service stock assessment scientists to a 2016 questionnaire related to aspects of spatial stock structure in their recent stock assessments. Respondents supplied information about stock assessments for 59 managed fish stocks (Table S1), representing all regions of the United States continental coastal waters, Alaskan coastal waters, and the Pacific Islands region. Respondents were allowed to choose one answer that best fit their assessment situation (panel A and C) or were allowed to choose all categories that applied to their situation (panel B). All responses were made voluntarily, and thus do not represent a random sample or census.

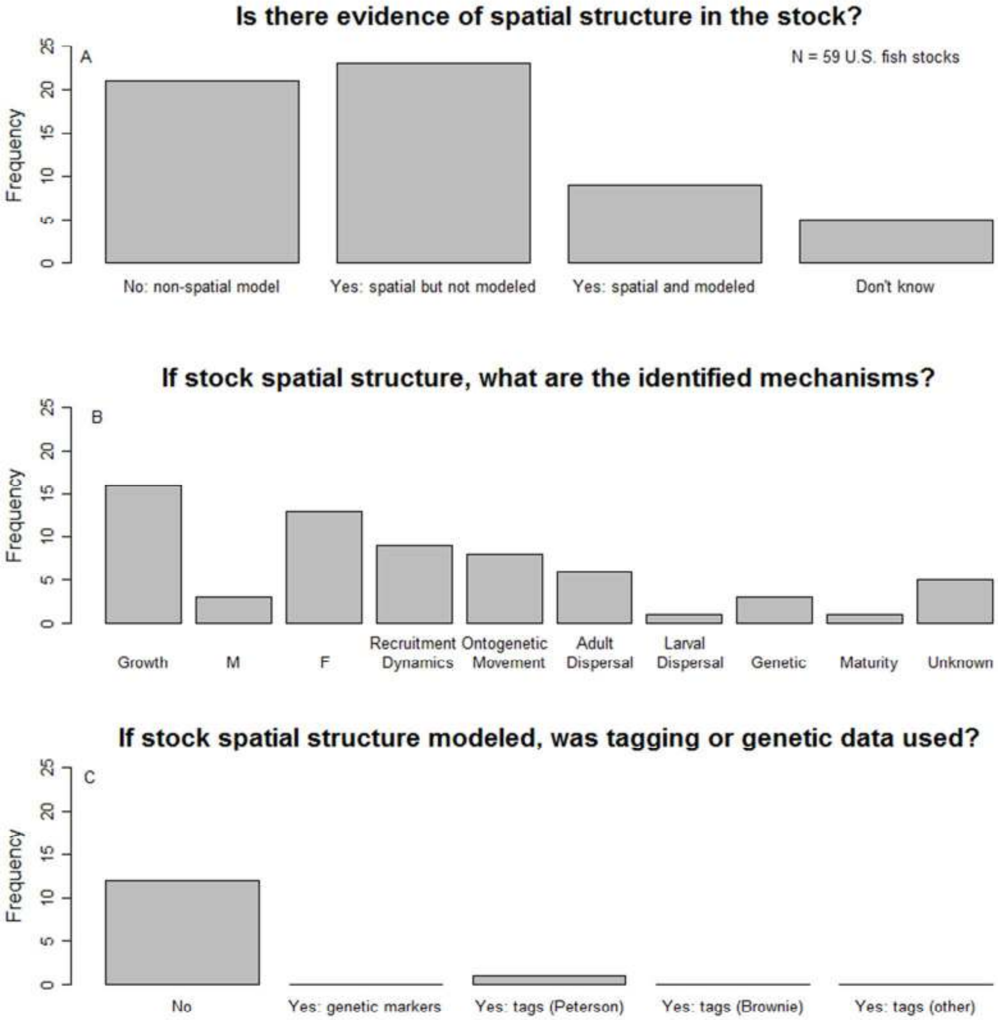


Figure 3. Conceptual diagram illustrating the synergistic approach to simultaneously utilizing species distribution models (SDMs) and demographically-structured models (DSMs). SDMs can be applied to the raw data to provide refined abundance indices that can be fed directly into spatially-explicit integrated assessment models (i.e., DSMs). Scientific advice from the DSMs is then incorporated into the management framework to set catches at the desired spatiotemporal scale. Based on real-time data collection, SDMs can again be applied to provide forecasts of species distributions, which can inform in-season management decisions in order to avoid bycatch or the exceeding of catch targets. In the long-term, management strategy evaluation (MSE) can be developed to determine the robustness of the assessment-management framework and to indicate if simpler approaches may be more suitable.

