# INTER-AMERICAN TROPICAL TUNA COMMISSION WORKSHOP ON SPATIAL ANALYSIS FOR STOCK ASSESSMENT 

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This report is organized into sections corresponding to the topics discussed at the workshop. Under each section, introductory text, taken from the background information provided to participants before the workshop, is given. Then abstracts for each presentation are provided. Finally, the discussions during the workshop about the focus questions are summarized. The report does not represent the consensus of the opinions of the workshop participants.

## 1. INTRODUCTION

It is clearly evident that stock and fishery dynamics vary spatially, and this variability should be considered in the assessment and management of fish stocks. As data collection methods improve, more fine-scale spatial data become available. These data can be analyzed to get a better understanding of the spatial variability of stock and fishery dynamics. Management strategies can then be designed to either exploit this spatial variability or to be robust to it, depending on the situation. Currently, few stock assessment models directly address spatial variability, and methods need to be developed to improve this situation. In the simplest form, stock assessment models either model spatial variability by separating fisheries into areas so that catchability and selectivity can differ or model each sub-stock separately. More complex models explicitly model separate sub-stocks and movement among them. These models are usually based on large areas, and do not model differences in biological parameters (e.g. growth) among areas. To aid in the development of spatially-explicit stock assessments, methods are needed to determine the appropriate spatial scales for separating stocks, sub-stocks, fisheries, or other factors included in the spatially-explicit stock assessment models. The goals of the workshop are to provide a forum to discuss the state of the art in spatial analysis in fisheries stock assessment and how it can be improved, and to motivate more applications.

## 2. SPATIO-TEMPORAL INTERACTIONS IN CPUE STANDARDIZATION

Standardization of catch-per-unit-of-effort (CPUE) data to develop an index of abundance is one of the most commonly conducted analyses in fisheries stock assessment. The standardization is conducted using a variety of approaches, e.g. general linear modeling (GLM), delta-lognormal, general additive modeling (GAM), neural networks, and habitat-based standardization. In these analyses the year (or other unit of time) effect is used to represent an index of relative abundance that is fit in stock assessment models.

Area (or some measure of space, e.g. latitude and longitude) is commonly included in the analysis and is frequently a significant variable included in the final model. Using area as a main effect in a GLM means that the trend over time is the same in each area, but the overall CPUE differs among areas. However, if there is a significant interaction term between area (or other factor) and year, this makes it difficult to interpret the year effect and the index of relative abundance. An interaction between area and year means that there are different trends in the CPUE in some of the areas.

There are several approaches to dealing with interactions between area and year. The first, and possibly
the most frequent, is to ignore the interaction term and not include it in the analysis. The other extreme is to produce separate indices of abundance for each area and apply separate stock assessments to each area. Methods have also been developed to deal with the interaction within the CPUE standardization. The interaction term is included as a random effect or the area-specific indices are area weighted to develop a single index.

Even if the interaction term is statistically significant, the differences in the year effects among areas may not substantially impact the management implications. Often there are so much data that any variable included in the analysis is significant. One method used to decide if variables (or interaction terms) should be included in the analysis is to limit the model to those effects that increase the explained variation by a least $\mathrm{x} \%$ (e.g. $5 \%$ ). If there is a significant interaction, the year effects should be contrasted among areas to see if the effect is meaningful. If there are multiple areas in the analysis, a single area may be different and causing the significant interaction. Analyses that group areas together and test which groups are the same should be carried out. On the other hand, if there is no significant interaction term, this does not necessarily mean that the areas have the same trend, but it may mean that there are insufficient data.

Sharing information about catchability among sub-areas in a spatially-structured population dynamics model can greatly increase the information content of the indices of abundance. For example, making the catchability the same for each sub-area will help estimate the relative abundance in each area. However, sharing catchability requires that the indices of abundance are calculated appropriately. The sub-areas are often of different sizes and contain different densities of fish. Therefore, the index should represent the relative abundance in each sub-area. In spatially-structured models of tuna in the western and central Pacific Ocean (WCPO), the Secretariat of the Pacific Community (SPC) shares catchability for standardized longline CPUE based indices of abundance among sub areas. First, standardized indices are calculated separately for each sub-area. Next, a temporal subset of the pooled data is modeled in a single analysis. Re-weighting is performed by summing the estimated $5^{\circ} \times 5^{\circ}$ area effects within each sub-area, and multiplying them by the sub-area standardized CPUE indices normalized over the period of the temporal subset. For more detail, see_Hoyle and Langley (2007).

### 2.1. Dealing with spatial-temporal interactions in CPUE standardization

## Mark N. Maunder

Significant area-year interaction terms are common in GLM analyses of fishery CPUE data. However, it is often difficult to determine if the resulting indices of relative abundance show substantially different trends. Four main methods have been used to deal with area-year interactions: explicitly ignore the interaction; average the year effects for each area; treat the interaction as a random effect; and model separate populations. The choice of which method should be used depends on the goal of the analysis and characteristics of the interaction. Analysis of Japanese longline CPUE data for bigeye tuna in the eastern Pacific Ocean (EPO) suggests that trends differ among areas, in which case modeling separate populations may be the best method to deal with the area-year interaction.

## FOCUS QUESTIONS

What is the best approach to deal with significant area-year interaction terms in CPUE standardization?
If the statistically-significant interaction between area and year explains only a small portion of the total variation (e.g. less than $5 \%$ ) and the differences in the year effect among areas is small, then the area-year interaction can be ignored. Caution should be taken in situations with limited data because there may be insufficient information to detect an interaction, even if one exists.

If the area-year interaction appears to be random (e.g. the residuals of the year effects for each area around a mean year effect for all regions appear to have no autocorrelation) then the area-year interaction can be treated as a random effect.

Differing CPUE trends do not necessarily imply separate populations. In a single stock with age-related spatial separation, CPUE trends will tend to differ due to 1) the time offset in cohorts passing through the fishery, and 2) the different levels of fishing-related depletion by age class. In some cases this situation can be modeled using separate fisheries.

If there are substantial differences among areas in the trend in the year effect, then the areas should be modeled as either separate populations or separate fisheries (see below). Sensitivity analyses should be conducted to determine the impact of spatial structure on the management advice.

In some situations, the interpretation of differences in the year effect is problematic. For example, if the stock contracts or expands its spatial extent as the abundance changes, the CPUE in the center of the distribution may be hyper-stable and the CPUE on the fringes of the stock may experience hyperdepletion (or a lack of data). In other situations, the center of the stock distribution and/or vessels may move over time (e.g. due to environmental changes).

