

# **Evaluating harvest strategies that account for fish population structure: an integrative review of key uncertainties and future research needs**

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# Approval

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## **Abstract**

Fisheries management decisions are guided by the outcomes from stock assessment models, which typically assume that fish stocks represent single homogenous populations. However, species normally exhibit complex spatial structure. Using outputs from spatially aggregated stock assessment models to inform harvest strategies in spatially structured fisheries could lead to management failure and erosion of biocomplexity. This paper summarizes how spatial population structure has been addressed in the fisheries literature and explores options for developing harvest strategies that address fish population spatial structure. I also highlight common pitfalls and data needs associated with spatial modeling and harvest strategies. Continued investment in spatial and finer-scale data collection and associated spatial analysis are necessary to develop effective spatial harvest strategies. I conclude that developing spatial modelling and harvest strategies for fishery species is an important step to address the complex nature of marine population structure.

**Keywords:** Spatial; population structure; harvest strategies; simulation; stock assessment; operating models

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# Chapter 1.

## Introduction

### 1.1. What is a population

Despite the prolific use of the term "population", there is no consensus on its definition or use from a fisheries management perspective (Waples and Gaggiotti 2006; Beamish *et al.* 2009). A variety of definitions exist in ecological-related textbooks and literature. Hilborn and Walters (1992) define a population as “an arbitrary collection of individuals of fish that is large enough to be essentially self-producing (abundance changes are not dominated by immigration and emigration), with members of the collection showing similar patterns of growth, migration and dispersal.” Similarly, Berryman (2002) defines a population as a collection of conspecific individuals in a closed region without immigration and emigration, where the dynamics are driven primarily by birth and death. Quinn and Deriso (1999) define a population (a unit stock) as an aggregation of fish individuals that can be managed as a discrete unit. In the review of Waples and Gaggiotti (2006) entitled “What is a population?”, they choose to define a population as “a group of organisms of the same species occupying a particular space at a particular time”. These definitions imply that populations of a certain species are self-sustaining and are largely isolated from each other. They also imply that fisheries do not take mixed catches from different populations, so the managers can apply one single management policy to different populations instead of customizing management policies to different populations. Ciannelli *et al.* (2013) expand Berryman’s (2002) definition according to the levels of aggregations: (1) sympatric discrete populations, (2) spatially complex populations, e.g. metapopulations and source – sink populations, and (3) panmictic populations. Ciannelli *et al.* (2013) define sympatric discrete populations as “reproductively and genetically isolated populations, which may occupy overlapping habitats, at least during one phase of their life cycles”. Spatially complex populations (metapopulation, source – sink) are “locally breeding subpopulations (deme) which may be genetically connected via dispersal”. Panmictic populations are “interbreeding individuals that are heterogeneously distributed over space”. Heterogeneous spatial population structure is defined as the underlying spatial

and temporal changes in physical and biological environment (Brown *et al.* 1995), individual behavioral responses (Planque *et al.* 2010), and intra- and inter-specific interactions (Ciannelli *et al.* 2013).

The fisheries literature increasingly recognizes that spatial homogeneity is not the rule, but is, instead, an exception for many fish populations (Heath *et al.* 2008; Kell *et al.* 2009; Ying *et al.* 2011; Berger *et al.* 2012; Benson *et al.* 2015). Although recent studies of stock identification show that fish populations exhibit a variety of spatial structure (Begg and Waldman 1999; Cadrin 2005; McBride 2014), spatial heterogeneity has rarely been incorporated into stock assessment models and harvest strategies (Cadrin and Secor 2009; Goethel *et al.* 2011; Berger *et al.* 2017). Furthermore, research suggests that dramatic and large-scale changes in fish spatial distribution patterns are one potential cause of fish population collapse (Hutchings 1996; Berkeley *et al.* 2004; Cao *et al.* 2014; Jiao *et al.* 2016). For example, in the debate about the collapse of Atlantic cod, some argue that failures were partly caused by a lack of spatial modeling of the density distribution of Atlantic cod, especially of the stock structure and fishing effort allocation (Hutchings 1996). Indeed, ignoring spatial structure in fish population dynamics models could bias stock assessment results, and lead to fisheries management failure (Fu and Fanning 2004; Sterner 2007; Hutchinson 2008) as different subpopulations have different optimal harvest levels resulting from variation in life-history parameters such as growth rate and natural mortality (Berger *et al.* 2012; Kerr *et al.* 2017).

Arguably, clear guidance on how to delineate the boundaries of subpopulations is lacking. Attributes that can be used to define separate subpopulations include area, genetic difference, population size, isolation level, demography, and the degree of exchange. Such guidance can suggest rules in defining a subpopulation (Goethel *et al.* 2016). For example, a subpopulation spatial area can be defined such that individuals within the subpopulation can produce 90% or more of recruitment within the boundaries. Similarly, management areas within the larger stock area can be defined such that 50% or more recruitment within the boundaries is produced internally. If the demographic data is not available to determine the spatial boundaries based on those thresholds, major geographic features, patterns of concentration of a species, maturity, growth type difference or habitat patches (benthic or oceanographic) could be reasonable means of population delineation (Pita *et al.* 2016). In reality, the historical development of the

fishery, the influence of policy, and advancement of scientific methods will also influence the definition of management areas (Kerr *et al.* 2014).

## **1.2. Drivers of population spatial structure**

The causes of spatial population structure include demographic heterogeneity (habitat distribution contributes to different characteristics among subpopulations and therefore causes spatial structure within a population), migration within fish species, and isolation forcing (Iles and Sinclair 1982; Ciannelli *et al.* 2013; Herbst *et al.* 2016). Fish habitat is distributed heterogeneously in space. Each subpopulation may have its own, seasonal spawning period (Iles and Sinclair 1982). Fish species move between spawning, rearing, feeding grounds. For instance, the isolation of population units of herring involves the spawning and pre-spawning aggregation stages (Iles and Sinclair 1982). On the other hand, for a closed population, there is a low degree of mixing during migration at the larval and spawning stage. Therefore, mixing during migrations maintains stock structure in metapopulations. Movement between populations can also keep subpopulations from local extinction and therefore preserve biodiversity (Smedbol and Stephenson 2001; Kerr *et al.* 2010b; Guan *et al.* 2013). Moreover, fish species life history traits can determine the degree of spatial structuring in different populations (Berger *et al.* 2012).