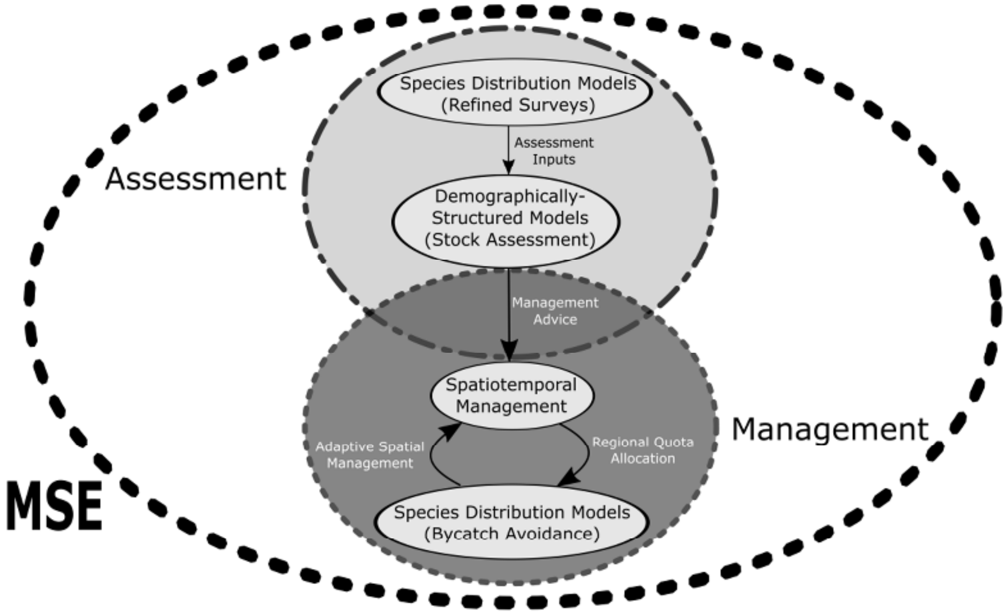