## 3. SPATIAL STRUCTURING OF FISHERIES IN ASSESSMENT MODELS

It is a common practice to separate the catch into several different fisheries before including it into a stock assessment model. These fisheries can differ by fishing method, time, area, or other appropriate characteristic. The reason for separating fisheries is generally because they capture different size/age fish or that the indices of abundance relate to particular components of the catch. The general assumption is that selectivity and/or catchability is constant over the whole time period of the fishery. It is obvious that some gears catch different-sized fish, so the catches for these should be separated. For example, tuna stock assessments generally separate purse seine-caught fish, which are smaller, from longline-caught fish, which are larger. Separating catch into different fisheries temporally can also be obvious when certain management measures are put in place (e.g. minimum legal size or mesh restrictions).

Fish caught in different areas can differ in size. This may be due to differences in the size of fish that inhabit each area or some characteristic that influences the size-specific availability or selectivity of the gear. Often, the differences in size of individuals in the different areas are modeled as different fisheries rather than sub-populations in order to reduce the complexity of the modeling.

Unless there are clear juvenile and adult areas, it may be difficult to determine how to model the groups in the different areas. The areas can be determined by spatial analysis of the catch characteristics, such as CPUE, age, and size. For example, Phillips et al. (2008) used regression trees to define fisheries for the Antarctic toothfish in the Ross Sea.

### 3.1. Stock structure of bigeye, yellowfin, and skipjack tunas in the eastern Pacific Ocean

## Kurt M. Schaefer

Regional fidelity has been demonstrated for bigeye, yellowfin, and skipjack tunas in the eastern Pacific Ocean (EPO), with low levels of mixing expected with stocks in the central and western Pacific Ocean (WCPO). The scientific information available to elucidate stock structure of these three species in the EPO has been reviewed, evaluated, and compiled in this document. The evidence indicates there are probably northern and southern sub-stocks of bigeye (with separation at about $10^{\circ} \mathrm{N}$ ), based on tagging data; northern and southern sub-stocks of yellowfin (with separation at about $15^{\circ} \mathrm{N}$ ), based on tagging, length-at-maturity, morphometric, and stable nitrogen isotope data; and northern and southern sub-stocks of skipjack (with separation at about $15^{\circ} \mathrm{N}$ ), based on tagging and length-at-maturity data. The spatial extent of those stocks and the levels of mixing are not yet well defined. Stock boundaries most likely oscillate within a few degrees of latitude relative to seasonal and annual variability in oceanographic conditions. Further research is needed to elucidate the extents and interactions of the sub-stocks.

### 3.2. Determining spatial structure length distributions of tuna catches using multivariate regression trees

## Cleridy E. Lennert-Cody and Patrick K. Tomlinson

Individual yellowfin length-frequency samples can be unimodal and symmetrical, but also highly skewed or multimodal. In order to explore whether this type of structure may be related to the location and date of the purse-seine sets that caught the fish, we applied multivariate regression trees to the port sampling data for purse seine-caught yellowfin tuna from 2000-2007. The response variable was the proportion of fish in each of 11 length intervals. The five degree latitude, the five degree longitude, and the quarter associated with each set were used as predictors. Trees were built on each year's data separately and on the data of all years combined. Spatial splits of the data were found to dominate over temporal splits. Spatial splits associated with the one-standard error trees were compared to the spatial strata currently used by the IATTC for computing total catch. Future work will include replacing the sum of squares loss function with a loss function more appropriate for the comparison of distributions, building trees over the full period used in IATTC stock assessments, and determining if the spatial post-stratification inferred from the regression tree analysis would provided a smaller variance for the estimated total catch than the current spatial stratification.

### 3.3. A new feature extraction method for very non-normal data: analysis of multivariate speciessize data from a tuna purse-seine fishery

## Mihoko Minami, Cleridy E. Lennert-Cody

We propose a new feature extraction method for very non-normal data. Our method extends principal component analysis (PCA) in the same manner as the generalized linear model extends the ordinary linear regression model. As an example, we analyze multivariate species-size data from the tuna purse-seine fishery in the eastern Pacific Ocean. The objective of this analysis is to explore species associations and their relationship to environmental factors, as a means of developing options for reducing the catches of unmarketable animals. The data contain many zero-valued observations for each variable (combinations of species and size). Thus, as an error distribution we use the Tweedie distribution, which has a probability mass at zero, and apply the Tweedie-generalized PCA (GPCA) method to the data.

## FOCUS QUESTIONS

What is the best approach to define fisheries and/or populations in stock assessment models?
The approach and information used to define fisheries and/or stocks depends on many factors specific to the stock under study. It also depends on the goal of the analysis (e.g. management or research). For example, evaluation of spatial closures and marine reserves may require finer spatial stratification than for the evaluation of total allowable catch (TAC)-based management.
Factors to consider when defining areas or fisheries include

## General

Simplicity
Statistical areas used to collect data or implement management
Management needs
Adequacy of amount of data available
Consistency among assessments of different species

## Fishery information

Abundance trends
Size data
Catch, effort, and/or CPUE distribution and magnitude

Gear type, method (e.g. purse seine set type), and target species

## Biological information

Geographic variation in life history characteristics (e.g. growth, maturity schedules)
Tagging data
Genetics
Morphometrics and meristics
Otolith microchemistry

## Isotopes

Biogeography Oceanography/Longhurst biomes
Larval distribution and dispersion
These factors differ in the information they provide on defining areas or fisheries. For example, a useful preliminary rule of thumb (as used by the SPC ) is to consider separate areas if the CPUE trends differ, and separate fisheries if the length frequencies differ. The biological data typically indicate whether the stock assessment should be separated into different areas (although see below about using fisheries to approximate areas). Tagging data are considered the most useful method to provide the necessary information to define areas and movement among areas for many species.

## Research

Extensive research (e.g. . simulation analysis) is needed to evaluate the value of each of the factors in defining appropriate areas and fisheries and to prioritize data collection. Statistical techniques need to be developed to extract information from each factor and to combine this information. Sampling programs need to be designed appropriately to provide the desired information.

Do longline and purse-seine fisheries operate on the same stock?
Restricted movement and spatial differences in the fisheries may cause the fisheries to operate on different components of the stock.

