ABSTRACT

Title of Thesis: ASSESSMENT OF POPULATIONS WITH SPATIALLY

EXPLICIT DYNAMICS AND THE CONSEQUENCES

FOR MARINE PROTECTED AREAS

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Spatial processes can have important consequences in the population dynamics of fishes and marine invertebrates. Therefore fisheries management should consider space in the techniques used to understand population dynamics. The purpose of this thesis was to investigate spatial dynamics of fish populations in Maryland's coastal bays (Chapter 2) and evaluate effects of spatial management (in the form of marine protected areas (MPAs)) on accuracy of abundance estimates (Chapter 3). In Chapter 2, I examined trawl survey data from Maryland's coastal bays to estimate trends in relative abundance of four commonly caught fish species using a generalized linear model that allowed region specific estimates. Species showed different responses in the two regions, but trends over time were not related to local habitat variables. In chapter 3, I examined the effects of an MPA on the accuracy and bias of estimates from spatially aggregate and explicit surplus production models (SPMs) using a simulation experiment. I found that spatially-explicit SPMs produced more accurate estimates of biomass than spatiallyaggregate SPMs, and that larger MPAs produced more accurate estimates than smaller MPAs.

ASSESSMENT OF POPULATIONS WITH SPATIALLY EXPLICIT DYNAMICS AND THE CONSEQUENCES FOR MARINE PROTECTED AREAS

By

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Chapter 1: Introduction

Spatial processes can have important consequences for the population dynamics of fishes and marine invertebrates. Therefore, fisheries management should consider space in the techniques used to understand population dynamics. For example, fleet dynamics have caused variable exploitation rates on different parts of the pacific salmon population in British Columbia (Hilborn and Ledbetter, 1979), which violates the common assumption in stock assessments that fishing mortality is evenly distributed across the entire population. Habitat selection can cause clusters of higher density in many species of marine fishes (Shepherd and Litvak, 2004), and understanding habitat selection can affect habitat conservation decisions. Finally, larval dispersal is known to play a role in the local densities of adult metapopulations, though this role is poorly understood (James et al., 2002). Spatial dynamics often have implications for fisheries management and require geographical resolution in data collection as well as spatially-explicit techniques for analysis.

Understanding spatial processes can provide important information for fisheries ecology and management. Identifying regions of high productivity or of higher densities of fish can help explain observed trends in fish density. The differences in productivity can be due to characteristics inherent in the region, such as better food resources (Harris et al., 2004), or external forcing, such as currents that force planktonic larvae into one area instead of another (Schwartz, 1964). Source-sink dynamics, where one or more highly productive regions provide new recruits for less productive regions, have been useful in understanding the consequences of spatial management strategies (Crowder et al., 2000; Kaplan et al., 2009). The interactions of fish populations when combined with

spatial dynamics can help describe fish communities, sometimes better than environmental variables (Magnan and Bertolo, 2006). Identifying these regions can then help us identify the factors important in supporting fish communities.

Incorporating spatial complexity in fishery models can also help managers make decisions about marine protected areas (MPAs) to maximize their positive effects on both the target species and the community as a whole (Pelletier and Mahevas, 2005). Several authors have considered spatial processes in the placement of MPAs. To determine the spatial arrangement of MPAs that would lead to the greatest conservation and recovery of the population, Kaplan et al. (2009) considered the total size of MPA, the distance of larval dispersal, depth of the protected area, and habitat suitability. They found that the effectiveness of a chain of MPAs is dependent on the placement of the MPAs in relation to suitable habitat (Kaplan et al., 2009). Neubert (2003) investigated optimal harvesting strategies in regions with MPAs in a more general way, viewing the only spatial heterogeneity of the population and habitat as that imposed by variable fishing rates. Neubert (2003) found that a large central MPA aids both the recovery and fishery yield of a population with a low growth rate that lives in a restricted habitat. These two studies are examples of how an MPA or a network of MPAs could aid in improving conservation and enhancing economic benefits for fisheries (Neubert, 2003; Kaplan et al., 2009).

Although MPAs have been increasingly used as management tools, it has been suggested that MPAs may hinder our ability to assess populations and provide scientific advice for future management using current methods (Field et al., 2006). Often, the models used to evaluate effectiveness of MPAs are often very different from those used to assess fish stocks (Punt and Methot, 2004). The evaluation of the effectiveness of

established MPAs may benefit from spatially explicit stock assessment techniques to capture the changes in the forces acting on the population, or spatial disaggregation, caused by management. However, Punt and Methot (2004) are among the few studies that have incorporated spatial dynamics in stock assessments and other types of stock assessments should be explored.

The objective of my thesis was to investigate spatial dynamics of fish populations in Maryland's coastal bays (Chapter 2) and evaluate effects of spatial management (in the form of marine protected areas (MPAs)) on accuracy of estimated population size and stock assessment advice (Chapter 3). Specifically, I employed spatially-explicit techniques to identify and assess regions that have different population dynamics. In Chapter 2, I compared trends in relative abundance from survey data across two regions in Maryland's coastal bays, and in Chapter 3 I compared the performances of spatially-explicit and spatially aggregate stock assessments after an MPA is implemented.

In Chapter 2, I developed standardized indices of abundances to estimate trends in four common species in Maryland's coastal bays and compared the trends with those of environmental and habitat variables to attempt to identify factors important in population dynamics in that region. The species I included in my analyses were Atlantic menhaden (*Brevoortia tyrannus*), weakfish (*Cynoscion regalis*), spot (*Leiostomus xanthurus*), and summer flounder (*Paralichthys dentatus*) and the environmental variables included were submerged aquatic vegetation (SAV) coverage, nitrogen to phosphorus ratio, temperature, salinity, dissolved oxygen concentrations, and three other factors. The Maryland (MD) DNR survey has been conducted since 1972 and the trawl distance, sites, and times of year sampled were standardized in 1989. Data collected before 1989 have

not been used in any indices of abundance generated by MD DNR. I used a generalized linear modeling (GLiM) approach to standardize survey data from Maryland DNR to capture the earlier 17 years of data. Inclusion of the earlier years provided valuable perspective on the trends in juvenile abundance, but using raw data from the years before the survey was standardized would bias the indices of relative abundance derived from the data if a GLiM was not used. In order to contrast the fish density supported by different parts of the bays, I compared the indices of abundance in two geographically distinct regions to assess whether the regions were also biologically distinct.

In Chapter 3, I conducted a simulation study to assess the accuracy of spatiallyexplicit and spatially-aggregate surplus production models (SPMs) when an MPA creates spatial heterogeneity of fishing mortality within a stock's range. I simulated a fish population and the corresponding fishery with a data generating model. In the simulation, an MPA was implemented when the population was at a low level. The data generating model provided indices of abundance and fishery catch data for the SPMs that were used to assess the population. I tested four different SPMs: a spatially-explicit SPM where migration was specified, a spatially-explicit SPM where migration was estimated, a spatially-aggregate SPM where indices of abundance were available from both the MPA and fished region, and a spatially-aggregate SPM where indices of abundance were only available from the fished region. The biomass estimates from the SPMs were then compared to the true biomass from the data-generating model. I considered effects of the size of the MPA, the migration rate of the stock between the MPA and fished areas, the variance of the indices of abundance, and absence of indices of abundance from within the MPA on the performance of the SPMs.

CHAPTER 2

Trends in relative abundance of fishes and the effects of changes in habitat on fish densities in Maryland's coastal bays during 1972-2009

Abstract

Maryland's coastal bays provide habitat for juveniles of many commercial and recreational species of shellfish and finfish. The Maryland Coastal Bays Trawl and Seine Survey has been conducted by the Maryland Department of Natural Resources since 1972 to provide a fishery-independent index of abundance of key species. The survey has undergone substantial spatial and methodological changes that affect the accuracy of indices of abundance of several fish populations monitored by the survey. I developed generalized linear models to standardize the indices of abundance of four commonly caught fish species (Atlantic menhaden *Brevoortia tyrannus*, weakfish *Cynoscion regalis*, spot *Leiostomus xanthurus*, and summer flounder *Paralichthys dentatus*). Since 1972 density declined significantly for menhaden and spot, and the northern bays had significantly higher densities than the southern bays for all species. Changes in relative abundance of the four species examined were not related to seagrass coverage, temperature, salinity, nitrogen to phosphorus ratios, and other habitat variables, but were likely caused by stock-wide recruitment patterns.

Introduction

Long term studies are necessary to determine changes in abundance and the effects of changes in habitat on marine populations (Peterson et al., 2003). However, sampling methods often change over time, complicating the interpretation of the trends in abundance. Survey catch per unit effort (CPUE) is frequently used as an index of abundance (Ricker, 1975; Maunder and Punt, 2004), but certain assumptions inherent in using CPUE as an index of abundance can be violated by changes in survey methodology. For example, changing the distribution or amount of effort over time can cause misleading indices of abundance. The critical assumption that is most commonly violated is that catchability, the proportion of a population caught by one unit of effort for a particular gear type, is constant over time (Arreguín-Sánchez and Pitcher, 1999; Wilberg et al., 2010). This assumption can be violated because the effectiveness of one unit of effort changes over time if the survey design changes (Ricker, 1975).

Habitat quality in coastal environments has significant effects on the density of fish those environments can support (Gibson, 1994). However, identifying the key features of habitat that relate to the ability of the habitat to support of fish populations is challenging and requires the analysis of multiple biological and physical parameters (Imhof et al., 1996; Rose, 2000). Seagrass, in particular, is thought to be an important nursery habitat for many juvenile fishes (Orth et al., 1984; Nagelkerken et al., 2002). Fish densities are higher in seagrass bed than over unvegetated areas (Guidetti, 2000; Jackson et al., 2001; Orth et al., 2006) because seagrass may serve as a refuge from predation or as a source of prey (Harris et al., 2004). Because of the purported link

between juvenile fish and seagrass, the decline in seagrasses around the world has caused concern in conservation and fisheries monitoring agencies (e.g. Wazniak, 2004).

However, in some areas, such as the Chesapeake Bay, relationships between juvenile fish abundance and seagrass have not been found, even on small scales within nearby vegetated and un-vegetated areas (Heck and Thoman, 1984). Abiotic factors are also important in defining the quality of habitat. Increased nutrient inputs from agricultural practices and urbanization can cause eutrophication, which leads to enhanced algal blooms that can prevent light from reaching submerged vegetation and can increase the area of hypoxic or anoxic waters when the algae decompose. In addition to water quality, the hydrodynamic regime (e.g. currents) also has a strong impact on how juvenile fish are distributed.

Maryland's coastal bays support a broad range of both fish and invertebrates and provide nursery habitat for many species of young-of-year fish (Bolinger et al., 2007). Several of the dominant species in the bays, such as Atlantic menhaden (*Brevoortia tyrannus*) and blue crab (*Callinectes sapidus*), have been a source of conservation concern in the Mid-Atlantic due to declining catch and observed recruitment classess (Lipcius and Stockhausen, 2002; ASMFC, 2010a, 2010b). The Maryland Coastal Bays Trawl and Seine Survey (MCBTSS) has been conducted by the Maryland Department of Natural Resources (MD DNR) since 1972 to monitor the populations of fishes and invertebrates in the Maryland coastal bay estuaries (Figure 1). A particular focus of the survey is juvenile fishes that use these areas as nursery habitats (Bolinger et al., 2007). The MCBTSS methods and sites were standardized in 1989. Prior to 1989, the time of year, the specific sites sampled and the duration of the trawl tows varied substantially

from year to year. These methodological and spatial changes during the survey time series make differentiating changes in abundance from changes in survey design difficult.

In this study, I estimated trends in relative abundance for four fish species in Maryland's coastal bays, and tested for effects of habitat and on relative abundance of four fishes in the northern and southern coastal bays of Maryland during 1972-2009. My specific objectives were to 1) determine the trends in abundance of four fish species in Maryland's coastal bays and 2) determine whether changes in abundance were related to changes in habitat. I used generalized linear models (GLiMs) to standardize abundance indices and analysis of covariance (ANCOVA) to test for temporal trends and the effects of habitat on relative abundance through time.

Methods

Data

Maryland's coastal bays are located on the eastern side of the Maryland portion of the Delmarva Peninsula and are separated from the Atlantic Ocean by two barrier islands (Figure 1). The largest of the bays, Chincoteague Bay (about 377 km²). is surrounded by predominantly forest and agriculture. The smallest bay is Newport Bay (about 16 km²), which is located north of Chincoteague Bay and is also surrounded by mostly forest and agriculture. Sinepuxent Bay is located to the northeast of Chincoteague Bay and is the second largest of the coastal bays at 24.1 km². It is surrounded by mostly wetlands, forest, and urban centers. North of Sinepuxent Bay is Isle of Wight Bay (surface area-21.1 km²) surrounded by forest, residential areas, and more urban centers. Assawoman

Bay (surface area - 20.9 km²) is the northernmost bay and is surrounded by forest, agriculture, and wetlands. The bays are largely well-mixed, with average salinities in all bays ranging on average between 27 and 31 ppt.