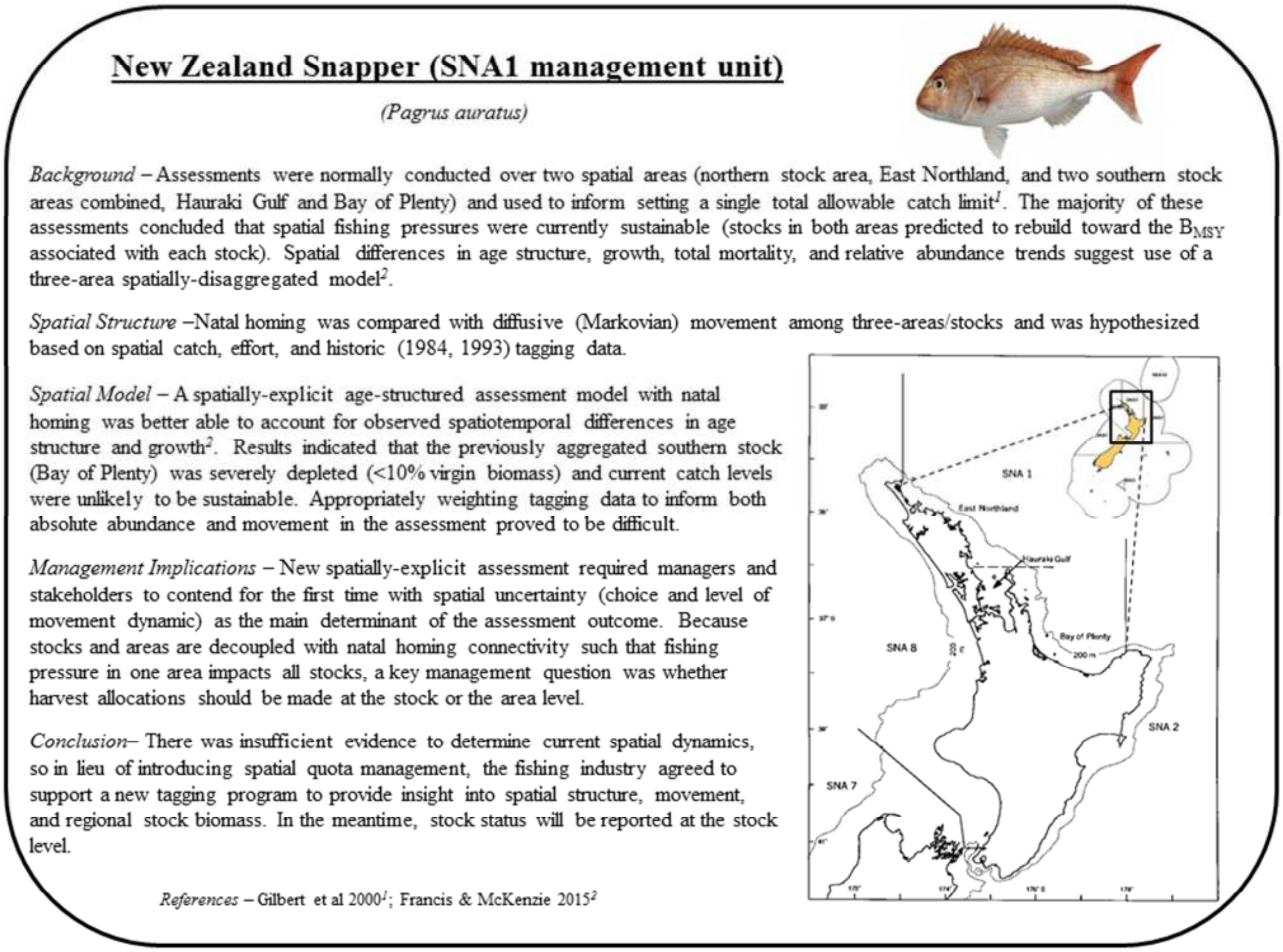