Landscape and hydrographic features may constrain individual dispersal and reproduction and therefore can set geographic boundaries of a population. For instance, the geographic range for sympatric populations and meta-populations is generated by the mechanisms that generate isolated groups of individuals reproductively or demographically (Ciannelli *et al.* 2013). Within a certain range of habitat of a population, small-scale environmental forcing and individual behavior mainly generate and maintain the spatial structure. For example, spatial structure within a panmictic population can be maintained by the underlying heterogeneity of the physical and biological environments such as currents, patches of food or local prey depletion, as well as be behavioral interactions among individuals within species (e.g. schooling and intraspecific competition) and among species (e.g. feeding aggregations and predation) (Ciannelli *et al.* 2013).

### 1.3. What can erode population spatial structure?

There are several mechanisms that can erode population spatial structure with the two main factors being a combination of exploitation and environmental forcing (Ciannelli *et al.* 2013). Overharvesting a population can cause depletion, which can lead to the erosion of spatial structure of the population (McQUINN 1997; Kell *et al.* 2009). For examples, exploitation is concentrated on particular local populations could deplete the local population leading to changes in metapopulation structure, thereby digging a 'hole' in the metapopulation's components (Kell *et al.* 2009). Such erosion of spatial variability in fish populations can reduce population productivity, resilience, and stability (Kerr *et al.* 2010b; Watson and Haynie 2018).

Environmental forcing can also contribute to the loss of spatial structure. Climate forcing can change dispersal and migration pathways (Perry *et al.* 2005; Nye *et al.* 2009; Tseng *et al.* 2011; Diop *et al.* 2018). Fish populations have optimal environmental conditions such as optimal temperatures, oxygen saturation (Tseng *et al.* 2011). Large-scale climate forcing can alter those conditions and thus alter the distribution of populations (Tseng *et al.* 2011; Gaines *et al.* 2018). There are many examples of alteration in species spatial distributions that are caused by large-scale oceanographic changes (Perry *et al.* 2005; Nye *et al.* 2009; Tseng *et al.* 2011; Hulson *et al.* 2013). For example, Tseng *et al.* (2011) explore the influence of sea surface temperature increase on potential habitats of the Pacific saury *Cololabis saira*. The results show an obvious poleward shift of the potential habitats of Pacific saury under different scenarios of sea surface temperature changes.

Human beings and environmental forcing can change the spatial population structure by changing the habitat patches and the population's occupancy (Bergek *et al.* 2010; Hulson *et al.* 2013). Human beings and environmental forcing can break the mechanisms that support the populations. For example, the sympatric populations are maintained by the mechanisms that generate reproductively or demographically isolated groups of individuals (Ciannelli *et al.* 2013). Metapopulations are maintained by the mechanisms leading to variation of demographic rates across the species range (Kritzer and Sale 2004; Ciannelli *et al.* 2013). And panmictic populations are maintained by individuals' behaviors and small-scale environmental forcing such as currents, patches of food (Ciannelli *et al.* 2013). Any changes of those mechanisms caused by humans

and /or environmental forcing can erode the spatial structure within the population. In addition, large-scale environmental changes and human interruption on habitat patches can affect population abundance, age structure and population spatial structure (Bergek *et al.* 2010). Accordingly, changing the population age structure can lead to the change of population spatial structure because different individuals with different age, sizes normally distribute differently over space (La Valley and Feeney 2013; Hulson *et al.* 2013).

#### **1.4. Consequences of eroding population spatial structure**

The consequences of eroding population structure are relevant to population management and conservation. For example, many studies (Jørstad *et al.* 1991; McQUINN 1997; Smedbol and Stephenson 2001; Kell *et al.* 2009; Libungan *et al.* 2015) show that herring populations consist of many subpopulations, and the number of subpopulations and the abundance of each subpopulation are proportional to the number and size of geographic areas that allow retention during the spawning stage or very early life stage. Each subpopulation is adapted to the local living environment and has different life history traits such as somatic growth, reproduction phenology, and maturing time (Smedbol and Stephenson 2001). Loss of any subpopulations will change the spatial structure and, potentially, reduce the ability of individuals to adapt to the changing environment (McPherson *et al.* 2001).

In addition, numerous studies indicate that genetic differentiation of many marine fish is more complex and may occur at much smaller scales than management units (Lin *et al.*; Grant 1985; McPherson *et al.* 2001; Reiss *et al.* 2009; Kocovsky *et al.* 2013). This creates problems associated with the mismatch between population structure and current fisheries management units (Reiss *et al.* 2009). Mismatches about lead to depletion of a subpopulation, triggering a decrease in genetic and phenotypic diversity. Moreover, preserving the biocomplexity of exploited populations is very important. For the locally adapted population, recovery of the abundance of depleted populations may take possibly longer than the time estimated by models that ignore population spatial and genetic structure in the models (Verspoor *et al.* 2005; Reis *et al.* 2009).

Eroding population spatial structure can also make the populations more sensitive to environmental fluctuations (Hsieh *et al.* 2008; Ying *et al.* 2011). For instance,

Hsieh et al. (2008) analyze a long-term data set on larval distribution off southern California, where populations that experience heavy commercial harvest appear more sensitive to environmental fluctuation. In turn, populations with depletion of subpopulations show more sensitivity in spatial distribution since the heterogeneity of spatial responses to environmental variation is reduced (Hulson et al. 2013).

The relationship between human-caused or climate-driven changes of population structure and the ensuing effects on population abundance suggest developing a more comprehensive approach to incorporate spatial population structure into the simulation and stock assessment models, as well as a more integrated approach to incorporating spatial population structure into the management process in which the spatial structure of a population is well monitored and catches are numerically and geographically reported.

In the chapters to follow, my first objective is to review how fish population structure has been considered in the current research. I begin by first reviewing the stock assessment approaches that account for spatial structure in estimation of stock status, and then review the simulation modelling approaches that have incorporated spatial dynamics, and finally I illustrate how operating models of fish populations can be formulated in a way that can account for spatial population structure. The second main objective of this paper is to document the ways that spatial structure can be incorporated and achieved in current harvest strategies. Third, I summarize common pitfalls and data needs when developing spatial modeling and conducting spatial harvest actions. Finally, I conclude that adaptive, spatial, and case-specific management strategies will be needed in the future.