Historically, there have been areas in the EPO in which longline fishing has dominated and purse-seine fishing has been limited. Purse seine fishing on fish associated with fish-aggregating devices (FADs) has recently expanded into these areas and produced favorable catch rates. This indicates that historically there may have been components of the EPO stock of bigeye that were fished by the longline fisheries, but not by the purse-seine fisheries.

Vertical distribution data obtained from archival tag data indicate that bigeye and yellowfin tuna are vulnerable to both purse-seine (surface) and longline (subsurface) fisheries in the same areas.

## Research

Analyses should be conducted to determine how to appropriately model changes in the spatial distributions of fisheries observed in the EPO. For example, the increase in recruitment that is estimated to have started when the purse-seine fishery expanded should be further investigated.

Tagging should be conducted on a wider range of ages and areas for yellowfin, bigeye, and skipjack.

## 4. SPATIAL POPULATION DYNAMICS MODELS

The first decision that should be made when there is spatial structure in the population dynamics is whether the sub populations can be adequately modeled as independent populations or if interactions (i.e. movement) among sub-populations should be modeled. Independent populations are probably the simplest for both assessment and management. If interactions are necessary, there are several different approaches that have been applied, e.g. advection-diffusion models, block transfer models, and movement models. The type of model used will depend on the data that are available and the types of questions
being asked.

## Advection-diffusion models

Advection-diffusion models are widely used in animal ecology (e.g. Skellam 1951 and Okubo 1980), and have been applied in population models of fish movements (e.g. Sibert and Fournier 1994; Sibert et al. 1999; Adam and Sibert 2002). The time development of the density of the tagged population is assumed to follow the advection-diffusion-reaction (ADR) equation. The ADR equation is solved numerically by a finite difference partial differential equation solver. The advection-diffusion models are usually fit to tagging data to estimate the model parameters.

## Block transfer

Most stock assessment models that include interacting sub-populations model each sub-population as a large spatial block with movement among the sub-populations. In general, these models require estimates of movement rates from tagging analysis. More recent analyses (Hampton and Fournier 2001; Maunder 2001) have integrated the tagging data directly into the population dynamics models. The movement among sub-areas may be structured, based on age, size, season, or some other characteristic.

## Movement

In some cases movement among sub-populations can be constrained due to understanding about movement patterns or may occur seasonally for reproductive purposes. This structure may facilitate the estimation of model parameters. For example, Fournier et al. (1998) were able to estimate movement parameters from CPUE and length-frequency data for albacore tuna in the southern Pacific Ocean because they assumed that recruitment occurred in only one area.

## Sub-stocks that mix when caught

In some species there are separate sub-populations that mix when they are feeding and are caught, but return to separate areas when they spawn (e.g. New Zealand hoki, salmon and other anadromous species, Atlantic bluefin, and Hawaiian black-footed albatross). This type of dynamics still requires joint modeling of the populations, but may not require explicit modeling of movement. Information on the proportion of the catch comprised of each population (e.g. from tagging or genetics) may be important to correctly model the populations.

## Sharing information among sub-populations

If multiple sub-populations are modeled, whether they interact or not, it may be useful to share information among the sub-populations. It is likely that some, if not all, the parameters from the subpopulations may have similar values. In addition, there may not be enough information for some of the sub-populations to reliably estimate the model parameters. Random-effects models can be used to share information among the sub-populations. These models can be implemented by using hierarchical Bayesian models and the Markov chain-Monte Carlo (MCMC) algorithm or in a Frequentist framework using AD Model Builder's (Otter Research 2004) random effects module.

## Fine scale spatial stratification

There have been several applications that model fine-scale spatial dynamics of fish populations (e.g. SEAPODYM). The models are often simulation models in nature, and require assumptions about the model parameters. However, recent applications have attempted to estimate the model parameters by fitting directly to data (Senina et al. 2008).

### 4.1. Analysis of two structural hypotheses about the dynamic of shrimp Heterocarpus reedi off the coast of Chile

## Carlos Montenegro, Mark N. Maunder, and Maximiliano Zilleruelo

The Chilean shrimp (Heterocarpus reedi, Decapoda, Pandalidae) inhabits the bottom of the continental
shelf and upper slope off central Chile, at depths between 150 and 550 m . The Subsecretaría de Pesca (SUBPESCA) declared the fishery to be fully exploited in 1995, and established a total allowable catch of 10,000 tons for 1996. Spatially, the management of the resource is based on two main zones: the northern zone, from latitude $26^{\circ} 03^{\prime} \mathrm{S}$ to $32^{\circ} 12^{\prime} \mathrm{S}$ and the southern zone, from latitude $32^{\circ} 12^{\prime} \mathrm{S}$ to $38^{\circ} 28^{\prime} \mathrm{S}$. As shrimp landings showed a marked decrease during 1997-2000, during 2001 individual quotas were introduced and total catch quota was split in a temporal and spatial fractioning that included the complete closure of the southern zone. Since then, alternate closures to regions in this zone have been applied annually, while the total catch quota has been maintained at around 5,000 tons per year. The administration of the fishery includes annual stock assessments studies, with the purpose of reviewing the available information of the resource, determining the status of the resource, evaluating the implications of different management actions, and recommending a total allowable catch for the next year. The goal of this analysis is to test whether there are differences in the population dynamics of Heterocarpus reedi in the large zone which it inhabits off the coast of Chile. We test if is better, from the stock assessment point of view, to model the stock as one unit in the whole area, or as two separate stocks. We use three versions of a surplus-production model, defined by the value of the shape parameter, and we test several scenarios. The scenarios differ as to which parameters are shared between the two zones and, consequently, in the number of parameters estimated. This analysis is used to determine if the virgin biomass, the biomass at the beginning of the modeling period (1989), or the production rate at maximum production, differs between the two zones inhabited by Heterocarpus reedi. Furthermore, we test whether the data suggest a better fit to a symmetric production curve ( $\mathrm{B}_{\mathrm{msy}} / \mathrm{B}_{0}=0.5$ ) or an asymmetric one ( $\mathrm{B}_{\mathrm{msy}} / \mathrm{B}_{0} \neq 0.5$ ). The results suggest that all model parameters except for the carrying capacity are similar in the two zones. Initial investigations suggest that carrying capacity per unit of habitat is similar in the two zones. The main difference between the two zones is local depletion caused by different catch histories.