I divided the coastal bays into two regions using the inlet to the Atlantic Ocean as a divider. The northern region included Assowoman and Isle of Wight Bays and the southern region included Newport, Sinepuxent, and Chincoteague Bays. The northern bays are only connected to the southern bays by the narrow inlet at the north end of Sinepuxent Bay. The land surrounding the northern bays is more developed than the southern region, so anthropogenic eutrophication is more prevalent in the northern region (Murphy and Secor, 2006). The northern bays have higher abundances of common fishes than the southern bays, possibly because the higher amounts of nutrients in the northern systems allow higher fish productivity, and support higher densities of common species, although species richness is higher in the southern bays (Murphy and Secor, 2006).

The MCBTSS samples with a bottom trawl in 20 different sites in the five coastal bays (Figure 1). The trawl survey is conducted in the middle of the coastal bays, in waters 0.75 to 2 m deep. The survey uses a fixed-site design. Sites were initially chosen to represent the range of trawlable sites, but the location of some sites changed over time. Since the survey was standardized in 1989, DNR has trawled at each site once a month from April to October. The trawls are conducted with a 4.9 m (16 ft) semi-balloon trawl with 3.18 cm (1.25 in) stretch mesh in the outer net, 2.86 cm (1.13 in) stretch mesh in the cod end, 1.27 cm (0.5 in) stretch mesh inner liner, and a tickler chain (Bolinger, 2007). Before standardization, the trawls varied in tow length and area covered, some samples were taken in winter months between November and March, and the sites were not

sampled every month during the other times of the year. In 1989, the deployments were standardized to a 6-min tow of the net at a speed of approximately 2.8 knots, for an area swept of about 17,040 m².

I examined data for four commonly caught species: Atlantic menhaden, weakfish (Cynoscion regalis), spot (Leiostomus xanthurus), and summer flounder (Paralichthys dentatus). The methods I used to standardize the indices required a large amount of data, and all four of these species had enough available data. From the data available it is likely that of the other species caught in the survey only bay anchovy (Anchoa mitchilli) and blue crab (Callinectes sapidus) would have fulfilled the data requirements of the analyses, however I chose not to use these last two species in by analyses. All of these species support important recreational or commercial fisheries and use Maryland's coastal bays as nursery habitat. These species were also selected because they represent a variety of life histories, use the coastal bays at different times of the year, and inhabit different areas of the bays.

The four species included in the analyses have distinct life histories, but they all use Maryland's coastal bays during their life cycles. All four species enter the coastal bays as larvae or early juveniles (Able and Fahay, 1998), although summer flounder can also enter as adults in the summer. Summer flounder and spot are demersal species, but spot prefer muddy bottom while flounder prefer harder sandy bottom (Froese and Luna, 2010; Luna and Froese, 2010). Weakfish and menhaden, on the other hand, are pelagic. Summer flounder and weakfish are piscivores, menhaden are planktivores, and spot are benthivores. Using species with this range in life histories allowed me to capture a broad picture of the types of fish in the coastal bays.

To develop indices of abundance I included data only from months when a species was expected to use the coastal bay habitat. Weakfish are present in the coastal bays from late July until November (Able and Fahay, 1998). Similarly, analyses for spot included observations from April to November, and the summer flounder models included March through November (Murdy et al., 1997) to reflect their seasonal migrations. The menhaden models included the whole year because some larvae enter the estuary in the fall and overwinter there as juveniles while the rest enter in the spring and remain throughout the summer and fall (Table 2.1; Murdy et al., 1997; Able and Fahey, 1998). Some sites and years were excluded from the analyses due to the large numbers of zero-catches in the dataset that caused year or site effects to not be estimable in the standardization model (Deroba and Bence, 2009; Table 2.2).

Environmental variables potentially indicative of habitat quality were available from a monitoring program conducted during 1993-2004 by the National Parks Service. Variables included total suspended solids, total nitrogen to phosphorus ratio, silicate concentration, chlorophyll a adjusted for phaeophytin concentrations, and dissolved oxygen. These variables were measured at 16 sites in the southern region but only yearly medians were available for my analyses. None of these variables were available for the northern region. The area of submerged aquatic vegetation (SAV) in each region was obtained for each year from 1993 to 2004 (unpublished data, J.J. Orth Virginia Institute of Marine Science). Temperature and salinity were recorded with each trawl tow from the MCBTSS. I calculated the monthly average for surface temperature and salinity for the sites in each region and then calculated a yearly average from the monthly averages.

Standardizing Indices of Abundance

I used generalized linear models with a negative binomial distribution and a log link function to standardize yearly indices of abundance for each of the species (McCullagh and Nelder, 1989; Maunder and Punt, 2004). The negative binomial distribution allows zero catches, which was necessary for this survey because about two thirds of the observations for each species are zeros. The model was

$$E(\log(C)) = \beta_0 + \beta_{\textit{Year}} + \beta_{\textit{Site}} + \beta_{\textit{Month}} + \beta_{\textit{Re gion *Year}} + \beta_5(\textit{Effort})$$

where E(log(C)) is the expected natural logarithm of catch for the given species, and year, site, month, a year-by-region interaction, and effort are main effects. A region effect was implicitly included in the model because the sites are nested within the regions. The region effect was the average of the individual site effect estimates within each region. The year effects and year by region interactions provided indices of abundance for the northern and southern bays. The site effects accounted for spatial variation across sites. The location of several sites changed over time; sites where the location was changed were treated as separate sites. The categorical month effect accounted for variation in catch due to time of year, and the continuous effort effect accounted for different lengths of trawls before the survey was standardized. All factors except effort were modeled as categorical. One unit of effort was 8,520 m² of area swept.

The same procedure described above was carried out for the seine portion of the survey. The trends over time for each species were then compared between the two gear types. The results from the seine survey analyses and the gear comparisons are described in Appendix I.

Characterizing Trends over Time and Effects of Habitat

I fitted ANCOVAs using proc glm in SAS 9.2 to estimate trends over time among species and differences in density between the northern and southern regions. The ANCOVAs were species-specific and included region as a categorical variable and year as a continuous covariate,

 $I = \beta_0 + \beta_{Re\ gion} + \beta_1 (Year)$, where I was the species-specific index was the same as that calculated by the GLiM, β_0 was the intercept, β_{Region} was the categorical region effect, and β_1 was the continuous year effect.

Region-specific regressions with year were conducted to estimate trends in abundance in each region over time. I used a Bonferroni correction for multiple comparisons to determine the p-value associated with an α level of 0.05: 0.0125 for comparing differences between regions and 0.0063 for comparing the slopes of region-specific trends over time. Univariate regressions of indices of abundance against each of the habitat variables were also conducted for each species, which were region-specific for the temperature and salinity data, but only data from the southern region were available for the other habitat variables. A Bonferroni correction was also used for the individual region regressions to determine the critical p-value of 0.0013 to correspond to an overall α level of 0.05.

Results

The four species analyzed showed different trends within each region over time (Figures 2.5). The variability of the indices was also different, with Atlantic menhaden

indices varying by 5 orders of magnitude (10,000 fold difference) over the time series and summer flounder varying by only two orders of magnitude (100 fold difference) from the smallest estimate to the largest. All four of the species were alike, however, in that they showed significantly higher densities in the northern bays than the southern bays (p<0.0001 for menhaden, flounder, and weakfish; p=0.0105 for spot; Figures 2.2-2.5).

Both spot and menhaden showed overall declines from the early 1970s in the northern region, and only menhaden showed a significant decline in the southern region (Figures 2.2 and 2.3; Table 2.3). Spot declined in both regions, but the decline was only significant in the northern region. The rate of decline in the northern region was 30% greater than the southern region (northern bays=-0.103 year⁻¹, southern bays=-0.079 year⁻¹). Similarly, while the decline in menhaden was significant in both regions, the northern region showed a greater rate of decline than the southern region (northern bays=-0.154 year⁻¹, southern bays=-0.134 year⁻¹). The decline in menhaden was largely driven by extremely high indices of abundance in the 1970s and early 1980s that were absent in the 1990s and 2000s (Figure 2.2). The decline in spot, on the other hand, was steady with periodic spikes in density that also declined over time (Figure 2.3)

Summer flounder and weakfish did not trend significantly in either region. Both species even had periods of increasing abundances in the 1990s and early 2000s.

Summer flounder had spikes in density in 1984 and 1986 in the northern region, but 1972 and 1973 had the highest densities in the southern region (Figure 2.4). Weakfish had highly variable indices of abundance, especially in the northern region. The highest densities occurred in 1995 and 1978 in the northern region and 2005 and 2003 in the southern region (Figure 2.5).

All of the habitat variables showed interannual variation, but the majority of the habitat variables did not exhibit significant trends over time (Figure 2.6). Only seagrass cover increased significantly from 1993 through 2004 (p<0.001; Figure 2.6). There were high correlations between the northern and southern regions for salinity (r=0.802) and temperature (r=0.837) over time. Only two habitat variables were highly correlated with one another; the nitrogen to phosphorus ratio was highly correlated with silica concentration (r=0.632), and dissolved oxygen was highly negatively correlated with salinity in the northern region (r=-0.716). Relative abundance was not significantly related to any of the habitat variables for any of the species (Table 2.4).

Discussion

Long-term surveys that span several generations of fish are necessary to explore trends in abundance over time. I developed statistically standardized indices of abundance for four fish species in Maryland's coastal bays that explicitly incorporated changes in location of survey sites, times of year sampled, and amount of effort used at each site. These standardized indices indicated significant decreases in spot and menhaden abundance during 1972-2008, but no significant trends in abundance for weakfish or summer flounder. The declines in abundance of spot and menhaden would not have been detected if I only used data since 1989, the year methods for the MCBTSS were standardized.

It is important to consider all of the available data to reach the best conclusions about fishery resources (Myers and Worm, 2003), because the years included to detect changes in population size frame our understanding of the magnitude of change. This has

been called the problem of "shifting baselines" (Pauly, 1995). However, it is also important to recognize potential shortcomings in using older data. There have been questions within Maryland DNR about the reliability of the data collected prior to 1989. The data have been checked against original field datasheets, examined for entries that were questionable, and corrected to the extent possible. Because the data were validated, I was confident in using all 38 years of the survey for my analyses. However, the most reliable data are from 1989 onward, and these are the data that have been used to inform stock assessments (e.g., ASMFC, 2010b).

Two of the species examined declined significantly in at least part of the coastal bays of Maryland. The decline in Atlantic menhaden likely reflects a decline across the east coast that has caused concern for managers in the last couple of decades (ASMFC, 2010a). Regional recruitment indices for Atlantic menhaden have been relatively low during the last twenty years (ASMFC, 2010a); the coastal bays indices I developed showed the same pattern. The trend in spot abundance has been punctuated periodically by large recruitment events, though the magnitude of the recruitment events has declined over time, so that high recruitment events in recent years are not as large as in early years. These spikes and the overall trend are also reflected in stock assessments for juveniles across the East Coast of the U.S. (ASMFC, 2010b; Rickabaugh, 2010), suggesting that the trends in abundance seen in the coastal bays are consistent with the trends seen on a broader scale for spot and menhaden.

The northern coastal bays had higher densities of all four of the species in my study than the southern region, which corresponds to previous results from Murphy and Secor (2006). The cause of higher density in the northern bays than the southern bays

could include higher primary production in the northern bays as a result of the extended retention time of water in the creeks flowing into the bays (Murphy and Secor, 2006) and may indicate a bottom-up effect of production on fish density. Schwartz (1964) also suggested that species composition may differ between the northern and southern bays as a result of stronger currents forcing more water, and potentially larvae and juvenile fish, into the northern bays. The differences in density between the two regions was opposite of what is expected based on water quality, however. Two of the southern bays, Chincoteague and Sinepuxent, consistently score better in almost every metric of bay health than the two northern bays (Franks, 2004; IAN et al., 2010). Indeed, Franks (2004) emphasizes the large amounts of commercial and residential development that has occurred along the edges of the northern bays compared to the relatively pristine environment of the southern bays has contributed increased eutrophication in the northern bays and is detrimental to their health. However, in spite of the perceived lower quality of habitat in Assawoman and Isle of Wight Bays (northern region), they supported significantly higher densities of fish, at least for the species considered here.

Changes in abundance of the four species investigated were not significantly related to any of the habitat variables examined. The habitat variables covered a wide range of possible factors, from nitrogen and phosphorus ratios to the abundance of seagrass. In particular, seagrass is often considered "essential fish habitat" for coastal species because it is thought to provide refuge and nursery habitat for the young-of-year fish that are so prevalent in those regions, though it has been noted that there is some ambiguity in the documentation of the nursery role of seagrass (Beck et al., 2001).

Seagrass may not be as important as overall habitat structure or refuge provided by other

sources such as oyster beds or coral reefs (Heck et al., 2003). In Maryland's coastal bays I did not detect a significant effect of seagrass coverage on the four prevalent species in spite of the steady increase of seagrass throughout the 1990s and early 2000s. While none of the other habitat variables significantly affected density, the effect of seagrass was often the least significant habitat variable with the smallest slope (Table 2.4).