## Chapter 2.

# Representing dynamics of spatially-structured fish populations

## 2.1. Spatially explicit stock assessment

Stock assessment models estimate key parameters for exploited populations, such as biological reference points (e.g., fishing mortality rate associated with MSY), which can then be used to provide advice on appropriate harvest levels (Hilborn and Walters 1992; Kuykendall *et al.* 2017; Archambault *et al.* 2018; Punt *et al.* 2018). Although most fish populations are recognized to exhibit complex spatial population structure, stock assessment models typically assume that individuals within a stock assessment region form a unit stock, i.e. a closed population (Fu and Fanning 2004; Lewy and Kristensen 2009). Generally this assumption is a result of management boundaries, data availability, and analytical convenience (Hilborn and Walters 1992; Fitzgerald *et al.* 2018). Allowing for complex spatial structure in assessment models requires more and better spatially-resolved data as well as an ability to represent connectivity between populations or otherwise interacting groups of fish in the model (Denson *et al.* 2017; Jardim *et al.* 2018).

The validity of the single unit stock assumption has been a research priority in recent years, particularly following simulation analyses that highlighted the risks associated with ignoring the spatial structure on population sustainability and recovery (Ying *et al.* 2011; Guan *et al.* 2013; de Moor and Butterworth 2015; Cao *et al.* 2017; Lee *et al.* 2017). Beverton and Holt (1957) first developed spatially explicit models that account for population spatial structure (e.g. they develop a population model that takes into account spatial variation in fishing intensity and movement of fish in section 10.2.2 of the book). Subsequently, a variety of software programs and models allow for spatial structure in stock assessment. For example, the MULTIFAN-CL software program (Fournier *et al.* 1998; Hampton and Fournier 2001) is developed to explicitly account for connectivity between subpopulations via mark-recapture information (Hampton and Fournier 2001). Similarly, Goethel *et al.* (2015a) include connectivity between subpopulation of New Zealand snapper (*Pagrus auratus*) and yellowtail flounder

(*Limanda ferruginea*) using a metapopulation dynamic model. The availability of tagging information can greatly benefit development of spatially explicit models. For instance, for the Atlantic bluefin tuna fishery, there are tag-integrated data from conventional, archival, and satellite tags, and catch compositions separated by stock based on otolith microchemistry (Taylor *et al.* 2011). Based on those data, Taylor *et al.* (2011) develop a spatially explicit stock assessment model. Taylor's model is perhaps the best example of a holistic spatially explicit, tag-integrated assessment based on the high-quality data available for this fishery. For data-poor fisheries, however, there is a need for a simpler approach. For example, skipjack tuna (*Katsuwonus pelamis*) distributed in the western and central Pacific Ocean are assumed to have six different populations living in six interconnected regions with connectivity existed among subpopulations (Langley 2001). However, the formal assessment model only considers two main regions situated in the equatorial Pacific (Langley 2001). The other four regions in the north have relatively less exploitation, and therefore less, and poorer quality data. The analytical benefit of including these data is assumed to be low. In addition, the authors point out that there are a number of problems encountered to estimate parameters for six regions and the movement rates between subpopulation because of the data limitation (Langley 2001).

The focus of spatial stock assessment models is initially on estimating reference points and the status of a fishery (Goethel and Berger 2017). However, there is growing interest in their use for providing advice on rebuilding trajectories for fisheries that have been overfished. For example, the yellowtail flounder fishery (*Limanda ferruginea*) off the northeastern United States has been over exploited, and the fishery is managed as three distinct stocks on Georges Bank, off southern New England, and in the waters immediately north and south of Cape Cod (Hart and Cadrin 2004). A comparison of rebuilding times under different stock structure assumptions found that recovery rates and future biomass levels are much higher when interactions among sub-stocks are considered in the model (Hart and Cadrin 2004).

Even though population spatial structure can be incorporated into stock assessment models, there are continuing barriers to implementing the model outcomes into management advice. There are relatively few real-world applications where spatially explicit assessment models have been used to provide management advice. One reason is the limited familiarity and communication problems among scientists, managers, fishermen, and other stakeholders and limited experience (Goethel *et al.*

2016; Berger *et al.* 2017). It is also unclear whether fisheries managers know how to translate the spatially explicit scientific outcomes into spatially explicit policies. Therefore, 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. Another important barrier to spatially explicit stock assessment models is their need for high-quality spatially resolved data, including catch and survey data, the estimates of exchange rates among subpopulations and life-history parameters for each subpopulation (Denson *et al.* 2017). Furthermore, the mismatch between the large number of parameters that need to be estimated and the small samples sizes for each spatial unit due to partitioning data streams can lead to high uncertainty of the outcomes (Berger *et al.* 2017). Therefore, most spatial stock assessment research remains limited to evaluating robustness and risks using simulation testing instead of applying the outcomes into management process. For instance, the bluefin tuna stock assessment discussed above has not been used to provide management advice. In the skipjack tuna fishery, the reference points for the skipjack are estimated, but the status for the stock is determined as an aggregate and not for each of the two regions considered in the model (Langley 2001).

## **2.2. Simulation modeling**

Simulation analysis plays an important role in testing the robustness and uncertainty of assessment results and the performance of different hypothesized spatial population structure, as well as the effect of the spatial scale of management units on fisheries sustainability (Butterworth and Geromont 2001; Pelletier and Mahevas 2005; Kerr *et al.* 2010a). Simulations are capable of mimicking the biological complexities in the real world using operating models (Hilborn and Walters 1992; Kerr *et al.* 2014). Therefore, simulations are able to use all kinds of information and knowledge that are available (e.g., experts' judgement or experience), and are not constrained by observed data (Hilborn and Walters 1992). The use of simulation analysis allows scientists to test different scenarios of spatial structure and movement parameters, and then to help identify what combinations provide the best fit to the observed spatial data or distribution (Goethel *et al.* 2015b). In this way, simulations can provide insights into the types and scales of spatial data (e.g. tagging data) needed to represent the true spatial population structure.