### 4.2. An evaluation of spatial structure in the stock assessment of bigeye tuna in the eastern Pacific Ocean

## Alexandre Aires-da-Silva and Mark N. Maunder

Tagging studies indicate restricted movements and regional fidelity of bigeye within the eastern Pacific Ocean (EPO). Such restricted movements, combined with the spatial heterogeneity of the fleet distribution and the catch, suggest that localized depletion patterns of bigeye sub-stocks may exist in the EPO. A preliminary evaluation of spatial structure in the stock assessment of bigeye in the EPO was made. The EPO was divided into four major sub-areas-inshore, central, northern, and southern-with no mixing of fish assumed among sub-areas. An independent stock assessment was conducted for each subarea. The preliminary analyses show differences in the longline CPUE trends and in the depletion levels among sub-areas in the EPO. These results suggest that smaller spatial scales are important to consider. However, similar trends in recruitment indicate that the sub-stocks may be connected through recruitment or similar recruitment processes.

### 4.3. A random-effects meta-population model of yellowfin tuna in the eastern Pacific Ocean

## Mark N. Maunder and Alexandre Aires-da-Silva

A random-effects meta-population model is applied to the yellowfin tuna stock in the eastern Pacific Ocean (EPO) to account for the spatial expansion of the longline and purse-seine fisheries. A PellaTomlinson (1969) model with the shape parameter fixed so that $\mathrm{B}_{\mathrm{msy}} / \mathrm{B}_{0}=30 \%$ ( $\mathrm{P}-\mathrm{T} 30 \%$ ) is used to model each $5^{\circ} \times 5^{\circ}$ area as a separate population. The estimated parameters of the models for each area share information by treating them as random effects. The model is fit to purse-seine catch per day of fishing data for each area. Movement among areas is ignored. The population dynamics model essentially smoothes the CPUE data and fills in spatiotemporal cells with no data. Sharing information about parameters among the areas using the random effects allows modeling areas that have insufficient data to estimate the model parameters. Initially, a simple model is run, assuming that the estimated catchability is the same for each area and that the production rate parameter is fixed and the same for each area. Spatial
distributions of estimated depletion levels and carrying capacities are consistent with current understanding of the yellowfin stock and fishery. Several improvements, including the use of spatial correlation in the random effects, could be made to the model.

### 4.4. Modeling fisheries and stocks spatially for Pacific Northwest chinook salmon

Rishi Sharma, Henry Yuen, and Mark N. Maunder

The Pacific Salmon Commission (PSC) was established in 1985. The primary objective was to manage for the conservation of different species of Pacific salmon in Alaska, Canada, Washington, and Oregon. One of the most valuable stocks, both commercially and recreationally, managed by the PSC is chinook salmon (Oncorhynchus tshawytscha). Currently, the PSC uses a cohort analysis algorithm that scales current abundance to a historic base period (1979-1982) abundance, and projects terminal run size or escapements for thirty different stocks by estimating environmental variability parameters to best fit observed terminal run data for that stock. We present an alternative to this model; an adapted catch-at-age model that uses the life history of chinook salmon and a time series of coded wire tag (CWT) data and terminal run data. Once estimates of catch (with precision) are generated external to this model, we fit the adapted age-structured model to ocean catches, terminal catches, and terminal escapement by estimating catchability and selectivity by fishery and time, maturation by stock and time, and recruitment deviates by time. The model presented is capable of addressing multi-stock and multi-fishery interactions by estimating different selectivity and catchability for different stocks by fishery. The added advantage of these methods is that we explicitly incorporate uncertainty into these assessments, can also account for varying quality (precision) of external data, including genetic data, and build in environmental processes into these models.

### 4.5. Modelling the interactions in time and space between black footed albatrosses and fishing effort

## Simon D. Hoyle and Mark N. Maunder

Two models of black-footed albatross population dynamics are being developed, using different approaches. We summarize the data used in both models and the structure and preliminary results from one model. The model is intended to be general enough to model the important aspects of population dynamics for a range of albatross species. Its structure includes sub-populations on island groups, with bycatch being taken from a pooled population. The statistical approach is to use integrated analysis, fitting to multiple data types within the one model. These include nest counts, fledgling counts, estimates of breeding success, survival, and state transition rates from mark-recapture data, and fishery bycatch. Fishing effort and bird distribution data are also included in the model, and assumed to be known without error. Long-term nest and fledgling count data show some interesting trends and dynamics, which suggest hypotheses and sensitivity analyses. For example, population trends appear to differ among islands, with long-term stability on Laysan Island, but substantial increases on most other island groups. This suggests that effects on or close to islands must be considered. Also, a decline in nests counted at French Frigate Shoals from the mid-1980s to the mid-1990s was contemporary with the disappearance of Whale-Skate Island (which held up to $40 \%$ of French Frigate Shoals breeding pairs), so to some extent may have represented skipping breeding until nest sites were re-established on other islands. Preliminary model results were presented, including diagnostic fits to the data, and estimates of total bycatch by fishery. These results are expected to change substantially as model structure and input data are improved.

### 4.6. A general covariate-based model for meta-populations

Mark N. Maunder, Carlos Alvarez-Flores, and Simon D. Hoyle
Spatial structure is common in many populations, but catch data are often not collected in such a way that the origin of the individuals is known, and this causes issues when estimating the impact of fishing. In addition, non-fishery impacts may differ spatially, and untangling the different impacts to determine the
fishery impact may be difficult. These issues are particularly relevant for species such as the Hawaiian population of black-footed albatross, which has sub-populations in several breeding colonies and islands. A general approach for modeling such populations is developed based on 1) using population dynamics models to model each population; 2) applying integrated analysis to fit to multiple data types; 3) modeling survival as a function of covariates, including fishing impacts and non-fishery related impacts; and 4) fitting to bycatch data aggregated from multiple populations. The method was applied to preliminary data for the Hawaiian population of black-footed albatross. The results indicate that even though the population is rebuilding, fishing has had a substantial impact on the population and that, due to the low productivity of the population, the impact of historical fishing lasts for a long time. Non-fishing impacts are also shown to be substantial for some of the populations and their inclusion improves the fit to the data.