Figure 4. Case study (New Zealand snapper; photo credit: Ministry for Primary Industries) describing the identification and incorporation of spatial population structure into stock assessment models, including complications that can emerge when developing and implementing these models for use as the basis for fishery management.



New Zealand Snapper (SNA1 management unit)

(Pagrus auratus)

Background – Assessments were normally conducted over two spatial areas (northern stock area, East Northland, and two southern stock areas combined, Hauraki Gulf and Bay of Plenty) and used to inform setting a single total allowable catch limit[1]. The majority of these assessments concluded that spatial fishing pressures were currently sustainable (stocks in both areas predicted to rebuild toward the B_{MSY} associated with each stock). Spatial differences in age structure, growth, total mortality, and relative abundance trends suggest use of a three-area spatially-disaggregated model[2].

Spatial Structure –Natal homing was compared with diffusive (Markovian) movement among three-areas/stocks and was hypothesized based on spatial catch, effort, and historic (1984, 1993) tagging data.

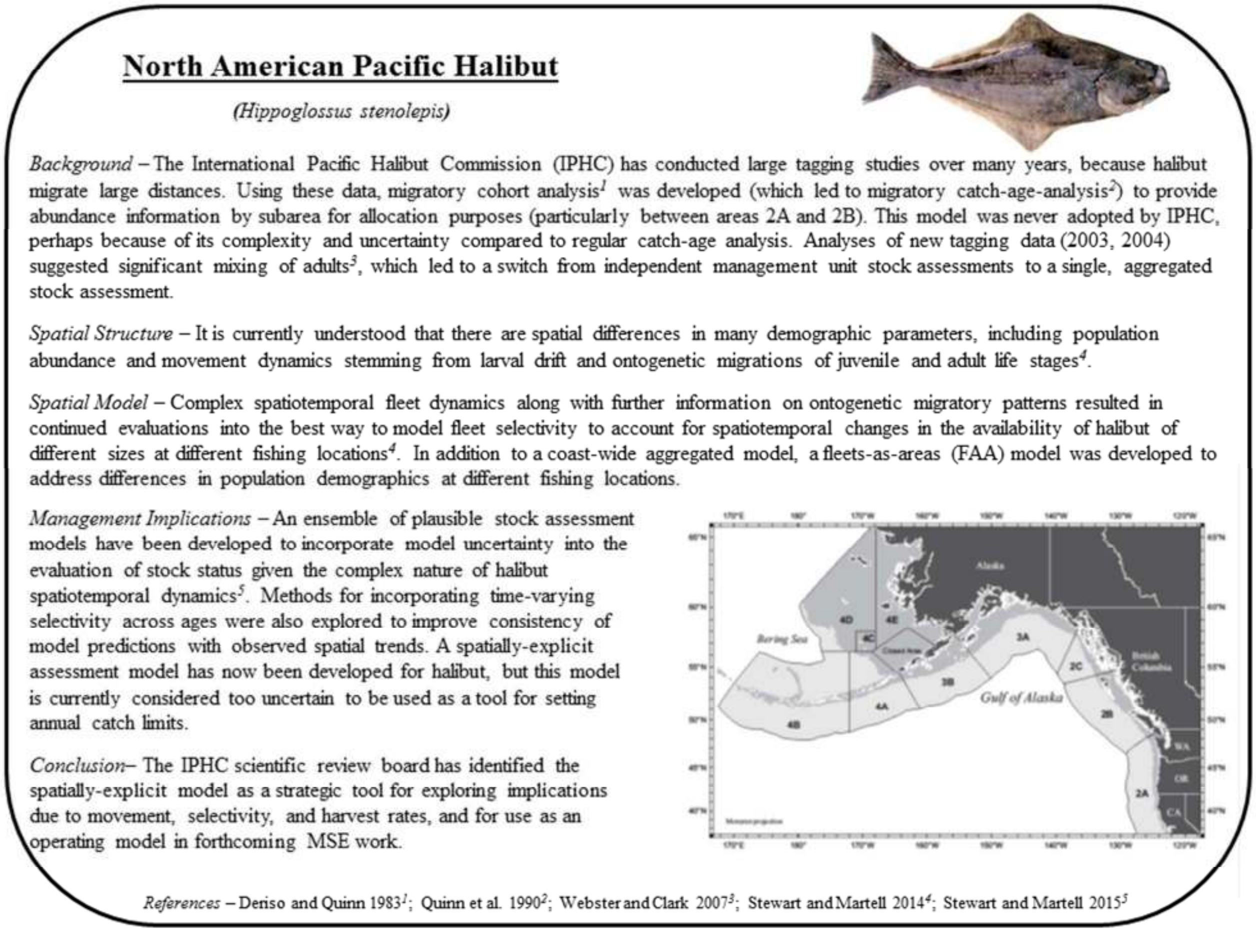
Spatial Model – A spatially-explicit age-structured assessment model with natal homing was better able to account for observed spatiotemporal differences in age structure and growth[2]. Results indicated that the previously aggregated southern stock (Bay of Plenty) was severely depleted (<10% virgin biomass) and current catch levels were unlikely to be sustainable. Appropriately weighting tagging data to inform both absolute abundance and movement in the assessment proved to be difficult.

Management Implications – New spatially-explicit assessment required managers and stakeholders to contend for the first time with spatial uncertainty (choice and level of movement dynamic) as the main determinant of the assessment outcome. Because stocks and areas are decoupled with natal homing connectivity such that fishing pressure in one area impacts all stocks, a key management question was whether harvest allocations should be made at the stock or the area level.

Conclusion– There was insufficient evidence to determine current spatial dynamics, so in lieu of introducing spatial quota management, the fishing industry agreed to support a new tagging program to provide insight into spatial structure, movement, and regional stock biomass. In the meantime, stock status will be reported at the stock level.