Simulation analysis can be used to explore the effects of spatial structure on the results of stock assessment models (Butterworth and Geromont 2001; Lewy and Kristensen 2009; Ying *et al.* 2011; Goethel *et al.* 2015b; Laretta and Goethel 2017). Ying *et al.* (2011) use simulation analysis to explore the risks of ignoring fish population spatial structure in fisheries management. The authors set up three population spatial structure scenarios for the simulation fishery: (1) metapopulation, in which subpopulations are connected by movement; (2) three independent subpopulation, in which the authors assume there is no movement between subpopulations, i.e. the subpopulation is completely isolated from each other; (3) a single unit population, in which the spatial structure is completely neglected in the population, i.e. it is a homogeneous spatially aggregated population. Similar simulation approaches are used in various fisheries (Kell *et al.* 2009; Guan *et al.* 2013; Punt *et al.* 2015). Simulation is also used to test the performance of spatially explicit models, by estimating different values of movement between subpopulations and the correlation rate among recruitment parameters and movement (Hulson *et al.* 2013; Goethel *et al.* 2015b; Herbst *et al.* 2016; Lee *et al.* 2017). In addition, some authors use simulation analysis to explore the improvement in stock assessment results by using spatial data in the models such as tagging data (Neat *et al.* 2014; Goethel *et al.* 2015a; Laretta and Goethel 2017). In general, all these spatial explicit models have been reported to perform well especially with high-quality tagging data. However, care must be taken when the population structure or movement mechanisms are not known or tagging data is not available or adequate to provide spatial information. In that case, research indicates that spatially aggregated approaches that assume populations are homogeneous can be more robust than the spatial approaches that assume incorrect population structure (Langseth and Schueller 2017). Therefore, scientists must be careful in using spatial and non-spatial models in simulation analysis.

The performance of spatial stock assessment models is affected by three factors: (1) the context and type of assessment models (e.g., the delay-difference model vs. surplus production model); (2) data availability and quality to provide spatial information such as tagging data; (3) the hypothesized combination of spatial structure of the population and its corresponding key parameters (e.g., assuming two or three subpopulations, the connectivity and movement parameters among subpopulations and the vital rates and recruitment) (Carruthers *et al.* 2011; Denson *et al.* 2017; Laretta and

Goethel 2017). For example, Benson *et al.* (2015) evaluate the risks of aggregated harvest management for a spatially structured herring fishery. The authors point out that under some scenarios of dispersal, fleet dynamics, and management errors, the results suggest that spatially aggregated stock assessment models provide robust management advice. However, Truesdell *et al.* (2016) use a fine-scale simulation of a sessile scallop resource to demonstrate that ignoring population spatial structure by assuming homogeneous fishing pressure (i.e., equal capture probability), the fishing mortality will be overestimated, and the biomass will be underestimated. Therefore, the performance of the spatial models is based on different context of fish species life history and fishery dynamics. Similarly, Porch *et al.* (1998) use a spatial model to simulate the performance of two scenarios of populations: metapopulation with a mixing movement, and two separate populations. The authors demonstrate that the two separate populations perform better than the metapopulation because the movement in the metapopulation is mis-specified. Therefore, in the spatial modeling, the assumed functional form of movement and the associated parametrization of movement in the estimation process can strongly impact the model performance.

Simulation models that include environmentally-driven spatial biomass and recruitment dynamics have been developed to evaluate the consequences of climate change on commercially important fish species (Perry *et al.* 2005; Hulson *et al.* 2013). For example, Hulson *et al.* (2013) investigate the effect of climate change on the distribution and recruitment dynamics for Bering Sea walleye pollock (*Gadus chalcogrammus*). Their research indicates that under climate change scenarios, directly estimating year-specific movement and the proportion of recruitment in the spatially explicit models can get more accurate population parameters estimation. Similarly, Denson *et al.* (2017)'s work illustrates that accounting for environmental forcing in spatial modeling through a covariate provides more accurate estimation of key parameters compared with the models that do not take environmental forcing into account. Although neglecting environmental forcing in stock assessment models can degrade performance of harvest strategies, spatial modeling does not guarantee better model performance because sometimes the adding spatial variables or environmental forcing into the models yields relatively little benefit to parameter estimation (Hulson *et al.* 2013; Goethel *et al.* 2015b). For example, Hulson *et al.* (2013) and Goethel *et al.* (2015b) point out in

their search that incorrect specification of movement parameters will lead to erroneous and biased management advice.

Spatially explicit simulation analysis can also be used to calculate spatially explicit biological reference points, which can be used to project sustainable catches (Ying *et al.* 2011). Ying *et al.* (2011) develop spatially explicit biological reference points for a metapopulation and demonstrate that assuming inappropriate population spatial structure (i.e., assuming single unit population or three isolated independent populations) may lead to the failure of harvest management and localized depletion. Similarly, Carruthers *et al.* (2011) develop and apply a spatially explicit surplus production model to incorporate multiple stocks with movement among sub-stocks. They illustrate the calculation of the reference point of a stock (e.g. dynamic  $F_{MSY}$ ) within the multi-stock surplus production framework. Kerr *et al.* (2014) compare the values of reference points (i.e.  $F_{MSY}$ ) estimated from complex spawning structure model and the spatial aggregated model using the case study of Atlantic cod.

### **2.3. Operating models for use in management evaluation**

Spatial modeling techniques have not been widely incorporated in the stock assessment and management processes although it is widely recognized that ignoring spatial structure could cause biased results in stock assessment models, while plenty of simulation studies reveal the potential consequences (Kerr *et al.* 2010a; Guan *et al.* 2013; Jiao *et al.* 2016; Denson *et al.* 2017). There are three key limitations: 1) data needs: most fisheries data are spatially aggregated and lack sufficient spatial resolution to support and match the scale of population structure (Denson *et al.* 2017); 2) models: it is difficult to make spatially explicit models operational, and there is a lot of uncertainty in the model performance (Lee *et al.* 2017); 3) management: it is still unclear how to use the spatial modeling techniques to provide advice for fisheries management (La Valley and Feeney 2013; Berger *et al.* 2017). The question is: how could these difficulties be overcome to incorporate spatial population structure into management? Management strategy evaluation (MSE) is increasingly used to evaluate different fisheries management strategies (Tuck and Possingham 1994; Grüss *et al.* 2016). The role of MSE is to assess the consequences across a range of management strategies or options and evaluate the trade-offs in performance of different management objectives (De La Mare 1998; Smith 1999). The MSE approach requires input from decision

makers (e.g. managers), technical experts (e.g. scientists), fishing industry, other community interests (e.g. fishermen) and MSE analysts (De La Mare 1998; Smith 1994). In the MSE framework, stock assessment models a key component of management procedures that link data to management decisions (Grüss *et al.* 2016). Therefore, the lack of spatially explicit stock assessment models makes the operational implementation of spatial management (and evaluation) difficult (Goethel *et al.* 2011, 2015a,b).