### 4.7. Spatial analysis of blue shark in the North Atlantic Ocean

## Alexandre Aires-da-Silva, Mark N. Maunder, Nancy Kohler, John Hoey, and Vincent Gallucci

This study presents a spatially-explicit tagging model to estimate blue shark movement and fishing mortality rates in the North Atlantic Ocean. The model uses the blue shark tag-recovery data of the U.S.NMFS Cooperative Shark Tagging Program (1965-2004). Four major geographic regions (two on each side of the ocean) are assumed, and annual rates of mixing among regions are estimated. The blue shark fishing mortality rates $(F)$ were found to be heterogeneous across the four regions. While the estimates of $F$ obtained for the western North Atlantic were historically lower than 0.1 per year, the estimates of $F$ over the most 1990s in the eastern side of the ocean are rapidly approaching an estimated reference point for conservation ( $F_{\max }=0.2$ per year).

### 4.8. Accounting for age-based and seasonal movement and other spatiotemporal effects, using regional and seasonal fisheries in a pooled-population model for South Pacific albacore

## Simon D. Hoyle

The South Pacific albacore stock assessment is currently modeled as a single region. Spatial and temporal variation in CPUE and size are accounted for with seasonal and spatial adjustments to catchability and selectivity. Before 1975, the assessment used four regions, and estimated movements among them. I discuss the tradeoffs between these two approaches, and compare the results. The single-region approach may be more reliable and stable when the trends in CPUE are similar for the different regions, as is the case for South Pacific albacore.

### 4.9. A spatially-explicit model of yellowtail flounder

## Daniel R. Goethel, Christopher M. Legault, and Steven X. Cadrin

Accurately modeling yellowtail flounder, Limanda ferruginea, is vital, because all three U.S. stocks are rebuilding from an overfished condition, and large discrepancies have occurred between model predictions and subsequent stock assessments. Recent tagging data demonstrate movements of yellowtail among stock areas, which may be affecting the model results, as negligible immigration and emigration is assumed in all three assessments. The purpose of this study is to evaluate the sensitivity of stock assessment results to movements of fish among stock areas. To do this, a spatially-explicit forwardprojection stock assessment model is being developed that includes a mark-recapture component (based on yellowtail tagging data) to the objective function to estimate movement. Future work will also include development of an external large-scale circulation model to assess the effects of egg and larval drift, both within and among stock areas, on recruitment. A simulation study will be performed on the integrated model to assess model performance, and to evaluate the types and amounts of movement that most affect the population dynamics of yellowtail flounder.

### 4.10. Exploring effects of fishing and migration on the distribution of Pacific halibut

## Juan L. Valero, Steven Hare, Ray Webster

Evidence of continuing movement beyond the age of recruitment to the fishery has recently challenged closed-area stock assessments of Pacific halibut. A coast-wide assessment currently in use has resulted in an estimated coast-wide harvest rate near the target; however, area-specific harvest rates are estimated to have been more than twice the target in the eastern areas and less than the target in the western areas. In order to illustrate the effects of movement and fishing on the distribution and population structure of Pacific halibut, we developed a simulation model with a user-friendly graphical user interface (GUI). The GUI allows the user to specify different movement patterns and fishing levels, run scenarios, and visualize the results of the simulations. The underlying model of the GUI is an age- and size-structured movement model. Scenarios using movement and fishing patterns close to those observed for Pacific halibut suggest that the current spatial distribution of halibut differs from that expected under no fishing conditions or under a spatially-uniform harvest rate, with higher levels of depletion in the eastern areas relative to the western areas. Preliminary results are consistent with recent and historical fishing patterns, recent coast-wide assessment estimates of realized harvest rates, and historical estimates of halibut distribution. Further work is needed to evaluate the effects of different levels of uncertainty and spatial variability in both population and fishery dynamics on the performance of alternative assessment approaches and harvest strategies for Pacific halibut.

### 4.11. Modeling ontogenetic changes in depth of sablefish, using spatial structure in Stock Synthesis

## Ian Taylor

Simulations of ontogenetic shifts in depth distribution of sablefish, Anoplopoma fimbria, can be adequately represented by a single-area model with depth-specific selectivity curves. However, both age and size selectivity must be considered. If the movement is age specific and selectivity is size specific (e.g. small fish escape through the trawl) then both age and size selectivity should be modeled. In the sablefish example, the size selectivity is logistic to model the escapement of small fish, and the age selectivity in the areas where young fish reside is reverse logistic to model the lack of old fish in that region.

### 4.12. Lessons from spatial tuna stock assessment applications in the western and central Pacific Ocean

## Simon D. Hoyle

I present an overview of spatial issues that are considered important for stock assessments of bigeye and yellowfin tuna in the western and central Pacific Ocean (WCPO). These fisheries are complex, with a multitude of fishing methods, fleets, and species. Spatial effects on population dynamics that may be considered include ocean conditions, including thermocline depth, seasonal changes, convergence zones, and seamounts, movements of the fish, age effects, and the Exclusive Economic Zones of the nations of the WCPO. The following issues are addressed in detail: regionalization of the model and the fisheries, defining regional boundaries, regional scaling of CPUE, estimating movement among regions, and spatial effects on biology that are not included in the model.

### 4.13. Likelihood selection for a spatially-resolved tag attrition model

## Eunjung Kim and John Sibert

The consequences of different choices of the likelihood function are compared in an advection-diffusion reaction model (ADRM). Tag attrition models are an important method for parameter estimation in analysis of tag return data. In previous studies, different likelihood functions were specified in tag attrition models without much consideration as to the consequences. Different likelihood functions may be sensitive to tag return numbers in ways that have a profound effect on the numerical values of the
estimated parameters. We applied three likelihood functions (Poisson, negative binomial, and lognormal) in ADRM applied to yellowfin tuna tag return data of the Regional Tuna Tagging Project of the Secretariat of the Pacific Community. The Poisson and negative binomial functions yielded the best fits to the observed tag return data. The lognormal likelihood function severely underestimated both fishing mortality and diffusion rate. Therefore, selection of the likelihood for tag attrition models should explicitly consider the effects on estimated parameters.

### 4.14. A multi-stock age-structured tag-integrated model (MAST) for the assessment of Atlantic bluefin tuna

## Nathan Taylor, Murdoch McAllister, Barbara Block, and Gareth Lawson

We present a Beta version of a spatial, multi-stock age-structured tag-integrated stock assessment model (MAST) for Atlantic bluefin tuna. MAST models two spawning populations (eastern and western) of Atlantic bluefin simultaneously in four areas, with quarterly time steps. The model estimates maximum sustainable yield (MSY) and fishing mortality corresponding to MSY ( $F_{\text {msy }}$ ) as leading parameters. Each stock has specific growth, maturity, and natural mortality parameters. The western stock is assumed to spawn only in the Gulf of Mexico (GOM, ICCAT area 1) and the eastern stock only in the Mediterranean Sea (MED, ICCAT area 6). Currently, the rest of the Atlantic Ocean is divided into two areas, ICCAT area 2 and a combination of ICCAT areas 3 and 4. In the model, fish are not permitted to move to the other stock's spawning area, but are otherwise allowed to move among any of the other areas in accordance with estimated movement transition matrices. During spawning periods, we assume that movement transitions from all areas to the spawning area of a given stock are given by that stock's maturity-at-age ogive. Non-spawning fish during that period move according to movement transition probabilities estimated for non-spawning fish, but are not permitted in spawning areas during this period.