The habitat variables tested in this study likely have a localized effect on population dynamics of fishes, but the spatial or temporal scales of data collection or analysis may not match the effects of habitat forcing on the populations. The trends in fish abundance in Maryland's coastal bays are most likely driven by forces on a much broader scale than trends in local habitat. Linking habitat variables with trends in juvenile abundance can be problematic because the juvenile populations as a whole may be more closely linked to stock size than local habitat. The similarity in trends between the juvenile indices on the coastal bay level and the Mid-Atlantic level for both menhaden and spot provide evidence that juvenile and adult populations are connected in both estuaries and the coast (Whitfield, 1989). Summer flounder also show the same overall trends in the last two decades in both coastal bays indices and in the stock assessments conducted for the Mid-Atlantic region (SAW, 2006). The populations that inhabit the coastal bays are mostly composed of single yearclasses that are replaced annually. The similarities of dynamics in the coastal bays combined with the overall deficiency of explanatory power that local habitat variables have in explaining changes in relative abundance point to the influence of large-scale, stock-wide forces on the densities of fish in Maryland's coastal bays.

In conclusion, the standardization of the survey data allowed me to evaluate long-term trends in relative abundance. Menhaden declined in density during 1972-2009 in both regions, and spot declined in the northern region. Summer flounder and weakfish showed no significant change through time. The observed declining trend in Atlantic menhaden and spot as well as the lack of overall trend in summer flounder matched trends in regional assessments conducted on these species. This is likely due to the coupling of coastal bay fish populations with the broader Mid-Atlantic stocks through recruitment. The northern region of Maryland's coastal bays, which is more eutrophic and has longer water retention time, supported higher densities of fish than the more pristine southern bays. However, the effects of habitat degradation may be evident in the steeper decline of Atlantic menhaden and spot in the northern region than in the southern region. Finally, because localized habitat variables were not related to relative abundance of any of the species, a coast-wide stock-recruitment relationship may explain long-term abundance trends better than local habitat variables.

Table 2.1. The months of the year included in the models for each species according to their expected inhabitation of the estuaries and the literature used to arrive at the included periods.

Species	Months in model	References
Atlantic Menhaden	Jan-Dec	Murdy et al., 1997; Able and
		Fahay, 1998;
Weakfish	July-Nov	Able and Fahay, 1998; Nemerson
		and Able, 2004
Summer Flounder	Mar-Nov	Murdy et al., 1997
Spot	Apr-Dec	Murdy et al., 1997

Table 2.2. Additional months, years, and sites removed from analyses and the reasons for removal.

Species	Region	Variable Level	Reason
		Removed	
All	All	1983	1 sample
Atlantic Menhaden	All	February	None Caught
Atlantic Menhaden	All	December	None Caught
Atlantic Menhaden	South	1986	None Caught
Summer Flounder	North	1972	None Caught
Summer Flounder	North	1974-1980	None Caught
Summer Flounder	South	1974	None Caught
Summer Flounder	South	1981	None Caught
Weakfish	All	Site 9(3rd loc.)	2 samples
Weakfish	All	1974	None Caught
Weakfish	All	1988	None Caught
Weakfish	North	1972	None Caught
Weakfish	North	1980	None Caught
Weakfish	South	1973	None Caught
Weakfish	South	1987	None Caught

Table 2.3. Results of ANCOVAs for trends by species and region over 1972-2009. Bold rows indicate statistically significant trends at α =0.0063, the level that corresponds to α =0.05 when corrected for multiple comparisons.

Species	Region	Slope	p-value
Atlantic Menhaden	North	-0.1537	<.0001
Atlantic Menhaden	South	-0.1335	<.0001
Summer Flounder	North	-0.0009	0.9349
Summer Flounder	South	0.0040	0.7568
Spot	North	-0.1030	0.0010
Spot	South	-0.0793	0.0086
Weakfish	North	0.0465	0.0698
Weakfish	South	0.0137	0.4979

Table 2.4. Results of habitat regressions. Variable designations are as follows: DO—Dissolved Oxygen, N:P Ratio—Nitrogen to Phosphorus Ratio, Silica—Silica concentration, Temp—Temperature (°C), Salinity—parts per thousand, SS—concentration of suspended solids, Chl a—Chlorophyll a concentrations. Temperature and salinity are evaluated for both regions; all other habitat variables are only evaluated for the southern region. Bold rows indicate statistical significance at α =0.0013, the level that corresponds to α =0.05 when corrected for multiple comparisons.

Species	Region	Variable	Slope	p-value
Summer Flounder	South	DO	0.0073	0.1617
Summer Flounder	South	Silica	-0.0181	0.1791
Summer Flounder	South	N:P Ratio	-0.1045	0.3105
Summer Flounder	North	Temp	-0.1656	0.3218
Summer Flounder	South	Temp	0.0653	0.6866
Summer Flounder	North	Salinity	0.0318	0.7053
Summer Flounder	South	SS	0.0116	0.7356
Summer Flounder	South	Salinity	0.0146	0.856
Summer Flounder	South	Chl a	0.0077	0.9179
Summer Flounder	South	SAV	-3.41E-07	0.9978
Atlantic Menhaden	South	N:P Ratio	0.5509	0.0551
Atlantic Menhaden	North	Temp	-0.9417	0.1503
Atlantic Menhaden	South	DO	-0.0181	0.2541
Atlantic Menhaden	South	Temp	-0.4582	0.3326

Atlantic Menhaden	South	Chl a	0.2089	0.3363
Atlantic Menhaden	South	SAV	0.0003	0.4267
Atlantic Menhaden	South	SS	0.0753	0.4572
Atlantic Menhaden	South	Salinity	0.1313	0.5821
Atlantic Menhaden	North	Salinity	0.1507	0.6553
Atlantic Menhaden	South	Silica	-0.0032	0.9398
Spot	South	Silica	-0.1082	0.0149
Spot	South	Chl a	-0.4084	0.1096
Spot	South	Temp	-0.8003	0.1556
Spot	South	Salinity	0.3587	0.2043
Spot	South	DO	-0.0193	0.323
Spot	North	Salinity	0.3158	0.3511
Spot	South	SS	0.0632	0.6138
Spot	South	SAV	0.0002	0.7095
Spot	South	N:P Ratio	-0.0910	0.8136
Spot	North	Temp	-0.0485	0.9452
Weakfish	South	DO	0.0214	0.0071
Weakfish	South	Chl a	0.2309	0.0481
Weakfish	South	Salinity	-0.2276	0.077
Weakfish	North	Temp	-0.3835	0.1233
Weakfish	South	Silica	0.0189	0.4303
Weakfish	North	Salinity	-0.0821	0.523
Weakfish	South	N:P Ratio	-0.0873	0.6314

Weakfish	South	SS	-0.0281	0.6361
Weakfish	South	Temp	-0.0328	0.9071
Weakfish	South	SAV	6.59E-06	0.9749

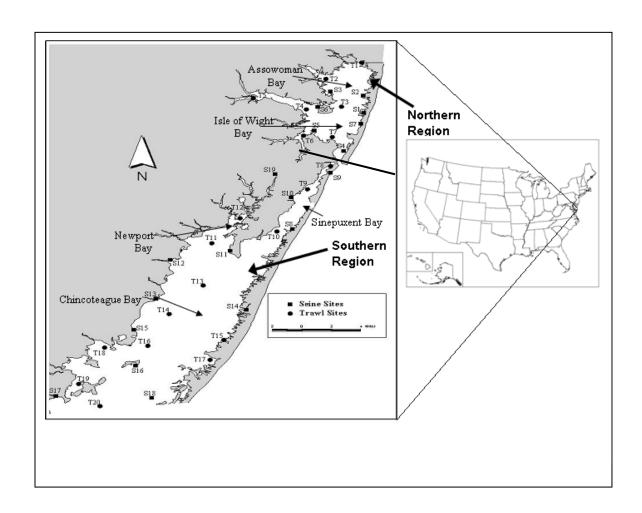


Figure 2.1. Map of Maryland's Coastal Bays and the trawl and seine sites of the MCBTS Survey. Sites with the prefix "T" indicate trawl sites. Sites with the prefix "S" indicate seine sites.

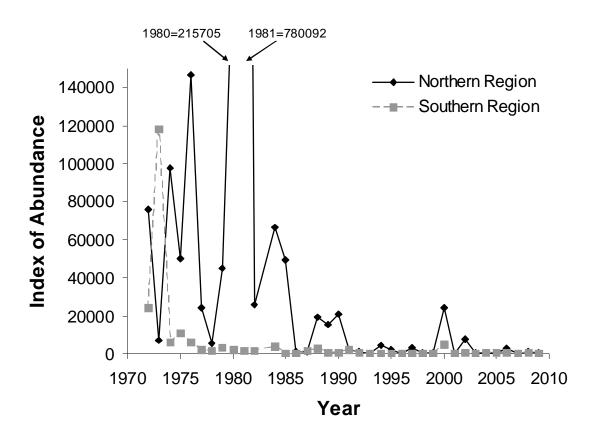


Figure 2.2. The model estimates of the trawl surveys for menhaden for each region. The missing values are the years where there were not enough data to form a reliable estimate.

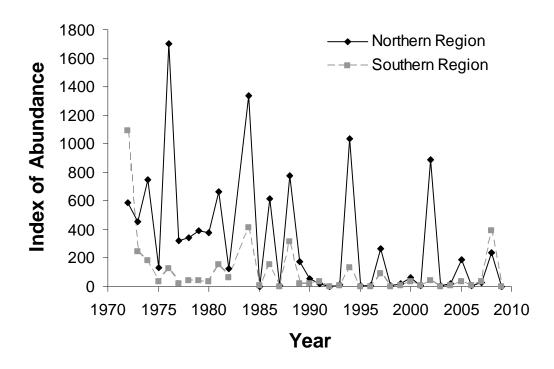


Figure 2.3. The model estimates of the trawl surveys for spot for each region. Missing values indicate year where there was not enough data to form a reliable estimate.

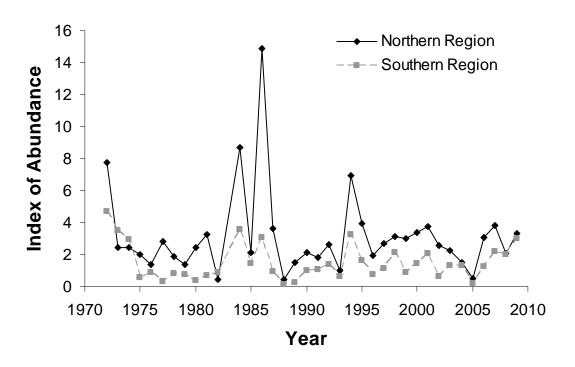


Figure 2.4. The model estimates of the trawl surveys for summer flounder for each region. Missing values indicate year where there was not enough data to form a reliable estimate.

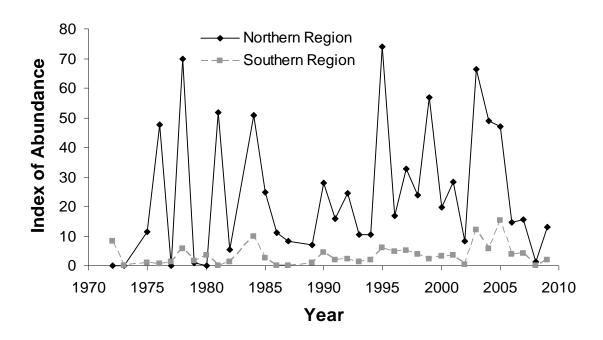


Figure 2.5. The model estimates of the trawl surveys for weakfish for each region.

Missing values indicate year where there was not enough data to form a reliable estimate.

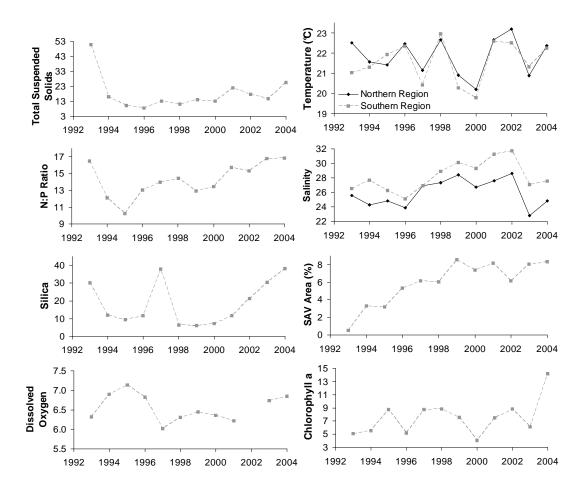


Figure 2.6. Trends of habitat variables from 1993-2004. N:P Ratio is the ratio of total Nitrogen to total Phosphorus. Submerged aquatic vegetation (SAV) Area is the percentage of bottom area in the southern region that has seagrass.