Difficulties parameterizing spatial operating models is the main constraint for spatial MSE (Goethel *et al.* 2016). It is extremely difficult to determine the accuracy of the key model parameters and to validate model performance, because it is usually difficult to verify outputs from the models with observed data collected from fisheries (Begg *et al.* 1999). Stock assessment models, on the other hand, can be used to estimate population parameters from observed data directly (Hilborn and Walters 1992). When spatially explicit data are available, the spatially explicit stock assessment models are able to estimate the values of spatially explicit parameters, which then can be used to construct the spatially explicit operating models that can evaluate different management strategies (Goethel *et al.* 2011). By constructing the spatially explicit estimation models as the operating models, the best-fit parameter values estimated from observed data can be input directly to the simulation framework.

MSE has five key ingredients which include: (1) management objectives that need to be clearly defined and specified; (2) developing quantifiable performance criteria for each management objective; (3) a set of alternative management strategies or options to be considered; (4) developing a mean of evaluating the performance of each management strategy or option using quantitative performance measures while accounting for suitable uncertainties; (5) conveying the results to decision-makers in a plain language (Smith 1994, 1999). MSE does not aim to seek an optimal strategy or decision for decision-makers; instead, decision-makers can apply their preferences and weightings to alternative objectives based on the information provided by MSE. At the implementation level, MSE fails if it cannot accommodate effective stakeholder participation and acceptance. At the technical level, MSE can be developed to incorporate spatial structure of a fish population in three ways: 1) spatially explicit parameter estimation, which is accomplished by developing a spatially stock assessment model and applied the model to observed data; 2) spatially explicit operating model development, which is achieved using the best fit spatial parameter

estimates derived from step one, along with different spatial assumptions in the model; 3) management evaluation, which means using the operating model developed in step two to test various hypothesized spatial structure scenarios and evaluate different management strategies.

The parameter estimation step is not expected to perfectly match the true scale of biological structure. Instead it aims to narrow down the possible range of values of the spatially explicit parameters in order to inform the following spatial operating model (Goethel *et al.* 2016). The spatially explicit operating models are assumed to represent the true spatial population structure in the natural world as closely as possible (Kerr and Goethel 2014). In the estimation-simulation framework, the estimation model is used to provide a first approximation of parameter values and spatial processes, then sensitivity analysis can be used to adjust or explore those estimates or spatial processes within the simulation model. It is not uncommon that there is a high degree of uncertainty associated with spatial modeling (Fay *et al.* 2011), so allowing for uncertainty or imprecision is critical in simulating potential states of nature. After parameters are obtained from the estimation model, uncertainty can be addressed by sampling from the posterior distribution of parameter estimates. Similarly, typical error sources can also be included by sampling observation errors from various data sources. In non-spatial operating models, as well as the spatial operating models, it is worth noting that the most important aspect of uncertainty is probably accounting for different alternatives of plausible operating models. Francis (2011) points out that, if there is no prior information available to narrow down the possible dynamics of populations, then scientists should develop as many operating models as they need to represent every plausible population scenario, and then compare the outputs for plausibility. Therefore, uncertainty and parameterization should be carefully considered and tested, especially when the parameters are assumed variables or from stochastic processes. Once the spatially explicit operating model is developed, it can be used to test the robustness and performance under different scenarios of assumed population structures (Kerr and Goethel 2014). The operating model in this step will determine how well each assessment model performs and which assessment models provide highly biased results that need to be abandoned. Finally, a variety scenario of simulation scenarios (both spatial and non-spatial) can be developed to evaluate the performance of different harvest strategies.

Although spatial modeling may improve scientific advice for many exploited fish populations around the world, it is necessary to clarify that non-spatial modeling approaches are still useful in providing scientific management advice and should not be abandoned (Hulson *et al.* 2013; Punt *et al.* 2015). It should become routine practice to test the robustness of both spatial and non-spatial approaches, particularly for management applications.

## Chapter 3.

### **Fishery harvest strategies that can account for complex fish spatial structure**

A harvest strategy is “a set of well-defined rules used for determining a management action in the form of a total allowable catch (TAC) or allowable fishing effort given input from a stock assessment estimator, or directly from data” (Kronlund *et al.* 2012). A harvest strategy often consists of a number of core components (Rayns 2007): 1) Objectives: fishery objectives define a desirable state of a fishery (e.g. biomass level) as well as the time frame for achieving those objectives; 2) Indicators track the performance of the fishery over time based on metrics such as biomass, catch rates, protected species interactions, etc.; 3) Reference points describe acceptable levels of performance in the fishery; 4) Harvest control rules / decision rules state what pre-determined management action will be taken under certain circumstances. This usually involves adjusting (through quota, management units or bag limits etc.) the catch or fishing pressure in the fishery. By being clear about what action will be taken and when, harvest strategies help remove much of the uncertainty around how a fishery will be managed. Harvest strategies can benefit both the fish and fishermen if designed correctly. Complex spatial structure in populations can be addressed by approaches that explicitly account for spatial structure in the model or can be implicitly considered in the harvest control rules (Tuck and Possingham 1994; Fay *et al.* 2011; Kritzer and Liu 2014). In addition, spatial management strategies can also be developed to increase the potential for meeting fisheries management targets and ensuring greater long-term yield by considering spatial structure in management processes (Woillez *et al.* 2009; Cope and Punt 2011). These strategies include distributing catch spatially through harvest control rule, and adopting finer-scale governance.

#### **3.1. Achieving spatial harvest strategies through harvest control rules**

Harvest control rules (HCRs) calculate recommended catch levels given estimates of present stock biomass or levels of fishing mortality (Tuck and Possingham 1994). Spatial variability, either in the population dynamics, fishery operations, or in data

collection, has the potential to impact HCR performance as they can drive variability in indicators used for stock assessment (Fay *et al.* 2011). HCRs are commonly selected for management based on pre-testing in simulation models. To be considered for implementation in a real-world setting, HCR must demonstrate an appropriate response to deviations from management targets, be robust to key uncertainties, and emphasize precautionary action given uncertainty (Fay *et al.* 2011). The latter point is particularly important for so-called 'data-poor' situations, when the reliability of indicators is likely questionable. As discussed above, spatially explicit stock assessment models can take important structural population patterns into account in the models and therefore can reduce uncertainties in estimating sustainable harvest levels (Cope and Punt 2011; Goethel *et al.* 2015a). However, spatial processes and attributes are not generally explicitly incorporated into HCRs, partly because incorporating spatial structure in the models increases the number of parameters that need to be estimated, which introduces greater uncertainty in the results compared to spatially aggregated models (Tuck and Possingham 1994).