We divided each mark-recapture data set into three groups, in accordance with whether the marked fish's stock of origin could be designated as western (1), eastern (2), or unknown (0). In a few cases with recently-marked fish, these designations could be made using genetic characteristics, but we designated the vast majority as eastern or western fish in accordance with whether they had been observed in one spawning area or another. In the cases for which it was not possible to assign fish to the western or eastern stocks, we assumed that the fish's stock of origin was unknown, and the fish could have been either a MED or GOM fish. Mark-recapture data were fit to discreet state-space likelihoods for electronic tag types. Here each fish has a mark-recapture history consisting of location (observed in areas 1-3 for GOM fish, or 2-4 for MED fish) or event states (captured by fishing gear g) or not observed (0). When making a stock designation was not possible, the situation was more complicated, since observations may be of either a GOM or MED origin fish. In those cases, twice the number of state combinations is possible. Here the tagged fish is assumed to be either a GOM or MED stock fish in areas 1-4, a GOM or MED fish caught in fishing gear in areas $1-4$, shed or dead, etc. In this case, the initial probability of the state, given the observation at the first time step, is given by the proportion of fish vulnerable to the gear and area in which it was initially marked. Currently we convert length at marking into ages outside the model.

We fitted MAST to ICCAT's indices of abundance for each area, to conventional mark-recapture data starting in 1950, and to archival and pop-up satellite tagging data. Abundance indices are fitted, using lognormal likelihoods, to the predicted vulnerable biomass (or number as applicable for each index), which is given by the sum of vulnerable biomasses for each stock, area, and quarter combination. Selectivities are modeled as a function of mean length at age, given by stock-specific von Bertalanffy growth parameters. The joint likelihood function therefore consists of 10 components for CPUE data, and for each stock designation $(0,1$, and 2 ) of each mark-recapture data type (conventional, archival, or popup). We show sample fits and discuss some problems with respect to the data and sampling programs used.

## FOCUS QUESTIONS

## When should sub-populations be modeled?

This question is answered above following the question "What is the best approach to define fisheries and/or populations in stock assessment models?"

## When can interactions between sub-populations be ignored?

The interactions between sub-populations can be ignored when simulation analysis indicates that the interactions do not impact management actions. For example, this may occur when movement among areas is low or if selectivity can account for age-specific movement.

Also, see the answer to the question below "Can region specific selectivity in a single region model account for movement?"

## Can region-specific selectivity in a single region model account for movement?

Generic simulations indicate that in some situations, region-specific selectivity in a single region model can adequately account for movement (see the abstract below "Evaluation of the impact of marine protected areas on stock assessment-based fisheries management"). This was shown to be true for ontogenetic shifts in depth distribution of sablefish using a single-area model with depth-specific selectivity curves (see the abstract above "Modeling ontogenetic changes in depth of sablefish, using spatial structure in Stock Synthesis").

In some situations it is clear that selectivity would not appropriately account for movement. For example, if there is a single juvenile area, but two adult areas, then different exploitation rates in the two adult areas could not be modeled appropriately using selectivity.

## Research

Simulation analyses should be extended to investigate a wider range of scenarios regarding spatial structure and movement.

## Is a Pacific-wide assessment of bigeye tuna necessary?

Initial tagging data indicate that movement of bigeye tuna is restricted. There are some issues with limited tagging data throughout the Pacific Ocean. There is also concern about the limited size and spatial distribution of bigeye tagged.

Preliminary analyses show differences in CPUE trends among subareas within the eastern Pacific Ocean and differences in the depletion levels of independent assessments based on these sub-areas. These results suggest that smaller spatial scales are important. However, similar trends in recruitment suggest that stocks may be connected through recruitment or similar recruitment processes.

A Pacific-wide bigeye tuna assessment is worthwhile for research purposes to confirm that the regional assessments provide similar conclusions, as previous studies have shown. Pacific-wide assessments also provide a forum for collaboration between scientists of the different regional fishery management organizations (RFMOs).

## Research

More comprehensive tagging data and life history samples throughout the Pacific Ocean are required. Stock assessments should be developed that include all the available tagging data, including those for experiments initiated during earlier years, which were analyzed by less sophisticated methods than those currently used. Fish and/or fishermen often behave differently in different years, so analyzing data for as many different years as possible may provide insights that would not otherwise be obtained. However, fishing effort has usually taken place in more extensive areas during recent years, so this must be taken into account when comparing the tagging results of experiments initiated in different years. Additional
analyses of the spatial structure in the bigeye tuna assessment are required.
Is it reasonable to assume that catchability and selectivity are the same among areas?
When the population is subdivided into separate areas, it can become difficult to estimate the relative biomasses in these areas. The WCPO assessments assume that catchabilities (under particular conditions) and selectivities for many of the Japanese longline fisheries are the same across areas. This assumption provides substantial information to the assessment on the absolute abundance by age/size across areas. The catchability assumption requires appropriate calculation of the habitat in each area and how it relates to the behavior of the fish.

There are several situations for which this assumption may be inappropriate, even for surveys. For example, if non-target species in one area interfere with the gear (e.g. dogfish removing bait from hooks) this may modify the catchability. Another example is seasonality factors that may differ on either side of the equator.

## Research

Data on bycatch should be evaluated to determine if it has an impact on the catch rates of the target species. Using individual hook data may allow the analysis of the time that bait remains on hooks.

More research is needed to determine the appropriate method to estimate the available habitat in each area so that catchability can be shared.

Is it important to model differences in biological processes (e.g. growth, maturity, natural mortality, and recruitment)?