References – Gilbert et al 2000[1]; Francis & McKenzie 2015[2]

Figure 5. Case study (North American Pacific halibut; photo credit: Washington Department of Fisheries and Wildlife) describing the identification and incorporation of spatial population structure into stock assessment models, including complications that can emerge when developing and implementing these models for use as the basis for fishery management. Inset map courtesy of the International Pacific Halibut Commission (http://www.iphc.int/).



North American Pacific Halibut

(Hippoglossus stenolepis)

Background – The International Pacific Halibut Commission (IPHC) has conducted large tagging studies over many years, because halibut migrate large distances. Using these data, migratory cohort analysis[1] was developed (which led to migratory catch-age-analysis[2]) to provide abundance information by subarea for allocation purposes (particularly between areas 2A and 2B). This model was never adopted by IPHC, perhaps because of its complexity and uncertainty compared to regular catch-age analysis. Analyses of new tagging data (2003, 2004) suggested significant mixing of adults[3], which led to a switch from independent management unit stock assessments to a single, aggregated stock assessment.

Spatial Structure – It is currently understood that there are spatial differences in many demographic parameters, including population abundance and movement dynamics stemming from larval drift and ontogenetic migrations of juvenile and adult life stages[4].

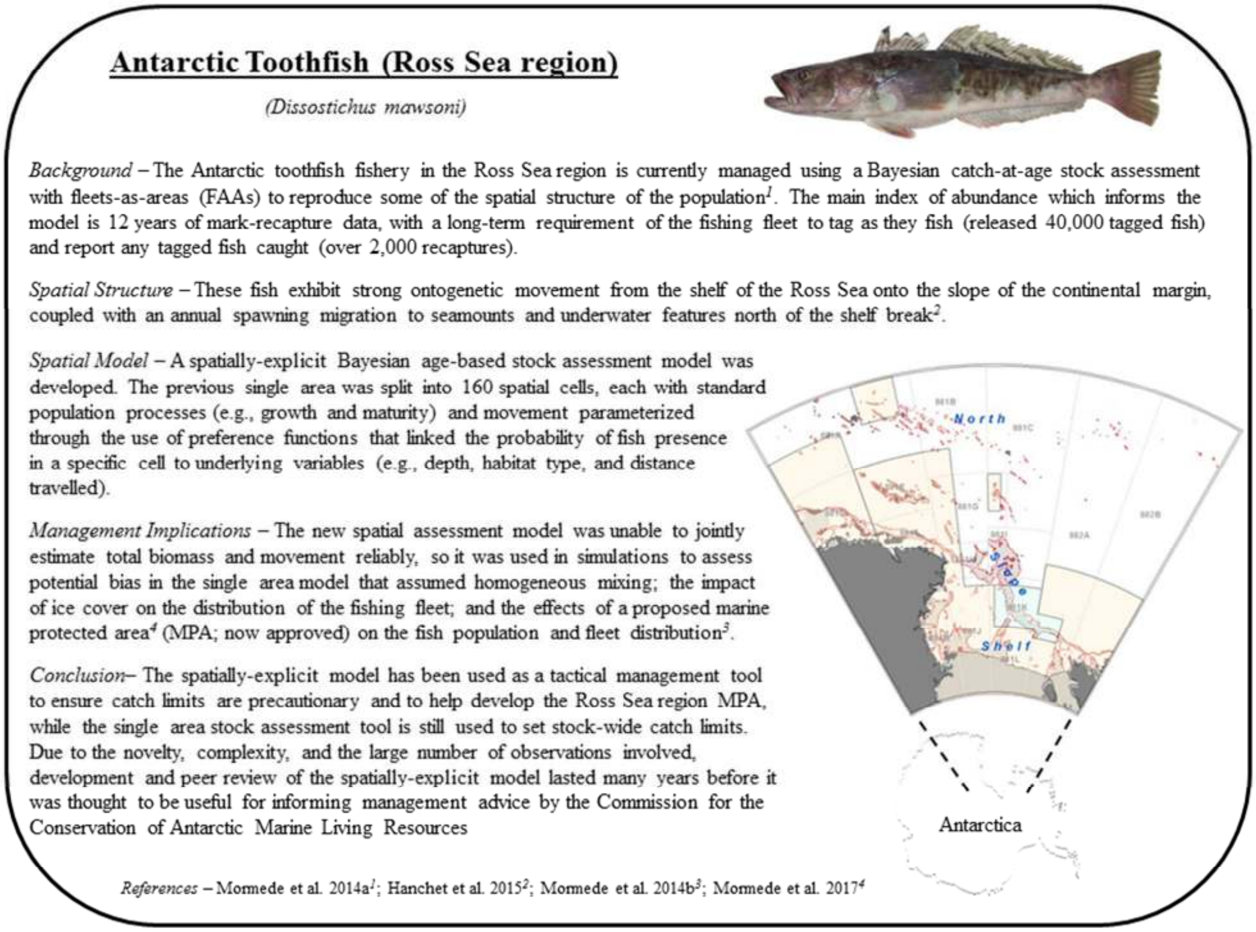
Spatial Model – Complex spatiotemporal fleet dynamics along with further information on ontogenetic migratory patterns resulted in continued evaluations into the best way to model fleet selectivity to account for spatiotemporal changes in the availability of halibut of different sizes at different fishing locations[4]. In addition to a coast-wide aggregated model, a fleets-as-areas (FAA) model was developed to address differences in population demographics at different fishing locations.