CHAPTER 3

Surplus Production Model Accuracy in Populations Affected by a No-Take Marine Protected Area

Abstract

Marine protected areas (MPAs) are an increasingly common tool used by fisheries managers to protect marine organisms from exploitation. However, implementation of an MPA violates commonly used assumptions for fishery stock assessments that are used to provide estimates of abundance and fishing mortality for management. Thus, it is important to understand the ability of assessments to incorporate the population dynamic and ecological impacts of MPAs on managed fish species. Age-structured assessments have been studied for their accuracy when a stock has an MPA in its range but less complex assessment techniques that could be more widely applied have not been evaluated. I conducted a simulation study to determine the effects of MPAs on accuracy of surplus production model (SPM) stock assessments. I simulated the dynamics of a population, which had part of its range in an MPA, and assessed that population with several surplus production models (SPMs). I tested the performance of spatiallyaggregated and spatially-explicit SPMs under a range of conditions including different sizes of MPAs, different migration rates between MPA and non-MPA regions, and scenarios with high and low observation error in the indices of abundance. I also considered a scenario in which no index of abundance was available within the MPA. I used the median of the absolute value of the relative error (MARE) and median relative error (MRE) from 200 replicates of each scenario to test the accuracy of the SPMs. SPMs showed a consistent pattern in accuracy and bias over time with increasing accuracy followed by decreasing accuracy in early years, increasing accuracy before the MPA was established, decreased accuracy with large positive bias after MPA implementation, and gradually increasing accuracy to the end of the simulation. The

accuracy of the assessments also increased as the MPA size increased except in the scenario with no index of abundance within the MPA, which increased in accuracy as the MPA size decreased. Monitoring the stock within the MPA is essential for conducting accurate stock assessments in areas with MPAs.

Introduction

Marine Protected Areas (MPAs) have been increasingly used and suggested as a fisheries management tool, often instead of or in addition to traditional management measures such as regulating the amount of harvest or fishing effort. While there are several types of MPAs, the most conservative is a no-take MPA where no harvest is allowed. One of the benefits of using MPAs in fisheries management is that the underlying theory is intuitive; when an area within a population's range is protected from fishing, it should develop a greater biomass of fish than fished areas. Increased biomass within the MPA should result in a "spillover effect" in fished areas where biomass shifts from the MPA to the fished area (Crowder et al., 2000; Halpern and Warner, 2002) thereby sustaining a fishery while conserving a large proportion of adult biomass. The spillover effect has been largely thought of as a larval subsidy to fished regions from the MPA (e.g., Punt and Methot, 2004). However, adult movement would create the same source-sink dynamics between the MPA and fished areas, but many species managed by MPAs have low movement rates as adults (e.g. Kaplan et al, 2009; for reasoning see Hilborn et al., 2004). Other benefits of MPAs include protection of habitat, refuge for populations that are at very low abundance, and protection for species not targeted by surrounding fisheries (Kelleher, 1999).

MPAs can have a substantial effect on the accuracy of stock assessment models that are used to provide estimates of abundance and fishing mortality for fishery management (Punt and Methot, 2004; Field et al. 2006). Stock assessments typically assume that each individual within a size or age class in a population is equally vulnerable, on average, to the fishery. Often the purpose of an MPA is to change the

vulnerability of a portion of the population to fishing by protecting it from fishing pressure. Thus, commonly used stock assessment techniques may not accurately portray a population that has an MPA within its range, which may result in biased estimates of fishing mortality rates and available biomass (Field et al., 2006).

Punt and Methot (2004) investigated the ability of spatially-explicit and spatially aggregated statistical-catch-at-age (SCAA) stock assessments to estimate biomass and fishing mortality rates of stocks whose spatial dynamics included an MPA. They found that spatially-explicit SCAAs are more accurate than spatially-aggregated SCAAs in predicting total biomass. In particular, spatially-aggregated SCAAs had very poor estimation performance, and spatially-explicit models were necessary to provide accurate estimates of fishing mortality and biomass. The characteristics of the MPA and population also affected assessment model performance. Larger MPAs, lower migration rates, and surveys with low observation error led to more accurate estimates of biomass from the stock assessment (Punt and Methot, 2004).

SCAAs are often impractical or impossible for stocks with incomplete or unavailable age data, but the performance of non-age-structured assessments has not been tested in scenarios that include use of MPAs in management. Surplus production models (SPMs) are a common method of assessing stocks where age-structured data are either incomplete or impractical to obtain (Prager, 1994). SPMs require less data than age-structured models and have fewer estimated parameters (Laloë, 1995). They include many aspects of population dynamics in a simple model, and they produce predictions that are easily translated into common reference points used to inform management such as maximum sustainable yield (MSY) or the equilibrium biomass that would produce

MSY (B_{MSY}; Jacobson et al., 2002). Although age-structured methods are often preferred, SPMs are still commonly used in assessing fish stocks in tropical regions where age-structured methods are impractical due to difficulties with accurately aging fish (Pauly, 1987).

The objective of my study was to examine the accuracy of SPMs for assessing stocks managed with MPAs. Specifically, the goal of this paper is to examine the accuracy of SPM estimates when part of the stock's range includes an MPA and the spatial resolution of the available data is confined to one region inside the MPA and one region outside the MPA. I also examined effects of size of MPA, migration rate, level of observation error in the index of abundance, and spatial aggregation of the data on estimates from spatially-explicit and spatially aggregated SPMs using simulations.

Methods

I conducted numerical experiments in which I simulated the dynamics of populations using a data-generating model (Figure 3.1). These populations were based on a stylized fish stock and followed a deterministic logistic growth pattern. I then produced time series of indices abundance such as might be available from fishery-independent surveys. Finally, I used several SPMs to estimate population biomass and other parameters of interest and compared the resulting estimates to the true values from the data-generating model to determine the performance (accuracy, precision and bias) of the assessment model estimates.

The data-generating model described the population dynamics for a range of MPA sizes and migration rates and produced data sets of catch and indices of abundance.

The assessment models were spatially-explicit or spatially-aggregated versions of SPMs and were fitted to the indices of abundance using a maximum likelihood approach. The SPMs were challenged with scenarios of different MPA sizes, migration rates, and data availability and quality. Each SPM was fitted to 200 replicate data sets for each scenario that differed in their random observation errors. All of the models were written in AD Model Builder (ADMB Project, 2010). The full model code is provided in Appendix II.

Data-Generating Model

The data-generating model was spatially explicit and tracked the population in two regions: one that became an MPA and one that remained open to fishing throughout the simulation. The type of MPA that is described here and assumed by the simulation is a "no take" or "no access" MPA, where no fishing is allowed (U.S. Dept. of Commerce/NOAA, 2010). Because the model required an informative pattern of fishing mortality over time, I created a scenario with a large amount of contrast in fishing mortality and biomass of the population over time. The simulation continued for 50 years, with the first year of the simulation also being the first year of the fishery. Fishing effort rapidly increased until the population was largely depleted and an MPA was established, at which point fishing effort gradually decreased in the fished region to the fishing mortality rate that would achieve MSY (F_{MSY}) due to concurrent regulations on the fishery in addition to the MPA (Figure 3.2). This pattern of fishing mortality was used to provide the models an informative data set, and to avoid the well known problem of uninformative "one way trip" data sets (Hilborn and Walters 1992). Spawning,

mortality, fishing, and the fishery-independent survey occurred sequentially at the end of each year.

The data generating model calculated the true total biomass at the end of each year, the observed index of abundance (observation error included), and the fishery catch in each region. The data generating model followed a discrete-time Schaefer (1954) production model with logistic growth, migration between two regions, and fishing (Hanneson, 1998; see Table 3.1 for definitions of variables):

$$\begin{split} B_{F}(t+1) &= B_{F}(t) + rB_{F}(t) \Biggl(1 - \frac{B_{F}(t)}{K(1-m)} \Biggr) + zm \Biggl[\Biggl(\frac{1-m}{m} \Biggr) B_{MPA}(t) - B_{F}(t) \Biggr] - F_{F}(t) B_{F}(t) \\ B_{MPA}(t+1) &= B_{MPA}(t) + rB_{MPA}(t) \Biggl(1 - \frac{B_{MPA}(t)}{Km} \Biggr) + \\ z(1-m) \Biggl[\Biggl(\frac{m}{1-m} \Biggr) B_{F}(t) - B_{MPA}(t) \Biggr] - F_{MPA}(t) B_{MPA}(t) \end{split}$$

Population parameters, r, K, z, and m, were constant across simulations within a scenario. Initial biomasses in each region were set at 90% of carrying capacity to represent a population that was only lightly exploited prior to the advent of a targeted fishery. The value for K was a generic maximum total biomass (Table 3.1) and r was similar to estimates of the maximum growth rates for the barndoor skate (*Dipturus laevis*; Gedamke et al., 2009) and South Atlantic albacore (*Thunnus alalunga*; Polacheck et al., 1993), but this level may be considered relatively high (Shepherd and Litvak, 2004). The migration rate (z) was defined as the probability that an individual will move from one region to the other within a year (Hannesson, 1998). The migration rate parameter represents a combination of a fish's propensity for movement and the size or arrangement of an MPA or complex of MPAs. For example, low z may represent a stock with a moderate movement with a single large MPA within its range, while a high z may

represent a stock with a low migration rate and a network of small MPAs within its range.

The index of biomass produced within the data generating model was the product of biomass, survey catchability, and a random lognormal observation error with a mean of zero and a standard deviation determined by the scenario,

$$S_{Area}(t) = B_{Area}(t) \cdot q_s \cdot e^{\sigma^* \delta(t)}$$
.

The random observation error was the only variable that changed in each replication of each scenario. Fishery catch in each region was calculated as the product of biomass and fishing mortality,

$$C_{Area}(t) = B_{Area}(t) * F_{Area}(t).$$

Scenarios differed in the size of MPAs, migration rates between the MPA and non-MPA regions, and the level of observation error in the indices of biomass. Sizes of MPAs considered were 5, 10, 20, and 40% of the stock area. The two largest MPA sizes were based on the methods in Punt and Methot (2004) as well as MPA sizes recommended or evaluated by several authors (Boersma and Parrish, 1999; Crowder et al., 2000; Jones, 2002). The two smallest MPA sizes were included to better represent actual MPA sizes implemented in current fisheries (United States Dept. of Commerce/NOAA, 2010). In order to simulate different types of populations and surveys I considered four levels of migration rate, 0.2, 0.3, 0.4, and 0.5 per year, and two levels of observation error, low (0.2 log-scale standard deviation (SD)) and high (1.0 log-scale SD). Figure 3.3 shows the true biomass of the simulated population over time for each combination of MPA size and migration rate. I also simulated one scenario in

which no index of biomass was available from within the MPA to model a situation where only fishery dependent data were available.

Estimation models

Data sets were fitted with spatially-explicit and spatially-aggregated SPMs. Spatially-explicit SPMs had the same form as the data-generating model, except that catch was subtracted each year. The migration rate parameters were assumed to be known at their true values in one version of the spatially-explicit SPM and were estimated in another. The dynamics of the spatially-aggregated model followed a simple Schaefer SPM (Hilborn and Walters, 1992),

$$B(t+1) = B(t) + rB(t) \left(1 - \frac{B(t)}{K}\right) - C(t)$$
.

The estimated parameters of the model were carrying capacity, the intrinsic rate of increase, the initial biomass as a proportion of carrying capacity, and survey catchability. Estimation models were provided the correct parameter values as starting values for the estimation to avoid potential problems caused by poor starting values. While analysts in the field would not have the correct values, the models were relatively insensitive to starting values. The parameters were estimated by minimizing the concentrated negative log likelihood functions. For the spatially-explicit scenarios the concentrated negative log likelihood function included components for the indices of biomass within and outside the MPA,

$$-LL = t_{\text{max}} * 0.5 * \log \left(\sum (\log(\hat{I}_F) - \log(I_F))^2 + \sum (\log(\hat{I}_{MPA}) - \log(I_{MPA}))^2 \right).$$

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For the spatially-aggregated SPMs, the concentrated negative log likelihood function included a spatially aggregated index of biomass,

$$-LL = t_{\text{max}} * 0.5 * \log \left(\sum (\log(\hat{I}) - \log(I))^{2} \right).$$

Assessment Evaluation

I evaluated the accuracy of SPMs by calculating the relative error of estimated biomass from the 200 simulated data sets for each estimation model,

$$B_{error} = \left(\frac{B_{pred} - B_{true}}{B_{true}}\right) * 100.$$

I summarized bias and accuracy of the models using the median of the relative error (MRE) or the median of the absolute value of the relative error (MARE) for each model under each MPA size, migration rate, and observation error scenario. I used the median instead of the mean because medians are not as susceptible to the influence of large outliers, which were present in the results. I used accuracy of estimated biomass in the last year of the simulation, or 30 years after the establishment of the MPA, to indicate overall accuracy of the model for most of the evaluations. I also estimated the relative error for the year the MPA was established, as well as five, ten, fifteen, twenty, and twenty-five years after establishment of the MPA.