Many species show variation in biological processes among areas. For example, yellowfin tuna in the eastern Pacific Ocean (EPO) exhibit differences in life history parameters with latitude. The growth rates of yellowfin also appear to vary within the western and central Pacific Ocean (WCPO), with lengthfrequency data in the north and otolith data in the central Pacific indicating growth rates that are different from those in the tropical western Pacific estimated from tagging and otolith data. The reproductive parameters of bigeye appear to be different in the EPO and the WCPO. These differences can affect management quantities. For example, assessment results from a Pacific-wide bigeye assessment differed, depending on whether the growth rates were based on EPO or WCPO data.

Yes, it is important to model differences in biological processes among areas. However, it becomes more difficult to model them if there is movement among the areas

## Research

Comprehensive biological sampling should be carried out across the spatial distribution of the stock to determine differences in biological processes, such as growth and maturity.

Spatial stock assessment models with movement that include different biological processes among the areas should be developed and evaluated.

How can archival tagging data be used to provide information about movement in stock assessment models?

The diffusion and/or dispersion estimates commonly obtained from the analysis of archival tagging data using state-space models could be used as a prior for movement in stock assessment models. Simulations would need to determine the block transfer rates, and would require assumptions about the distribution of fish within a region.

Alternatively, the archival tag data could be integrated directly into the stock assessment model by aggregating the fine-scale temporal archival data into quarterly time steps to estimate movement rates among large areas.

## 5. INF ORMATION ABOUT MOVEMENT AMONG SUB-POPULATIONS

Modeling interacting sub-populations requires information about movement among the sub-populations. The obvious source of information is from tagging data that directly estimate movement (Maunder 2007). Information can also be provided by genetics, micro chemistry, morphometrics, parasites, and unique spawning grounds, but these data may not provide the type of information that is needed. It may indicate whether there is some or no movement, but not the amount or if it is sufficient to impact management recommendations.

In integrated assessment models, data other than tagging data may also provide information about movement. For example, differences in age or length-frequency data among areas can provide information on movement, particularly if recruitment can be assumed to occur in only one area. However, this information may be from noise in the age-frequency data or model misspecification and not actual signal about movement. In some cases, the age-frequency data can overpower the information in the tagging data, producing movement estimates that are counter to those from the tagging data, which is unrealistic.

### 5.1. Movements, behavior, and habitat utilization of bigeye and yellowfin tunas in the eastern Pacific Ocean, as determined by tagging experiments

## Kurt Schaefer and Daniel Fuller

Preliminary results are presented on the movements, behavior, and habitat utilization of bigeye and yellowfin tuna tagged and released with geolocating archival tags in the eastern Pacific Ocean between 2000 and 2008. A total of 323 bigeye ( $49-136 \mathrm{~cm}$ in length, mean $=89.8 \mathrm{~cm}$ ) were tagged and released, and $162(50.2 \%)$ were recaptured and their tags returned. A total of 698 yellowfin (51-161 cm in length, mean $=82.1 \mathrm{~cm}$ ) were tagged and released, and $254(36.4 \%)$, were recaptured and their tags returned. Analyses of the archival tag data sets presented include estimation of the most probable movement paths and parameters obtained using the unscented Kalman filter. Results indicate restricted movements, by both species, with fidelity to the areas where they were tagged and released. The discrimination and classification of the proportions of days and frequency of events in which these species exhibited various unique behaviors, and the ontogenetic changes in those behaviors, are described. Species-specific vulnerabilities, to capture by longline and/or purse-seine vessels, inferred from these behaviors, are discussed. Horizontal and vertical habitat utilization distributions are also presented, and discussed with respect to physical oceanography.

## FOCUS QUESTIONS

Should age- or length-frequency data provide information about movement?
Age- and length-frequency data by area often provide information on movement. In some cases, for which there are distinct areas in which a component of the population (e.g. juveniles) are located, it may be appropriate to allow age data to provide information on movement. However, the signal in the data may be due to variation in unmodeled processes not related to movement. Therefore, in these cases, the amount of information about movement contained in age- and length-frequency data should be reduced. Down weighting the age data not only reduces the information on movement, but also on selectivity, recruitment, fishing mortality, and other processes. Therefore, the reduction in information may more appropriately be achieved by adding additional process variation to the model (e.g. annual variation in selectivity or growth).

## Research

Simulation analysis should be conducted to determine the appropriate methods to include additional process error in stock assessment models.
Does genetics (or other data e.g. otolith micro-chemistry, morphometrics, isotopes, etc.) provide useful information on movement?

These data can be used in an integrated model to represent the proportion of each stock in an area at a particular time. This may provide information on movement. For example, genetic data (or otolith microchemistry) of a fish at a given age caught in a certain area could provide information on movement, but this case is limited to only a few species with spawning site fidelity (e.g. bluefin tuna). Otolith microchemistry might be used to determine the general location of an individual at different periods in its life. This can be treated as a natural archival tag and used in an integrated assessment model.

## Research

Research should be conducted to determine how useful these data are for estimation of movement. This work would require extensive simulation analysis. Cost-benefit analysis should be conducted to prioritize data collection, in particular with comparison to tagging data. Genetics and otolith micro-chemistry data have shown limited value for tropical tunas.

What characteristics should a tagging program have to provide adequate information to parameterize a spatial stock assessment model?

The spatial distribution of the releases of tagged fish should be proportional to the abundance and agestructure of the population (as attempted by the International Pacific Halibut Commission and the Commission for the Conservation of Marine Living Resources) and over several years. Recoveries should be made in all areas in which tagged fish occur and of fish of all sizes. This may require effort to make sure that recoveries are taken by a variety of fisheries. Estimates of reporting rates are essential.

Comprehensive tagging of yellowfin tuna appears to be needed due to initial tagging data indicating that yellowfin show more movement in open-ocean areas than in coastal areas and in the vicinity of seamounts and islands. This also implies that different diffusion parameters would have to be calculated for these different areas.

## Research

Research is needed on external visual queues that can be used to uniquely identify fish carrying coded wire or passive integrated transponder (PIT) tags.

More work is needed on both theoretical and practical design of tagging studies.

## 6. SPATIAL ANALYSIS OF FLEET DYNAMICS

Not only do the fish move around, but the vessels that fish on them move as well, which complicates the interpretation of the data and management of the stocks. A better understanding of the fleet dynamics will help in constructing stock assessment models and management measures. For example, evaluation of closed areas requires an understanding of where the vessels will operate when the area in which they would normally fish is closed.