Uncertainty buffers are used in some cases where spatial structure is unknown, and is hard to reduce based on data (Punt *et al.* 2012). Uncertainty buffers are increasingly used in fisheries management to implement risk-averse harvest control rules by limiting the allowable catch to values lower than implied by assessment outcomes (Restrepo 1999). In other words, an uncertainty buffer is the difference between the catch limit given perfect information and the actual implemented catch limit. Having a buffer would reduce the chance of a depleted biomass where information about the stock or catch rates is found to be inaccurate, or where significant environmental changes pose a threat to the stock. Allowing a buffer can lower the target catch from that which would otherwise be set based on direct application of assessment outcomes and therefore can provide another level of precaution where TACs are set on uncertain MSYs. In cases where the stock is threatened, a buffer also gives the management agency time to enact emergency measures, or to go through the process of reducing the TAC (Punt *et al.* 2012). The magnitude of the buffer can be based on the inherent attributes of the population that make it either more resilient or more vulnerable, the risk policy that applied to the fishery, or the nature and extent of the uncertainty decided by fisheries managers (Restrepo 1999). Punt *et al.* (2012) applied an uncertainty buffer to management of Red King Crab (*Paralithodes camtschaticus*) in Bristol Bay, Alaska. Ying

*et al.* (2011) evaluated use of an uncertainty buffer and demonstrated that target biomass levels can be reached by setting the fishing mortality at a lower level to create an uncertainty buffer for the catch when complex spatial structure exists in a fishery, but is not explicitly recognized. Ying *et al.* (2011) showed that uncertain buffers in the form of lower fishing mortality rates can generate stability in both catch and biomass, but at the cost of yield and economic benefits from the fishery. Woillez *et al.* (2009) demonstrate an approach that can potentially fine-tune harvest control rules instead of simply applying an uncertainty buffer on the catch coarsely and giving up yield. Their approach adjusts uncertainty buffers on catch based on estimates of resilience or vulnerability of the stock obtained from spatial data and/or models.

The traffic light approach is an option for considering spatial structure in harvest control rules independent to the assessment process (Caddy 2002). It is particularly useful for the data-poor fisheries or fisheries that are highly sensitive to environmental changes. The traffic light approach can be used to assess fish stocks using a wide range of indices relative to different attributes of fish populations. The different indicators are first mapped on a common color scale to display whether reference values have been crossed. The use of thresholds and reference points is central to mapping the indicator series into a traffic light table. The assessment is then achieved by some form of integration of the colors, which may be based on weighting or grouping of the indicator responses. Lastly, management actions are taken based on the assessment and following decision-making rules laid down beforehand. This traffic light approach is model-free and presents the time series of fish stock status visually and allows different attributes of the stock (e.g., length structure, spatial distribution and abundance) to be monitored using a variety of indicators, but is limited by the lack of a statistical framework. The cumulative sum (CUSUM) is a statistical method that detects deviations from a reference mean, according to defined performance criteria. Petitgas (2009) suggested the use of CUSUM monitoring scheme (Hawkins and Olwell 1997) as a suitable statistical framework in this context. The framework is applied to the North Sea cod stock to illustrate how a fishery-independent integrated assessment can be achieved using a suite of indicators derived from research survey data only. The indicators used are related to the spatial distribution, abundance, length structure, length at maturity and apparent mortality. The traffic light approach combined with CUSUM can be used to formally account for the spatial structure in output of a stock dynamic model in which

spatial population structure is not explicitly considered. Models that address ecological and physical interactions beyond the biology of a single species are undergoing increasing attention and development as part of the rise of ecosystem-based management approaches (Grüss *et al.* 2016). The development of spatially explicit simulation and stock assessment models for management is normally constrained by data availability and the huge number of increased parameters that need to be estimated from the limited spatial data, approaches that utilize information of spatial structure in decision-making, without necessarily modeling it, opens another door for incorporating spatial structure in fisheries management.

Incorporating spatial population structure in assessment models and translating the assessment outcomes to management policies is difficult, and therefore, other ways of addressing this issue may be necessary. One approach mentioned in the current literature is to distribute catch in a finer-scale space than coast-wide scale (NEFMC 1999; NEFSC 2012). Distributing catch spatially in a finer-scale can reduce the risk of serial depletion and erosion of spatial population structure. Catch in the Atlantic herring (*Clupea harengus*) fishery located in the northeast coast of USA provides one example of spatial catch distribution in fisheries management (NEFSC 2012). Although there are a few distinct spawning components and known complex spatial population structure in Atlantic herring, stock assessment scientists still assume a single unit stock because of large uncertainty in population biomass, dynamics, and movement rates among subpopulations (NEFSC 2012). However, the potential for spatial population structure is accounted for in management by allocating quotas estimated from single-stock assessment models among four management areas. Such management action aims to avoid overfishing any spawning components accidentally (NEFMC 1999).

Rotational harvest strategies represent another type of spatial catch distribution procedure (Kuykendall *et al.* 2017) commonly found in shellfish fisheries. In Alaska's Cook Inlet, for example, commercial fishing for mussels and clams adopts two policies to achieve the spatial distribution of catch (Trowbridge *et al.* 2000). The first management action is that only half of the beaches that are certified for commercial fishing are open for fishing in any given year (Trowbridge *et al.* 2000). This management action aims to allow for growth and recruitment to the population before all individuals are vulnerable to the commercial harvest. Secondly, areas that are considered to be the most important for the population dynamics (e.g. source population) and recreational shellfish fishing

remain closed for commercial harvest (Trowbridge *et al.* 2000). This second management action aims to preserve the population and reduce conflicts among users.