I used analysis of variance (ANOVA) with absolute relative error (ARE) in the last year of the simulation as the dependent variable, and model, MPA size, migration rate, and observation error scenario as independent variables to compare the performance of the estimation models. Paired t-tests were also performed to determine the point at which the average error in estimated biomass was statistically similar to the last year of the simulation in each model and scenario.

Results

The populations in all of the scenarios began at 90% of carrying capacity and then declined rapidly for 20 years until they reached slightly less than 10% of carrying capacity (Figure 3.3). After the MPA was established at year 20, the populations slowly increased for 25-27 years until reaching equilibrium. This equilibrium varied with different MPA sizes. When only 5% of the total area was included in the MPA the populations recovered to about 51.7% of carrying capacity. When the MPA included 40% of the total area the populations recovered to around 71.9% of carrying capacity. Differences in migration rate affected the final equilibrium biomass by ~0.5%.

The general pattern of MARE in the assessment models changed over time (Figure 3.4). In the spatially-explicit model with low observation error and the scenario with 10% MPA and a migration rate of 0.3, after an initial slight decline MARE increased steadily before the establishment of the MPA until year fifteen of the simulation. The MARE then declined until three years after the MPA was established, at which point it sharply increased more than four-fold until seven years after the MPA was established. The error then slowly decreased until reaching a low equilibrium at about 20 years after the establishment of the MPA. The MRE also had a clear change from negative bias before the MPA was established to positive bias afterwards (Figures 3.4 and 3.5). The spatially-explicit and spatially-aggregated estimation models generally showed this same pattern of error, but the magnitude of the error was different among model and scenario combinations. The MARE of biomass in the last year was two to seven times less than the MARE five to ten years after the MPA was established on average. The

highest median errors were above 30% in the low-observation error scenarios (Table 3.3, Figure 3.5). Most of the highest errors were in the five and ten years after the establishment of the MPA, and the errors declined gradually so that the assessment at thirty years after the establishment of the MPA usually had the lowest errors, even compared to before the MPA was established. The t-tests showed that on average the MARE of the last year of the simulation was significantly lower (p<0.05) than the 23 to 28 years after the MPA was established.

The spatially-explicit SPMs produced more accurate estimates of biomass in the last year than spatially-aggregated SPMs (p<0.0001). For the scenarios with low observation error, the range of MAREs for spatially-explicit SPMs was 0.7 - 4.2% (Figure 3.6a and 3.6b; Table 3.4). In contrast, the spatially-aggregated SPMs had MAREs of biomass in the last year 2-4 times larger (range 2.5 - 8.8%) than the spatially-explicit SPMs in the low observation error scenario (Figure 3.6d). MAREs were higher in the scenarios with high observation error, as expected, but the relative difference between spatially-explicit and spatially-aggregated models was substantially smaller. The spatially explicit SPMs still performed significantly better than the spatially-aggregated versions (p<0.0001), with an MARE range of 4.9 - 17.1% (Figure 3.6c) compared to 5.7% - 19.4% in the spatially-aggregated SPMs (Figure 3.6f).

The spatially-explicit SPMs with migration rate as an estimated parameter had approximately the same MAREs as the SPMs where migration was assumed known at the correct value for the three lowest migration rates. Interestingly, in the highest migration rate scenario, the SPM that estimated migration rate had a significantly lower MARE of biomass in the last year than the scenario that specified migration rate

(p<0.0001). However, as this difference was only about 0.5%, the two were about equal in their accuracy.

Most of the scenarios showed significant trends of decreasing error as MPA size increased (p<0.0001). However, when no indices of abundance were available within the MPA error increased with increasing MPA size regardless of migration rate (Figure 3.6e). Only the spatially-aggregated model under the low observation error scenarios showed diverging trends in MAREs across levels of MPA sizes and migration rates (Figure 3.6d). In these scenarios estimated biomass had higher MAREs under lower migration rates and the MAREs generally increased with increasing MPA size. In the spatially-explicit SPMs with low observation error the highest migration rate had significantly higher MAREs than the lower migration rates (p<0.0001) when MPA size was 10, 20, or 40%. Finally, MAREs of estimated biomass increased with increasing MPA size and decreased with increasing migration rates in spatially-aggregated SPMs with no index of abundance in the MPA. The accuracy of the other models and scenarios were not affected by migration rate (p>0.05).

Discussion

MPAs have a negative effect on the accuracy of spatially aggregated SPM stock assessments. Modifications must be made to the traditional single stock model to account for differences in population dynamics between MPA and non-MPA areas. The spatially-explicit SPM was still relatively simple compared with spatially explicit agestructured approaches, and the parameters were estimable given informative data. The

complexity of the model was not greatly increased from a traditional spatially aggregated SPM, but the accuracy of estimated biomass was markedly improved.

Despite improvements in accuracy with spatially-explicit SPMs, there were unexpected patterns in both the MAREs and MREs even with the correctly specified model. Spatially-explicit and spatially-aggregated SPMs had large positive bias in estimated biomass soon after the establishment of the MPA. The pattern of error caused by MPA implementation persisted for about twenty years, even when data were available from within the MPA (Figure 3.4). However, accuracy during the later years of the assessment depended on a relatively accurate index of abundance before and after the establishment of the MPA.

Some authors have suggested that MPAs must occupy at least 20% and up to 40% of a population's habitat in order to be effective conservation measures (Jones, 2002; Boersma and Parrish, 1999). However, most actual MPAs occupy a much lower percentage of the total habitat, and less than 1% of marine resources are considered to be fully protected from fishing (Boersma and Parrish, 1999). Many of the modeling studies in the past have recommended and focused on large MPAs occupying between 20% and 70% of the population's range (e.g., Sumaila, 2002; Punt and Methot, 2004;), though some have explored the effects of smaller reserves (10-15% of the range) (e.g., Watson et al., 2000). Specifically, these studies have focused on the recommendations that emphasize large, "no-take" reserves (e.g., Pauly et al., 1997), which are different from other forms of MPAs that vary widely in the level of protection afforded to them. The results from this study suggest that large MPAs that are monitored can provide better

information about a population and improve the accuracy of analyses of stocks in the MPA by managers.

In my study, larger MPAs usually produced a more accurate stock assessment. Punt and Methot (2004) report similar results for SCAAs. The only assessment model in my study that had increasing errors with increasing MPA sizes was the spatially aggregate model with no indices of abundance from within the MPA. The trend in performance of models without information from within the MPA was expected because the assumptions of the assessment are violated to a lesser degree with a small MPA than a larger MPA. Thus, with large MPAs, indices of abundance from within the MPA are extremely important for accurate assessments.

Migration rates can also affect accuracy of stock assessments when an MPA is part of the management for a fishery. Punt and Methot (2004) found a decrease in accuracy of stock assessments with increasing migration rates. In my study migration did not have as much of an effect on accuracy as MPA size. When there was an effect of migration rate, increased migration rates increased the accuracy of the assessment, which was the opposite pattern from that in age-structured methods (Punt and Methot 2004).

My results, and the results from Punt and Methot (2004), tested a single large MPA, but they may be able to be extrapolated to a network of smaller MPAs (Field et al., 2006). This is important because of the SLOSS (Single Large Or Several Small) debate among ecologists (McNeill and Fairweather, 1993; Roberts and Hawkins, 1997; Walters, 2000). Because MPA size in the data-generating and estimation models in my study was in terms of proportion of carrying capacity biomass protected by the MPA, the results may be interpreted as the effects of several different kinds of MPAs on the accuracy of a

SPM. For example, a scenario that involves a large MPA could have the same proportion of carrying capacity protected as a series of smaller MPAs, but the migration rate would be higher for a network of smaller MPAs. However, my study assumes a closed population, so the results are not applicable to a subpopulation with extensive migration from outside the modeled area.

Information on trends in abundance within the MPA substantially improved total biomass estimates. The lack of information from within the MPA forces any assessment to be spatially aggregate and assume that dynamics within the MPA are the same as those outside of the MPA. The estimated biomass from scenarios without indices of abundance in the MPA was negatively biased, and the bias increased with larger MPAs and higher migration rates. The SPMs without indices from within the MPA were less accurate than those from the spatially-aggregated models that had data from within the MPA. Thus, survey information on relative abundance or biomass within the MPA is essential for accurate SPM assessments, especially in situations with large MPAs. Only 29% of MPAs, however, have sufficient information available to evaluate progress against their management objectives (Jones, 2002), and presumably to develop indices of abundance.

My study likely provides a best-case scenario for how well SPM assessments will perform when MPAs are implemented because, in most cases, the assessment model was exactly the same as the data generating model. My simulations assumed no error in the catch and deterministic population dynamics. My assessments also assumed that MPA size was known. MPA size is likely to be known, but the spatially-explicit SPM requires an assumption about the proportion of carrying capacity within the MPA, which may differ from the spatial extent of the MPA because limiting resources for the population

may not be evenly distributed. Other requirements for a successful SPM in this study were an informative fishing mortality scenario and indices that were actually proportional to population size. The results may be less accurate if fishing mortality is assumed to be constant or if there are flaws in the survey that make the indices disproportional to population size.

In spite of the potential benefits of MPAs, few MPAs have shown sufficiently good management to have substantial improvement in the biomass of fish they were established to protect (Kelleher, 1996; Hilborn et al., 2004). Positive effects on fish stocks from an MPA are highly dependent on variables other than MPA size such as the characteristics of the area, the behavior and life-history traits of the fish (Holland, 2002), and the success of management in actually protecting the area. Larger MPAs have a greater positive effect on fish populations than smaller MPAs, provided that the protected regions are of similar quality (Pelletier and Magal, 1996; Nowlis and Roberts, 1999). However, an MPA with higher quality habitat can lead to better results than a larger protected area of low quality (Lundberg and Jonzen, 1999; Rodwell et al., 2003) because higher-quality areas can support greater densities of fish. Moreover, the timing of dispersal behaviors also have a substantial effect on the regions where the majority of recruitment occurs, and therefore on the efficacy of an MPA (Morgan and Botsford, 2001; Pelletier and Mahevas, 2005).

In conclusion, accuracy of estimates from SPM stock assessments, like agestructured assessments, can be substantially affected by inclusion of an MPA within the stock's range. However, substantial improvements in accuracy can be made by collecting indices of abundance within the MPA and using a spatially-explicit SPM to model the population. The movement rate of the species only seemed to matter when very large MPAs were present, and large MPAs usually provided the most accurate biomass estimates in spatially explicit models. SPMs where the migration rate was estimated produced as accurate or more accurate results than models where migration was specified at its correct value and should be preferably used over SPMs where the migration rate is assumed known. A substantial period is necessary for biomass estimates to become unbiased after MPA implementation. However, the SPMs modeled here performed well in a broad range of circumstances and could be useful in stock assessments where an MPA is involved.

Table 3.1. Definitions of the symbols used in data-generating and assessment models.

	- 4
Symbol	Definition
$I_{\mathrm{Re}\mathrm{gion}}$	Biomass in one of the regions, Fish and MPA
	denote fished and MPA regions
ĵ	Predicted biomass in one of the regions, Fish
Re gion	and MPA denote fished and MPA regions
r	Intrinsic rate of increase: 0.4
K	Carrying capacity of the entire population:
	1000 units
m	Proportion of the total area in the MPA
Z	Migration rate
σ	Standard deviation of observation error
δ	Normally distributed observation error
F_{Area}	Annual fishing mortality rate
q_s	Catchability of the survey: 0.005
t_{max}	Number of years in simulation: 50
С	Total annual catch
В	Biomass

Table 3.2. Description of the six versions of the surplus production models.

Model & Scenario Set	Spatial Structure	Migration Estimated?	Survey Within MPA?	Observation Error log- scale SD
А	Spatially Explicit	no	yes	0.2
В	Spatially Explicit	yes	yes	0.2
С	Spatially Explicit	no	yes	1
D	Aggregate	no	yes	0.2
E	Aggregate	no	no	0.2
F	Aggregate	no	yes	1

Table 3.3. Overall error of all MPA sizes and migration rates from each model and scenario. The first row is the percent of the median of the absolute value of the relative error (% MARE) from each model and set of scenarios through time, beginning with the year the MPA was established. The numbers in bold are the two highest errors for that set of scenarios. The second, italicized row is the upper bound of the 95% confidence interval.

				MARE			
	Year	Year	Year	Year	Year	Year	Year
Model, Scenarios	20	25	30	35	40	45	50
Explicit, low error	14.8	13.0	13.9	7.1	3.5	2.5	2.0
	23.5	30.7	30.0	21.9	16.3	13.7	11.9
Explicit, migration							
estimated	14.5	14.6	15.7	7.6	3.3	2.3	1.9
	21.8	33.2	32.3	22.0	14.5	12.4	11.0
Explicit, high error	20.9	21.9	21.9	19.4	15.7	12.3	9.9
	51.0	113.7	102.3	75.0	51.0	47.6	64.8
Aggregate, low error	11.5	18.3	18.2	10.2	5.9	4.8	4.5
	20.8	40.6	36.5	27.2	19.6	14.6	11.9
Aggregate, no IA in MPA	23.7	16.0	18.7	24.4	25.5	22.2	16.2
	35.5	46.3	56.8	63.3	63.3	58.2	47.5
Aggregate, high error	22.7	32.5	32.1	24.2	17.3	14.0	10.9
	65.9	140.5	116.4	84.3	61.1	<i>57.4</i>	67.3

Table 3.4. Median relative error (MRE) of total biomass and bounds of the 95% confidence intervals from each combination of MPA size, migration rate, and SPM version.