### 6.1. Modeling fleet dynamics using neural networks and cellular automata

## Michel Dreyfus

Fishermen's behavior is a driving force that should be modeled or represented in simulations in order to describe the spatial dynamics of fishing effort. Tools like artificial neural networks and cellular automata are worth considering for that purpose, and some frameworks directed toward that goal are described. Maximization of economic return is considered to be the main driving force, but some considerations regarding human interactions from the field of sociology are also incorporated into the modeling.

### 6.2. On the trail of tuna: studying movements of purse-seine vessels

Richard Berk, Andreas Buja, Cleridy Lennert-Cody, Michael Freiman, Brian Kriegler, and Nickolas Vogel

Purse-seine vessel trip paths show an amazing diversity of types of features that are related to the vessel's
mode of fishing, searching techniques, interactions with other vessels, weather, and economics. A computer-intensive algorithm is being developed to predict purse-seine vessel movements as a means of providing insight into fishing effort. The algorithm extends the machine learning procedure, gradient boosting, to vector outputs. Inputs to this algorithm include the vessel's current location, activity, and status, plus information on its current and previous searching behavior, previous locations of successful fishing, and the locations and activities of cooperating vessels. Because no data are explicitly collected on vessel interactions, this project has also focused on the development of statistical measures for quantification of cooperative interactions among vessels. Visualization of potential vessel interactions has been greatly facilitated by the development of a program in the statistical freeware R for interactive animation of spatiotemporal data. Cooperating vessels will be identified by analyses of normalized counts of the numbers of times vessels' paths converge over short time periods.

## FOCUS QUESTIONS

## What contribution can spatial analysis of fleet dynamics make to stock assessment?

Analysis of movements of tuna purse seiners (fleet dynamics) has the potential to provide insights into how fishing/searching behavior differs among vessels, within and across fishing trips. Results of such analyses might lead to suggestions for stratification of calculations regarding fishing effort (e.g., days "fishing") by groups of vessels, where the groups are defined in such a way that vessels within the each group appear to have similar behavior or similar modes of fishing. For example, in the eastern Pacific Ocean (EPO) purse-seine fishery, there are vessels that set almost exclusively on fish associated with floating objects, which are most often man-made fish-aggregating devices (FADs) that are deployed on one trip with the intention of visiting them on the next trip in the hope that fish have aggregated around them. However, there are also vessels that set on fish associated with dolphins and/or on unassociated fish that make sets on fish associated with floating objects. When a vessel makes a set on fish associated with a floating object, that floating object is no necessarily a FAD that was deployed by that vessel; it may be flotsam, or a FAD deployed by some other vessel. Currently there are no distinctions made among the different types of behavior when computing purse-seine effort.

Understanding the vessel dynamics will help develop better catch-per-unit-of-effort indices, particularly for the purse seine fishery. Maunder (2005) discusses the development of indices of abundance from purse-seine catch and effort data.

## What management advice can be provided by spatial analysis of fleet dynamics?

Spatial analysis of fleet dynamics can provide information on appropriate delineation of closed time/areas and likely reallocation of effort when closed area management is implemented.

Research
Comprehensive unique marking of FADs would greatly enhance analyses of fleet dynamics in purse-seine fisheries for tunas.

## 7. MANAGEMENT OF SPATIALLY-HETEROGENEOUS POPULATIONS

Spatial heterogeneity in population dynamics or dynamics of the fishing fleet may require different management compared to what is currently used for stocks treated as single populations. Low amounts of mixing among areas may result in local depletion if the fishing effort is not evenly spread over the range of the stock. In this case, separate catch quotas should probably be applied to each sub stock. Differences in growth rates may require different minimum-length limits. Marine reserves and closed areas explicitly require the consideration of space and movement in any evaluation of management procedures. Other management consequences of spatially-structured populations may not be as apparent. Simulation analysis is required to better understand current and new management strategies applied to populations that are spatially structured. These simulations will require spatially-structured population dynamics models.

### 7.1. Evaluation of the impact of marine protected areas on stock assessment-based fisheries management

## Carey McGilliard and André E. Punt

Fish populations occur heterogeneously in space naturally, and as a result of anthropogenic influences such as spatial management. Few stock assessments account for spatial heterogeneity, assuming instead that the populations (or fishing mortality) are distributed evenly across space. A special case of spatial management is the use of no-take marine reserves. In this study, we use simulation modeling to analyze the ability of three stock assessment methods to estimate current biomass, unfished biomass, and depletion after the implementation of a single large no-take marine reserve. We use age- and sexstructured two-dimensional spatial operating models representing five patterns of ontogenetic movement to represent the "true" underlying population dynamics. Results show that assessing populations as a single stock without accounting for the large no-take marine reserve results in severe underestimation of biomass. Performing separate assessments for fished and protected areas leads to improved estimation performance in the absence of movement between assessment areas, but can severely overestimate biomass in otherwise.

### 7.2. Comparison of Pacific-wide, western and central Pacific, and eastern Pacific assessments of bigeye tuna

## John Hampton and Mark Maunder

Pacific-wide assessments of bigeye tuna have been conducted several times over the last ten years. The results of these assessments have been compared with results of assessments conducted independently for the eastern Pacific Ocean (EPO) and the western and central Pacific Ocean (WCPO) by the IATTC and the SPC, respectively. In general, the results of the Pacific-wide assessments are similar to those of the respective EPO and WCPO assessments. The greatest differences are due to the assumptions about the lengths at age used in the models, as the results are sensitive to the lengths at age and to the assumption about the asymptotic lengths used in the growth curves. The differences in the lengths at age between the two sides of the Pacific Ocean should be considered in any Pacific-wide assessment. More research on spatial differences in growth rates is needed for bigeye and other tunas.

## FOCUS QUESTIONS

## Can stock assessment models be used to evaluate the effects of closed areas?

Stock assessments have a potential to evaluate the effects of closed areas. However, the spatial stratification of the population dynamics model and data must be consistent with the closed area. The success of the analysis will depend on the available data and understanding of the stocks dynamics. Equally important, the dynamics of the fishing fleets should also be modeled.

## Research

More rigorous simulation testing of spatially-explicit models and their ability to evaluate closed areas is required.

Can we devise management strategies that are robust to spatial and stock-structure uncertainties that might not ever be properly characterized by data?
There is a potential to develop management strategies that are robust to spatial structure. The success of these strategies will depend on the type of spatial structure and the data that are available.

## Research

Extensive simulation analysis is needed to identify management strategies that are robust to a variety of different spatial structure scenarios.

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## 9. APPENDIX A: PARTICIPANTS

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