Another example of a spatial management system is the sea urchin (*Evechinus chloroticua*) fishery in New Zealand (Miller 2011). As the fishery developed, scientists and fishermen noticed that the distribution of sea urchin was highly patchy and likely represented complex spatial structure of the population. A quota management system was introduced to the sea urchin fishery in 2002 (South Island) and 2003 (North Island) (Miller 2011) (Miller 2011). There are 12 quota management areas for sea urchin in New Zealand, with the commercial catch concentrated in four of areas: SUR1B (Auckland - South), SUR4 (Chatham Islands), SUR7A (Marlborough Sounds), and SUR5 (Southland) (Miller 2011). Catch data which was reported at the 12 quota management areas were obtained from the Ministry of Fisheries Customary database. Those catch data also include a range of input information from a range of participants such as commercial fishers and processors (Miller 2011). The commercial participants aided the interpretation of commercial data. Since the quota management system was introduced into the sea urchin fishery, the number of vessels fishing has decreased, and the average catch per vessel per year has increased. Miller 2011 concludes that management of sea urchin fishery in New Zealand can be achieved by managing and monitoring the fishery at a smaller spatial scale than currently occurs. Another sea urchin fishery that uses spatial catch allocation management strategies is Chile's red sea urchin (*Loxechinus albus*). This fishery is the largest sea urchin fishery in the world, contributing more than half of the urchin roe yield of the world (Moreno *et al.* 2007). Chile's red sea urchin fishery was fully open and accessible for all fishermen in the late 1990s but started to decline in 1998. Stock assessment scientists began to evaluate this fishery using non-spatial models, and the stock was managed based on a single-stock assumption (Moreno *et al.* 2007). However, the management failed to curb depletion and the sea urchin population exhibited serial depletion, likely due to a failure to account for complex spatial structure in management (Orensanz *et al.* 2005). The Fisheries Research Fund in Chile initiated a project for the rotation of areas in the sea urchin fishery. The basic idea of the project is to explore spatially-explicit strategies, such as rotation and reserves consistent with the nature of the fishing process (Moreno *et al.* 2007). This project requires joint work among scientists, managers, processors and fishers. The main element of this project is to implement spontaneous rotation of fishing

areas at different scales (Orensanz et al. 2005; Moreno et al. 2007). Details on the spatial allocation and overall effectiveness of the approach at rebuilding stock structure are not currently available.

### **3.2. Achieving spatial harvest strategies by adopting nested- and finer-scale governance**

Another way to solve the challenges with complex spatial population structure is assign the management actions to a smaller-scale governance entity. A finer-scale management policy is able to focus on smaller scales of population status and may be more responsive for local populations. Enhanced stewardship of spatial structure may be achieved via fine-tuning management strategies combined with localized authority and access (Ostrom 2009; Camp *et al.* 2018). Such nested and fine-scale management may be required for fisheries that have the most complex spatial structure, the most numerous and smallest scale vessels, and the most numerous and widely scattered landing sites (Orensanz *et al.* 2005).

One well-known study using nested- and finer-scales of governance is the abalone (*Concholepas concholepas*) fishery in Chile (González *et al.* 2006). The fishery once was very productive and entered demanding Asian markets in the late 1970s (González *et al.* 2006). This success led to increasing fishing effort was entering the fishery, and by the late 1980s, the fishery became overfished and at risk of collapse (González *et al.* 2006). The federal government of Chile closed the abalone fishery from 1989 to 1992 and reformed its fisheries laws. When it was reopened, the managers decide to use the spatial catch allocation scheme mentioned in the Section 3.1 of this thesis. However, the fishery continued to collapse due to a limited capacity to set and control catch using quotas alone. The management strategy changed to an area-based allocation system of territorial user rights of fishing (TURF) (González *et al.* 2006). The TURF management strategy was enforced in 1997 and has appeared to be successful. Local communities are now fully involved in the management of local populations. Local communities can propose harvest strategies and plans for abalone or other species based on third-party scientific advice, and an area for limited fisheries effort that can enter (González *et al.* 2006). As a result, the abalone yield has stabilized or increased in many fine-scale areas managed by local communities along the Chilean coast. CPUE now increases compares to the CPUE before the fishery closure. More importantly, the

density of abalone has dramatically increased as a result of the management system and possibly with some help of environmental forcing to the fishery recovery as well. It is important to recognize that abalone density in some TURFs areas remains low. This may be attributed to poor local communities' management, environmental forcing that prevents the fishery from recovery, or emigration of abalone to the neighboring areas outside of the TURFs (González *et al.* 2006; Lester *et al.* 2017). There is no coordination between areas managed using TURFs and those that are not. Given the fact that larval dispersal and adult movement exist among TURFs and non-TURFs areas, the management might be improved by taking that fact into account (Steneck and Wilson 2010). This problem emphasizes the importance of retaining higher-level governance at the metapopulation scales when creating finer-scale management institutions. Steneck and Wilson (2010) illustrate that such approaches can also be effective in more developed countries with stronger governance capacity, using the American lobster (*Homarus americanus*) fishery in Maine (U.S.) as a case study.

## **Chapter 4.**

### **Common pitfalls and data needs associated with spatial modeling and harvest strategies**

Lack of high quality spatially resolved data is an important limitation in developing and adopting spatially-explicit management strategies. Beverton and Holt (1957) develop a spatial-explicit model by incorporating movement rates within the model. The authors then point out that the spatial units in the spatial modeling must be “as small as is consistent with the accuracy of commercial statistics of catch and effort, since the smaller the size the more faithful will be the representation obtained.” Another factor in spatial modeling associated with data is data sample size. Cope and Punt (2011) state that scientists need to balance the trade-offs between sample size and biological accuracy. The authors demonstrate that “greater spatial resolution in assessments decreases the amount of data available for each assessed area, therefore potentially increasing the uncertainty associated with the assessment.” Therefore, stock assessment scientists and managers need to decide how small the spatial scale should be for spatial modeling and harvest management strategies based on the availability of finer spatial scale data quality and sample size.

Besides data quality and data sample size, data diversity among data sets is also a critical factor for carrying out spatial stock assessment and management (Denson et al. 2017). For example, data sets with less variety can be correlated with each other (e.g., there could be correlation between movement rates and fishing mortality or selectivity) and therefore lead to high uncertainty in the outcomes using those data sets (Francis 2011). Hulson et al. (2011) found that increasing data diversity in tagging data reduces correlation between movement coefficients and other parameters can be achieved by designing the tagging study well and effectively. In addition, they show that the data from a well-designed tagging study can help to reduce the uncertainty in other parameter estimation such as mortality rates, which can help to achieve the goal of improving the results of spatial modeling in multiple ways (Hulson et al. 2011).

Spatial modeling is more data intensive compared to the non-spatial modeling because spatial modeling needs data to support existence of multiple populations.

however, it is not uncommon that different sources of data would show contradictory results (Francis 2011). Therefore, incorporating a variety of data sets does not guarantee improved assessments, may instead increase the uncertainty in parameter estimation. Under this circumstance, data weighting is necessary before incorporating different data sources in the model. Francis (2011) reviewed how to weight different data sets when the data sets provide contradictory results on the population dynamics. Francis concluded that when contradictory signals exist in the data set, weighting different data components is a challenge and there is no formulaic answer to this problem. Developing different models that use different data sets and then comparing the results from models would be a possible solution (Francis 2011), along with the use of the knowledge of experts, understanding of how those data sets are collected (Francis 2011; Hulson et al. 2011; Denson et al. 2017). Despite the possibility of contradictory signals arising from data sets, data collection protocols should consistently include spatial attributes whenever it is possible.