Spatially-explicit						Spatially-aggregated			
Model Version	Migration Rate	MPA Size	Median	Lower 95%	Upper 95%	Model Version	Median	Lower 95%	Upper 95%
A	0.2	5%	-0.7%	-12.5%	10.6%	D	1.5%	-10.3%	14.6%
Α	0.2	10%	-0.3%	-10.5%	7.9%	D	4.2%	-5.5%	13.0%
Α	0.2	20%	-0.3%	-7.3%	3.3%	D	7.9%	2.4%	11.5%
Α	0.2	40%	-0.1%	-2.0%	1.8%	D	8.8%	4.9%	11.2%
Α	0.3	5%	-0.7%	-12.6%	10.3%	D	0.4%	-11.4%	13.5%
Α	0.3	10%	-0.3%	-11.2%	7.7%	D	2.3%	-7.5%	11.0%
Α	0.3	20%	-0.3%	-7.1%	3.0%	D	5.0%	-0.4%	8.4%
Α	0.3	40%	0.0%	-2.3%	1.7%	D	5.8%	2.4%	8.0%
Α	0.4	5%	-0.7%	-13.0%	10.2%	D	-0.2%	-12.1%	12.9%
Α	0.4	10%	-0.4%	-11.0%	7.4%	D	1.3%	-8.6%	10.1%
Α	0.4	20%	-0.3%	-6.7%	3.0%	D	3.4%	-2.2%	6.7%
Α	0.4	40%	0.1%	-2.5%	1.8%	D	4.2%	0.8%	6.2%
Α	0.5	5%	-0.8%	-12.8%	10.1%	D	-0.5%	-12.4%	12.7%
Α	0.5	10%	-2.3%	-13.9%	9.2%	D	0.7%	-9.3%	9.7%
Α	0.5	20%	-1.3%	-14.5%	4.0%	D	2.4%	-3.4%	5.9%
Α	0.5	40%	1.5%	-20.5%	3.7%	D	3.2%	-0.1%	5.1%
В	0.2	5%	-0.7%	-13.4%	10.6%	Ε	-7.6%	-22.2%	7.5%
В	0.2	10%	-0.4%	-11.3%	7.7%	Е	-12.6%	-26.8%	2.3%
В	0.2	20%	-0.3%	-7.4%	4.0%	Ε	-18.9%	-35.0%	-1.6%
В	0.2	40%	-0.2%	-3.9%	2.8%	Е	-38.1%	-54.1%	-12.7%
В	0.3	5%	-0.7%	-13.1%	10.4%	Ε	-7.5%	-21.9%	7.5%
В	0.3	10%	-0.4%	-11.3%	7.4%	Е	-12.4%	-26.3%	2.3%
В	0.3	20%	-0.4%	-7.2%	3.4%	Е	-19.6%	-34.0%	-4.2%
В	0.3	40%	-0.2%	-3.2%	2.3%	Е	-36.9%	-52.6%	-17.0%
В	0.4	5%	-0.7%	-12.9%	10.3%	Е	-7.4%	-21.7%	7.6%
В	0.4	10%	-0.4%	-11.3%	7.3%	Ε	-12.2%	-25.9%	2.5%
В	0.4	20%	-0.3%	-7.0%	3.3%	Ε	-19.3%	-33.5%	-4.6%
В	0.4	40%	-0.2%	-3.1%	2.0%	Ε	-33.5%	-53.0%	-7.9%
В	0.5	5%	-0.7%	-12.8%	10.2%	Ε	-7.3%	-21.5%	7.7%
В	0.5	10%	-0.6%	-11.2%	7.3%	Ε	-12.0%	-25.6%	2.5%
В	0.5	20%	-0.2%	-6.9%	3.4%	Ε	-19.1%	-33.4%	-4.5%
В	0.5	40%	-0.1%	-3.1%	1.8%	Ε	-30.2%	-50.3%	-6.1%
С	0.2	5%	-5.6%	-70.1%	24.7%	F	-3.1%	-71.7%	38.4%
С	0.2	10%	-5.4%	-64.4%	19.7%	F	2.0%	-63.8%	33.1%
С	0.2	20%	-4.9%	-52.7%	13.8%	F	4.5%	-44.3%	28.3%
С	0.2	40%	-2.5%	-33.5%	13.1%	F	6.8%	-26.7%	40.0%
С	0.3	5%	-6.5%	-72.1%	25.3%	F	-4.6%	-73.0%	36.0%
С	0.3	10%	-5.9%	-65.9%	18.6%	F	-0.8%	-66.5%	30.3%

С	0.3	20%	-4.4%	-57.6%	13.9%	F	0.8%	-48.6%	30.0%
С	0.3	40%	-2.3%	-31.6%	13.0%	F	3.4%	-30.3%	34.8%
С	0.4	5%	-6.2%	-73.3%	24.2%	F	-5.9%	-73.7%	34.7%
С	0.4	10%	-5.5%	-69.1%	18.4%	F	-2.1%	-67.5%	28.9%
С	0.4	20%	-4.5%	-61.1%	13.6%	F	-0.7%	-52.7%	27.9%
С	0.4	40%	-2.4%	-31.6%	13.5%	F	1.9%	-32.5%	30.6%
С	0.5	5%	-6.3%	-71.6%	24.5%	F	-6.5%	-74.1%	34.2%
С	0.5	10%	-6.3%	-72.6%	18.9%	F	-3.7%	-67.8%	28.1%
С	0.5	20%	-5.3%	-61.8%	13.2%	F	-1.4%	-54.8%	26.0%
С	0.5	40%	-2.1%	-29.6%	13.4%	F	0.7%	-33.5%	27.6%

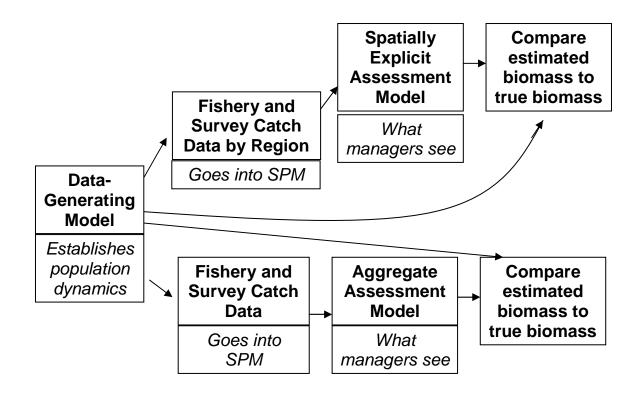


Figure 3.1. Flow chart of the models and datasets created in the simulation.

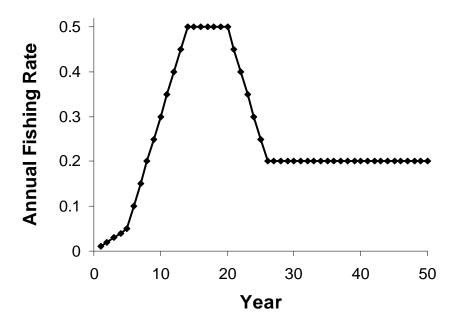


Figure 3.2. Pattern of annual fishing mortality in the fished region of the simulation. The first twenty years of the simulation also apply to the region that becomes the MPA.

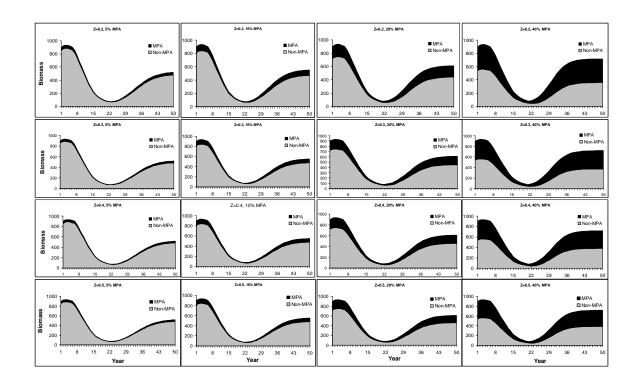


Figure 3.3. Biomass in both regions from every combination of MPA size and migration rate. Columns from left to right are in order of increasing MPA size and rows from top to bottom are in order of increasing migration rate.

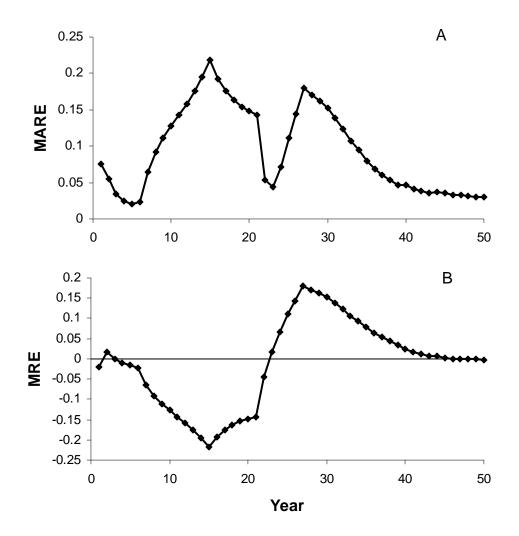


Figure 3.4. Median of the absolute value of the relative error (MARE, panel A) and the median of the relative error (MRE, panel B) for each year of the spatially explicit model where the MPA size was 10%, migration rate was 0.3, and observation error was 0.2.

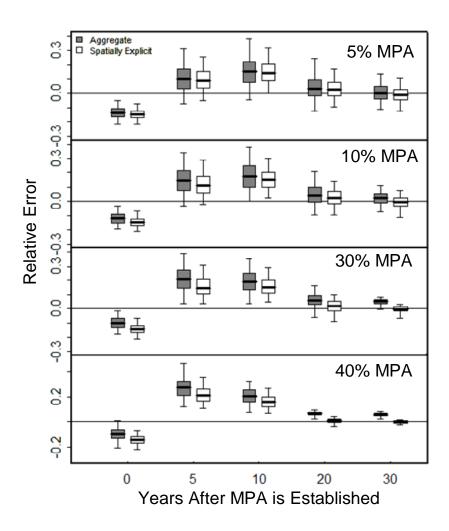


Figure 3.5. Boxplots showing the error in total biomass in the low observation error scenarios for both spatially explicit and aggregate assessment models through time.

Migration rate is 0.4 in every case shown. Boxes show interquartile range, dark line is the median, and whiskers are 95% confidence interval.

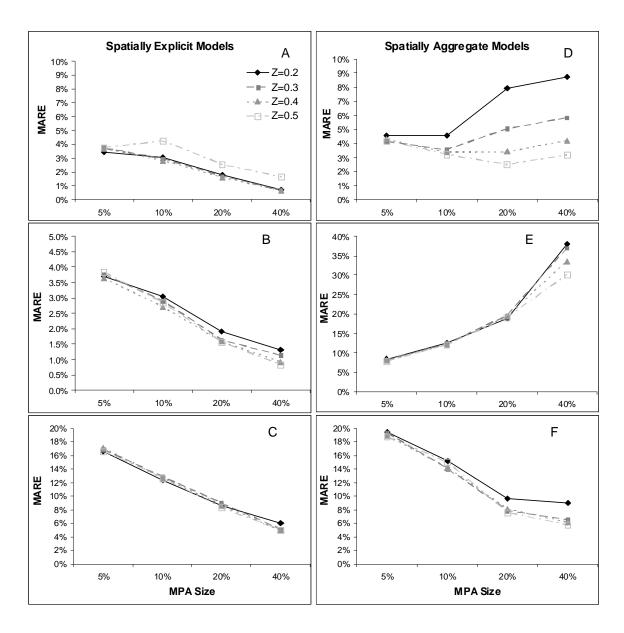


Figure 3.6. Median of the absolute value (MARE) of the relative error in biomass in the last year of the simulation from all models and scenarios. The letter in the top right corner of each panel corresponds to the model and scenario set defined in Table 2. Z indicates migration rate.

Chapter 4: Results and Summary

The objective of my thesis was to employ spatially-explicit techniques to identify regions that have different population dynamics and develop and compare assessment methods for stocks with spatial patterns of exploitation. The specific objectives of Chapter 2 were to develop indices of abundance of four common species caught in the Maryland Coastal Bays Trawl and Seine Survey (MCBTSS) and compare trends in abundance of four fish species across two regions within the Maryland's coastal bays. To achieve these objectives, I developed generalized linear models (GLiMs) to develop statistically standardized indices of abundance that accounted for changes in survey methodology and used the models to generate indices of abundance for 17 years of data prior to the standardization of the survey. I compared trends in indices of abundance for each species between the two regions and tested for effects of habitat on changes in abundance. My objectives in Chapter 3 were to assess the accuracy of surplus production models (SPMs) on a population with a spatially heterogeneous exploitation pattern because of a no-take marine protected area (MPA). I conducted a simulation study to evaluate the performance of SPMs when part of the range included an MPA. I tested several versions of SPMs under a range of conditions including proportion of the range protected by an MPA, migration rate between MPA and non-MPA regions, and quality and availability if indices of abundance.