Management Implications – An ensemble of plausible stock assessment models have been developed to incorporate model uncertainty into the evaluation of stock status given the complex nature of halibut spatiotemporal dynamics[5]. Methods for incorporating time-varying selectivity across ages were also explored to improve consistency of model predictions with observed spatial trends. A spatially-explicit assessment model has now been developed for halibut, but this model is currently considered too uncertain to be used as a tool for setting annual catch limits.

Conclusion– The IPHC scientific review board has identified the spatially-explicit model as a strategic tool for exploring implications due to movement, selectivity, and harvest rates, and for use as an operating model in forthcoming MSE work.

References – Deriso and Quinn 1983[1]; Quinn et al. 1990[2]; Webster and Clark 2007[3]; Stewart and Martell 2014[4]; Stewart and Martell 2015[5]

Figure 6. Case study (Antarctic toothfish; photo credit: National Institute of Water and Atmospheric Research) describing the identification and incorporation of spatial population structure into stock assessment models, including complications that can emerge when developing and implementing these models for use as the basis for fishery management.



Antarctic Toothfish (Ross Sea region)

(Dissostichus mawsoni)

Background – The Antarctic toothfish fishery in the Ross Sea region is currently managed using a Bayesian catch-at-age stock assessment with fleets-as-areas (FAAs) to reproduce some of the spatial structure of the population[1]. The main index of abundance which informs the model is 12 years of mark-recapture data, with a long-term requirement of the fishing fleet to tag as they fish (released 40,000 tagged fish) and report any tagged fish caught (over 2,000 recaptures).

Spatial Structure – These fish exhibit strong ontogenetic movement from the shelf of the Ross Sea onto the slope of the continental margin, coupled with an annual spawning migration to seamounts and underwater features north of the shelf break[2].

Spatial Model – A spatially-explicit Bayesian age-based stock assessment model was developed. The previous single area was split into 160 spatial cells, each with standard population processes (e.g., growth and maturity) and movement parameterized through the use of preference functions that linked the probability of fish presence in a specific cell to underlying variables (e.g., depth, habitat type, and distance travelled).

Management Implications – The new spatial assessment model was unable to jointly estimate total biomass and movement reliably, so it was used in simulations to assess potential bias in the single area model that assumed homogeneous mixing; the impact of ice cover on the distribution of the fishing fleet; and the effects of a proposed marine protected area[4] (MPA; now approved) on the fish population and fleet distribution[3].

Conclusion– The spatially-explicit model has been used as a tactical management tool to ensure catch limits are precautionary and to help develop the Ross Sea region MPA, while the single area stock assessment tool is still used to set stock-wide catch limits. Due to the novelty, complexity, and the large number of observations involved, development and peer review of the spatially-explicit model lasted many years before it was thought to be useful for informing management advice by the Commission for the Conservation of Antarctic Marine Living Resources

References – Mormede et al. 2014a[1]; Hanchet et al. 2015[2]; Mormede et al. 2014b[3]; Mormede et al. 2017[4]