Defining the biologically accurate management boundaries is another overarching challenge because it is associated with the biological characteristics of the species as well as the management laws and politics (Stephenson 1999). A number of simulation studies have simulated the risks of mismatch between management units and biological units of the species (McPherson et al. 2001; Reiss et al. 2009; Kerr et al. 2014). Kerr et al. (2014) indicate that when the mismatch exists, the constant population life history parameters assumed in the assessment models (e.g. natural mortality) will be applied to multiple distinct populations, and the outputs and the corresponding biological referent points for management will be applied homogeneously over multiple subpopulations, and therefore increase uncertainty in assessment outcomes and management strategies.

Another overarching issue in spatial modeling and harvest strategies is the difficulty in conveying the multidimensional aspects of spatial modeling to stakeholders and managers. Communication skills that can promote the understanding of model results and increase the comfort with model outputs among stakeholders and managers is needed to be improved (Berger et al. 2017). Spatial models appear much more complex than the spatially aggregated models, and therefore receive more criticism of the model outputs. Some people say the spatially explicit models are over-parametrized or unstable in performance (Carruthers et al. 2011). And of course, spatially explicit models

require more data analysis. However, similar challenges also exist for complex statistical but spatially aggregated models. For example, parameter correlation and data weighting still need to be dealt with when using spatially aggregated models (Francis 2011).

Development of spatial models and increasing availability of spatially explicit data sets, has increased the potential for applying spatial techniques and modeling in many fisheries (Hampton and Fournier 2001; Pelletier and Mahevas 2005; Mormede et al. 2017). In spite of the limitations and challenges with spatial modeling and harvest management, incorporation of spatial techniques can provide more robust and sustainable management strategies at desired spatiotemporal scales (Montenegro et al. 2009). Spatial modeling can represent fisheries populations in a more realistic way that can better match population heterogeneity in spatial processes and therefore prevent local depletion (Goethel et al. 2011). Hence spatial modeling and corresponding harvest management will continue to be a popular area of research in the future.

## Chapter 5.

### Summary and conclusions

Factors contributing to the effectiveness of a given management strategy include spatial population structure and potential ecosystem interactions within the system (Punt *et al.* 2016; Grüss *et al.* 2016). To evaluate a proposed harvest policy, it is necessary to define an objective function and test performance of the proposed harvest strategy within a stochastic simulation analysis (Deroba and Bence 2008). The influence of potential spatial structure in the simulated population needs to be carefully considered and explicitly incorporated into the evaluation.

Approaches such as the estimation-simulation framework already exist for spatial modeling and harvest strategy evaluation, however, large application gaps still exist in the research of implementing spatially explicit harvest policies. One reason for the gap may be the difficulty in explaining model complexities to stakeholders and managers, in contrast to the traditional single stock approach that is well understood and generally accepted (Berger *et al.* 2017). However, when complex population dynamics (e.g. source-sink metapopulation dynamics or basin dynamics) exist in the fishery of interest, it is important to account for spatial attributes of population dynamics and local productivity (Crowder *et al.* 2000), and ultimately to achieve the goal of developing effective spatially explicit harvest control rules for spatial management.

Another important factor that contributes to difficulties in application of spatially explicit modeling and harvest strategies is the scale of data collection. Data that can support spatially explicit operating models is rarely available (Kerr and Goethel 2014). The estimation-simulation framework introduced in the section 2.3 helps to address some of these problems by using observed data to estimate parameters used in the operating models. In the future, the increased collection of small-scale data will be necessary for evaluating spatial harvest strategies (Denson *et al.* 2017). One possible way of doing the collection of small-scale data in the future could be a collaborative academic-industry-government approach (Doherty *et al.* 2017) where commercial fishermen could help to collect small-scale data based on the scientific input of the specific scales for data collection. Fortunately, fine-scale spatial data is increasingly

available in many fisheries (Neat *et al.* 2014; Denson *et al.* 2017). Therefore, I anticipate that spatially explicit models and harvest strategy development will continue in the future.

Two critical questions in the field of spatial modeling, relate to the appropriate dimension and level of spatial complexity should be included and addressed in the biological operating model, and when is spatially explicit modeling needed given large other uncertainties such as climate and fishermen behavior (Kritzer and Liu 2014; Goethel *et al.* 2016)? To answer those questions, I recommend that scientists should have a thorough review about the existing information for the fisheries such as what types of data are available, what dimension of complexity is happening of the fishery and resource, and what mechanisms influence the fishery. A thorough analysis of the existing information may clarify whether to represent population spatial structure in the fisheries and what level and dimension of spatial complexity to include in the modeling. If population spatial structure exists in the fishery and is known, and the movement rates and other spatial parameters among subpopulations can be well estimated with low uncertainties using the existing information and data sets, then it is necessary to incorporate the population spatial structure into the modeling process. It is important to note that transitioning to spatially explicit modeling is not always necessary or feasible. For example, research in yellowtail flounder populations has showed some degree of connectivity and varying vital rates within the populations (Hart and Cadrin 2004; Goethel *et al.* 2015a). However, simulations suggest that assessing yellowtail flounder as a closed population perform relatively well compared to the complex modeling that takes connectivity and vital rates into account (Goethel *et al.* 2015a). Therefore, spatially aggregated models can be more robust than the spatially explicit modeling, especially when uncertainties exist in parameterizing connectivity and other spatial parameters (Goethel *et al.* 2015a). This result is specific to yellowtail flounder, and therefore decisions should be carefully made on a case by case basis. Generally, spatial approaches can be advantageous when critical components of spatial structure can be observed, and spatial data collection exists.

In conclusion, this review has illustrated that scientific understanding of marine spatial processes is increasing, along with recognition of the importance of incorporating spatial structure through spatial modeling and maintaining spatial biocomplexity through spatial harvest strategies (Kritzer and Liu 2014; Goethel *et al.* 2016; Berger *et al.* 2017;

Le Cornu *et al.* 2018). However, experience in the development and application of spatial modeling is limited, and therefore spatial complexity is not a key focus of most harvest strategy evaluations. Ongoing collection of fine-scale spatial data and growing recognition among managers and stakeholders will likely continue to drive model development in the near-term.

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