In Chapter 2, I showed that GLiMs could be used to account for spatial, temporal, and methodological changes in the MCBTSS. Since 1972 juvenile populations of Atlantic menhaden (*Brevoortia tyrannus*) and spot (*Leiostomus xanthurus*) have declined in Maryland's coastal bays, while summer flounder (*Paralichthys dentatus*) and weakfish

(Cynoscion regalis) did not have a significant trend over time. I also found that bays in the northern region, north of the inlet to the ocean, had significantly higher densities of these fishes than the southern region. However, none of the environmental variables, including seagrass area, were related to changes in relative abundance of any of the species through time. This is likely due to the coupling of coastal bay fish populations with the broader Mid-Atlantic stocks through yearly recruitment. The northern region of Maryland's coastal bays, which is more eutrophied and has longer water retention time, supported higher densities of fish than the more pristine southern bays. However, the effects of habitat degradation may have been reflected in the steeper decline of Atlantic menhaden and spot in the northern region relative to the southern region. Finally, because localized habitat variables were not related to relative abundance of any of the species, a coast-wide stock recruitment relationship may explain long-term trends better local habitat variables.

In Chapter 3, I showed that SPMs were able to be used as an accurate method of assessing the biomass of a stock where an MPA is involved. However, perhaps the most interesting result was that accuracy of the assessments changed substantially in the years immediately after the MPA was established. Up to twenty years was necessary for the error in the SPMs to return to more accurate levels. Spatially explicit assessments performed far better than spatially aggregate methods. Also, having indices of abundance from within the MPA was crucial to estimate the biomass of the total population accurately, and GLiM models from Chapter 2 could be used to develop spatially-explicit indices for populations with an MPA. The movement rate of the species only seemed to matter when very large MPAs were present, and large MPAs usually provided the most

accurate biomass estimates in spatially explicit models. SPMs where the migration rate was estimated produced as accurate or more accurate results than models where migration was specified at its correct value and should be preferably used over SPMs where the migration rate is assumed known. SPMs performed well in a broad range of circumstances and could be useful in stock assessments where an MPA is involved.

Appendix I: Trawl and Seine Survey Comparisons

Introduction

In addition to analyzing the trawl survey data as described in Chapter 2 of this thesis, I also analyzed the seine survey data in a similar manner and compared the two gear types. I also compared the indices of abundance from the generalized linear models I developed with the indices of abundance currently used by the Maryland Department of Natural Resources (MDNR) in their reports. The results of those analyses are described in this appendix.

Methods

The seine portion of the MCBTSS samples 19 different sites in the same five bays as the trawl survey (Figure 2.1). Since the survey was standardized in 1989, MDNR has seined at each site in June and September (July and September for 1989-1992). The seine survey was conducted with a 30.8 m X 1.8 m seine (100ft X 6ft) with 0.63 cm mesh (0.25in) (Bolinger et al., 2007). The seine survey is conducted adjacent to the edges of the bays, mostly in depths of less than one meter. The seine survey was not fully standardized spatially until 1993. The seine samples are not standardized by time, but rather the seine is pulled across a specific length of shore that varies among sites depending on the amount of exposed shoreline.

As with the trawl survey, I excluded some sites and years from the analyses. Site S19 was excluded because it has a very different salinity regime and other physical

properties from the other sites and can only be sampled at high tide. Other exclusions are detailed in Table I.1. The generalized linear model used to calculate the indices of abundance was the same as the trawl models (See Methods section in Chapter 2) but with no effort term, as one seine pull was considered one unit of effort. Weakfish were not caught enough in the seine survey to be able to calculate indices of abundance using the generalized linear model, so only menhaden, flounder, and spot were analyzed. Trends over time were analyzed by region with ANCOVAs as with the trawl models. A Bonferroni correction was used so that a significant p-value is reduced to 0.00833.

Index and Gear Comparisons

MDNR currently uses a simple catch per seine or catch per trawl averaged over all sites and samples within a year to arrive at one index per year for each species and gear type. I conducted correlations to compare the indices estimated by the standardization models with the indices used by MDNR. I compared the generalized linear model-based indices to the log-transformed yearly mean CPUEs for each species, gear type, region, and period (all years of the survey, years before standardization, and years after standardization). If the factors included in the model are important, the mean CPUE indices and the model estimates will have a higher correlation in the post-standardized years of the survey than the pre-standardized years.

I also compared the trawl and seine survey indices for each species to see if they provided consistent trends over time. If both gears are highly and positively correlated, they provide consistent indices of abundance. If they are not well correlated then one or both gear types show inaccurate indices of abundance. I used correlations between the regional year effect estimates of the models to assess the similarities in trends between

the year-effect results of the trawl and seine models. If both regions are highly and positively correlated, they are equally suitable for the species used in the analyses and can be considered one large region.

Results

The indices of abundance from the seine survey showed very different trends than the indices from the trawl survey for summer flounder and spot. Menhaden still showed a decreasing trend as in the trawl survey (only significant in the southern region, Table I.2, Figure I.1), but flounder showed a significant increase in the southern region (Figure I.2). Spot, which showed a significant decrease in the northern region and no overall increase or decrease in the southern region in the trawl survey, showed an increase in the southern region in the seine survey (Figure I.3).

The correlations between the trawl and the seine models varied greatly among species. A total of six gear correlations were performed, one for each region in the flounder, spot, and menhaden models (Table I.3). They ranged from -0.330 to 0.611 with menhaden being the most similar of the three species.

A total of 14 sets of correlations (42 total correlations, 40 were significant) were performed between the simple mean catch and the generalized linear model indices of abundance, and 12 of them were higher in the post-standardized years than the prestandardized years (Tables I.4 and I.5). The full models changed the index of abundance estimates more during the period when sampling was inconsistent than when the survey was standardized in 11 of the 14 sets of correlations. The correlations ranged from 0.363 to 0.981 (Tables I.4 and I.5). The majority of the generalized linear models followed the same trends as the simple catch per trawl or seine.

Discussion

The wide differences between the trawl and the seine surveys are an indication of the importance of gear choice in developing indices of abundance. The seine is limited to shallow near-shore areas. In the coastal bays, the trawl is limited to channels deep enough for the boat to pass, an important limitation in the coastal bays where the average depth is only about one meter. There are often large areas in between sites that cannot be reached by either the trawl or the seine. This combined with the very low correlations in trends between the trawl and seine (Table I.3) make it probable that the two gears are sampling somewhat different portions of the fish populations, or that one gear is sampling sub-optimal habitat for a species causing the trends to be different.

Because of the differing trends in the trawl and seine surveys, one gear must be used over the other to provide indices of abundance in the coastal bays. For the purposes of this thesis, I have made the assumption that the trawl provides a more accurate view of the trends in young-of-year fish of the species I studied, both because of the behaviors of the species and the range of the gear. The parallels between the trends seen in the trawl surveys and the mid-Atlantic stock assessments provide more support for the premise that the trawl survey provides more accurate indices of abundance. In spite of this decision, however, it may be useful to describe the trends seen in the seine survey.

Unlike the trawl survey, the northern region of the coastal bays did not have significantly greater densities of fish in the seine survey. There was also only one instance of significant decline in a species as opposed to the three instances in the trawl survey. Only menhaden in the southern region declined significantly during 1972-2009.

However, both flounder and spot showed significant increases in the southern region during the same time period (Table I.2, Figures I.2 and I.3). No significant changes were seen in any of the three species in the northern region.

Standardizing the survey in 1989 should have allowed a simple catch per trawl or seine to be an accurate index of abundance. If the full models developed in this project can produce a more accurate index of abundance, one would expect the models to change the estimates for the years before standardization more than the years after standardization. This hypothesis was substantiated by the correlations performed between the indices of abundance from the two methods (Tables I.4 and I.5). The generalized linear models were more correlated with the years in the survey post-standardization in 12 of the 14 species, gear, and region combinations, suggesting that the survey standardization improved the accuracy of the CPUE as an index of abundance and that the generalized linear models improved the accuracy of the indices of abundance prior to survey standardization.

Many of the overall increases or decreases in abundance were only apparent if the time series had more than ten or fifteen years, and more were necessary to ascertain whether the trend continued. For example, the time period for which the habitat data used in Chapter 2 was available (1990-2004) showed a significant increase in weakfish abundance, but when the entire time series from MCBTSS (1972-2009) is used no significant upward or downward trend is apparent. During 1990-2004 there was also no significant trend in menhaden or spot, but when the entire time series is taken into account both showed significant declines in the trawl portion of the survey. Thus, including the earlier data revealed trends that we would otherwise not have seen.

Table I.1. The years, months, and sites excluded from the seine survey analyses and the reasons for excluding them.

Cnasica	Dogion	Variable	Doggon
Species	Region Variable		Reason
		Level	
		Removed	
All	All	1983-1986	<6 samples
Menhaden	North	1980	None
			Caught
Menhaden	All	October	None
			Caught
Flounder	All	May	None
			Caught
Flounder	All	October	None
			Caught
Flounder	All	1973	None
			Caught
Flounder	All	1977	None
			Caught
Flounder	South	Site S14	None
			Caught
Flounder	All	1979	None
			Caught

Table I.2. The slopes and p-values of the trends for each species and region evaluated from the seine portion of the survey. Bold rows are statistically significant at α =0.008, the level that corresponds to α =0.05 when corrected for multiple comparisons.

Species	Region	Slope	p-value
Menhaden	North	-0.0615	0.2346
Menhaden	South	-0.0837	0.0034
Flounder	North	-0.046	0.0427
Flounder	South	0.0574	0.0051
Spot	North	0.0564	0.0196
Spot	South	0.0957	<0.0001

Table I.3. The gear comparisons between the trawl and seine full models for each species in two regions where the models for both gears converged.

Flounder		Menh	Menhaden		Spot	
North	South	North	South	North	South	
-0.330	0.367	0.487	0.611	0.071	-0.031	

Table I.4. The trawl survey correlations between the full generalized linear model and the simple average catch per trawl. Correlations are by region and species for all years (1972-2009), pre-standardization (1972-1988), and post-standardization (1989-2009). Stars indicate statistical significance at α =0.05.

Species	Region	All	Pre-	Post-
		Years	Standardization	Standardization
Spot	North	0.9794**	0.9719**	0.9812**
Spot	South	0.9667**	0.9126**	0.9896**
Menhaden	North	0.9102**	0.8258**	0.8425**
Mendahen	South	0.8370**	0.4921	0.9273**
Flounder	North	0.9287**	0.9520**	0.9613**
Flounder	South	0.9213**	0.8845**	0.9814**
Weakfish	North	0.8174**	0.7821**	0.8632**
Weakfish	South	0.6932**	0.3630	0.9510**

Table I.5. The seine survey correlations between the full generalized linear model and the simple average catch per seine. Correlations are by region and species for all years (1972-2009), pre-standardization (1972-1992), and post-standardization (1993-2009). Stars indicate statistical significance at α =0.05.

Species	Region	All	Pre-	Post-
		Years	Standardization	Standardization
Spot	North	0.9507**	0.9746**	0.9658**
Spot	South	0.9686**	0.9607**	0.9323**
Menhaden	North	0.8353**	0.8664**	0.8734**
Menhaden	South	0.7671**	0.5447**	0.8110**
Flounder	North	0.9305**	0.9318**	0.9596**
Flounder	South	0.8503**	0.7838**	0.9768**

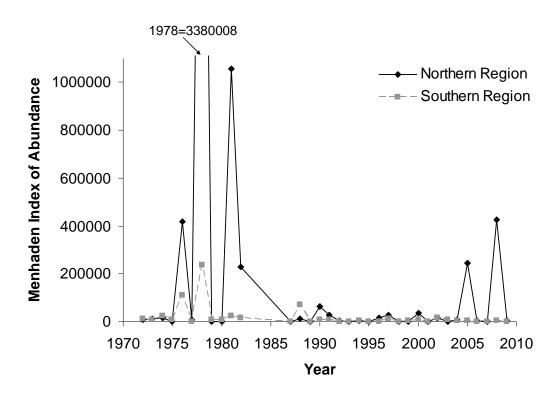


Figure I.1. The model estimates of the seine survey for menhaden for each region. The missing values are the years where there was not enough data to form a reliable estimate.

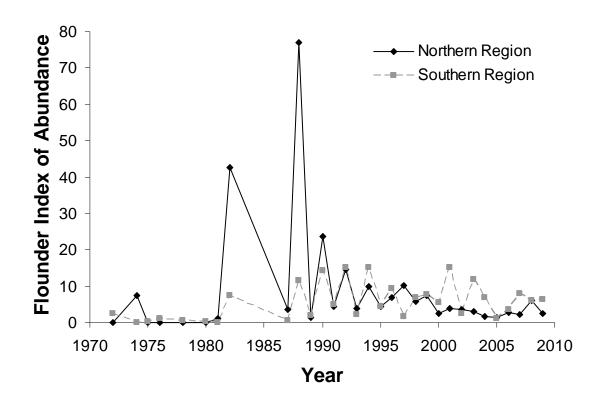


Figure I.2. The model estimates of the seine surveys for flounder for each region. The missing values are the years where there was not enough data to form a reliable estimate.

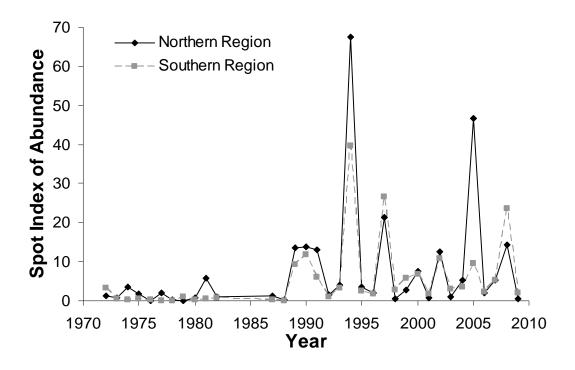


Figure I.3. The model estimates of the seine surveys for spot for each region. The missing values are the years where there was not enough data to form a reliable estimate.

Appendix II: Surplus Production Model Code

Data Generating Model

```
//Jennifer Barkman
//Chapter 2 2-Area Simulation Surplus Production Model
//Created June 30, 2010
// Last edited July 15, 2010
DATA_SECTION
 init_int tmax
                    //# of years in model
 init_vector F1(1,tmax) //Fishing pressure in non-MPA area
 init_vector F2(1,tmax) //Fishing pressure in MPA area
                     //intrinsic rate of growth
 init number r
 init vector m(1,4)
                      //proportion of area that is MPA
 init_number K
                      //Carrying capacity
 init number sq
                     //survey catchability
 init_vector z(1,4)
                     //migration rate
 init number sigma //st dev of observation error on log scale for survey data
                 //number of sumulations to run
 init int nsims
                //random number generator seed
 init int seedi
 init vector test(1,3)
 vector S1(1,tmax) //Survey catch in non-MPA
 vector S2(1,tmax) //Survey catch in MPA
 vector ST(1,tmax) //Survey catch in total area
 vector N1(1,tmax) //Abundance for non-MPA region
 vector N2(1,tmax) //Abundance for MPA region
 vector NT(1,tmax) //Abundance for total area
 vector C1(1,tmax) //Catch in non-MPA
 vector C2(1,tmax) //Catch in MPA
 vector CT(1,tmax) //Catch in total area
 int i //year counter
 int j //migration counter
 int k //sim counter
 int n //MPA size counter
 int seed
 vector S1 err(1,tmax)
 vector S2_err(1,tmax)
LOCAL_CALCS
 //cout << test << endl;
```

```
//cout << m << endl;
//exit(2);
END_CALCS
PARAMETER SECTION
 objective_function_value f
LOCAL_CALCS
//create random number generator seed
 seed=seedi:
 random_number_generator rng(seed);
 //run entire program and estimation model multiple times
 for(k=1;k\leq nsims;k++)
  //change rndnumbseed to create diff values
  seed+=2;
  S1_err.fill_randn(rng);
  S2_err.fill_randn(rng);
  //loop over migration rates
  for(j=1;j<=4;j++)
   for(n=1;n<=4;n++)
    //I output counters so I could see how far along the program was while it was
    cout << k << "" << z(j) << "" << m(n) << endl;
    //inital biomass
    N1(1)=(1.-m(n))*0.9*K;
    N2(1)=m(n)*0.9*K;
    NT(1)=N1(1)+N2(1);
    //fill in N vectors
    get_numbers();
    //create data file for 2-area est model
    ofstream ofs("estmodel.dat");
     ofs << "#tmax" << endl;
     ofs << tmax << endl:
     ofs << "#proportion of area that is MPA" << endl;
     of << m(n) << endl;
     ofs << "#migration rate" << endl;
     ofs \ll z(j) \ll endl;
     ofs << "#Abundance in total area" << endl;
     ofs << NT << endl:
```

```
ofs << "#Catch in non-MPA area" << endl;
      ofs << C1 << endl:
      ofs << "#Catch in MPA area" << endl;
     ofs << C2 << endl;
      ofs << "#Abundance in non-MPA area" << endl;
      ofs << N1 << endl;
     ofs << "#Abundance in MPA area" << endl;
      ofs \ll N2 \ll endl;
     ofs << "#survey catch in non-MPA area" << endl;
     ofs << $1 << endl;
      ofs << "#survey catch in MPA area" << endl;
     ofs << S2 << endl;
     ofs << "#test" << endl;
     ofs << "1 2 3" << endl;
    //create data file for one-area model
    ofstream one("oneareamodel.dat");
     one << "#tmax" << endl;
     one << tmax << endl;
     one << "#proportion of area that is MPA" << endl;
     one \ll m(n) \ll endl;
      one << "#migration rate" << endl;
     one \ll z(j) \ll endl;
      one << "#Abundance in total area" << endl;
     one << NT << endl:
      one << "#Catch in total area" << endl;
     one << CT << endl;
     one << "#survey catch in total area" << endl;
      one << ST << endl:
      one << "#test" << endl;
     one << "1 2 3" << endl;
    //create file to display population dynamics of the two areas
    //the ios::app appends data to the file in every iteration instead of deleting and
rewriting it
    ofstream bio("popdy.txt",ios::app);
      bio << z(j) << m(n) << endl;
      bio << N1 << endl;
     bio << N2 << endl;
     bio << NT << endl;
```

```
/*
                 //output seed numbers
                 ofstream out("rndnumseed.txt",ios::app);
                    out << seed << " " << endl;
                     out << N1 << endl;
                  */
                 //call estimation model 2-area and 1-area
                 system("estmodel.exe");
                 system("oneareamodel.exe");
   cout << "model finished" << endl;</pre>
   exit(0);
  END_CALCS
PROCEDURE_SECTION
FUNCTION get_numbers
   //Fill in N matrices
    for (i=1;i<tmax;i++)
        m(n)/m(n)*N2(i)-N1(i)-F1(i)*N1(i);
        N2(i+1)=N2(i)+r*N2(i)*(1.-(N2(i)/(K*m(n))))+z(j)*(1.-m(n))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))+z(j)*(1.-m(n))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))+z(j)*(1.-m(n))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))+z(j)*(1.-m(n))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))+z(j)*(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m(n)))*((m(n)/(1.-m
m(n))*N1(i)-N2(i))-F2(i)*N2(i);
        NT(i+1)=N1(i)+N2(i);
   //This checks to make sure biomass is positive
    if (NT(i)<0.)
        cout \ll N1 \ll endl;
        cout \ll N2 \ll endl;
        cout << NT << endl;
        exit(3);
```

```
*/
 }
//Fill in Catch matrix and survey catch matrix with the random error
 for (i=1;i \le tmax;i++)
  C1(i)=N1(i)*F1(i);
  C2(i)=N2(i)*F2(i);
  CT(i)=C1(i)+C2(i);
  S1(i)=N1(i)*sq*exp(sigma*S1_err(i));
  S2(i)=N2(i)*sq*exp(sigma*S2\_err(i));
  ST(i)=S1(i)+S2(i);
//This was for a version where no data was available in the MPA for the last 30 years of
the simulation
 /*
for (i=1;i<=20;i++)
  S2(i)=N2(i)*sq*exp(sigma*S2_err(i));
  ST(i)=S1(i)+S2(i);
 */
//cout << S1 << S2 << endl;
//cout << C2 << endl;
//cout << CT << endl;
//exit(2);
```

REPORT_SECTION

Spatially-Explicit Estimating Model

```
//Jennifer Barkman
//Chapter 2 2-Area Estimation Surplus Production Model
//Created June 30, 2010
// Last edited July 15, 2010

DATA_SECTION
init_int tmax //number of years of data
init_number m //proportion of area that is MPA
init_number z //migration rate
init_vector BTtrue(1,tmax) //Biomass in total area
init_vector C1obs(1,tmax) //Catch in non-MPA area
init_vector B1true(1,tmax) //Catch in MPA area
init_vector B1true(1,tmax) //non-MPA area
```

```
init_vector B2true(1,tmax) //MPA area
 init_vector S1(1,tmax) //survey catch from non-MPA
 init_vector S2(1,tmax) //survey catch from MPA
 init\_vector test(1,3)
 //I needed a 2nd catch vector that was not from the .dat file for the program to work,
though I don't remember why
 vector S1obs(1,tmax) //survey catch for non-MPA area
 vector S2obs(1,tmax) //survey catch for MPA area
 vector C1(1,tmax)
 vector C2(1,tmax)
 //counters
 int i
 int j
LOCAL CALCS
 //cout << test << endl;
 //exit(2);
 for(i=1;i \le tmax;i++)
  S1obs(i)=S1(i);
  S2obs(i)=S2(i);
  C1(i)=C1obs(i);
  C2(i)=C2obs(i);
END_CALCS
PARAMETER SECTION
 init number log sq(1) //survey catchability
 init_number log_K //carrying capacity
 init_number log_r(1) //growth coefficient
 init_number log_prop_B0 //B0 as a proportion of K (one less parameter)
 //init_number log_B0(1) //initial biomass
 init_number log_zest(1) //estimated value of migration rate
                     //predicted biomass in non-MPA area
 vector B1(1,tmax)
 vector B2(1.tmax)
                     //Predicted biomass in MPA area
 vector BT(1,tmax)
                      //Predicted biomass of 2 areas combined
 vector S1 pred(1,tmax) //Predicted survey catch in non-MPA
 vector S2_pred(1,tmax) //Predicted survey catch in MPA
 vector F1(1,tmax)
                     //Annual fishing rate in non-MPA
 vector F2(1,tmax)
                     //Annual fishing rate in MPA
```

```
number sq
              //survey catchability
 number K
              //carrying capacity
             //growth coefficient
 number r
 number B0
             //initial biomass
 number Bpen //penalty on negative biomass
 number zest //estimated value of migration rate
 number SS
              //sum of squares used in objective function
 objective_function_value f
LOCAL_CALCS
 //starting values are correct from the data-generating model
 \log_{\text{sq}} = \log(0.005);
 \log_K = \log(1000.);
 log r = log(0.2);
 \log_{prop_B0=\log(0.9)};
 log_zest=log(z);
//\log_B0=\log(900.);
PROCEDURE_SECTION
//convert all parameters back from log scale
 sq=exp(log_sq);
 K=\exp(\log_K);
 r=exp(log_r);
 B0=exp(log_prop_B0)*K;
 zest=exp(log zest);
//cout << B0 << " " << m << endl;
//exit(2);
//fill in first year of biomass vector
 B1(1)=B0*(1.-m);
 B2(1)=B0*m;
 BT(1)=B1(1)+B2(1);
 Bpen=0.;
//cout << " " << B2(1) << endl;
//exit(2);
 //fill in rest of biomass vectors
 for(i=1;i < tmax;i++)
```

```
B1(i+1)=B1(i)+(r*B1(i)*(1.-(B1(i)/(K*(1.-m)))))+(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)))-(zest*m*(((1.-m)/m)*B2(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1(i)-B1
C1(i);
              B2(i+1)=B2(i)+r*B2(i)*(1.-(B2(i)/(K*m)))+zest*(1.-m)*((m/(1.-m))*B1(i)-B2(i))-(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m))*(m/(1.-m
C2(i);
            BT(i+1)=B1(i+1)+B2(i+1);
            //cout << "biomass vectors" << endl;
            //exit(2);
            //penalty so biomass will not go negative in the final estimation
            if(B1(i+1)<0.)
                   Bpen+=square(B1(i+1));
                   B1(i+1)=0.1;
            if(B2(i+1)<0.)
                   Bpen+=square(B2(i+1));
                   B2(i+1)=0.1;
            //cout << "B penalty" << endl;
            //exit(2);
       }
     //cout << B1 << endl;
     //cout << B2 << endl;
     //exit(2);
     //fill in survey index values
      S1 pred=B1*sq;
     S2_pred=B2*sq;
     //calculate exploitation rate
     F1=elem_div(C1,B1);
     F2=elem_div(C2,B2);
     //likelihood function
     SS = norm2(log(S1\_pred) - log(S1obs)) + norm2(log(S2\_pred) - log(S2obs));
     f = double(tmax)*0.5*log(SS)+Bpen;
      /*
     cout << "B1true B1 B1diff B2true B2 B2diff" << endl;
     for(i=1;i \le tmax;i++)
```

```
cout << B1true(i) << " " << B1(i) << " " << B1(i)-B1true(i) << " " << B2true(i) << " "
<< B2(i) << " " << B2(i)-B2true(i) << endl;
 cout << f << " " << SS << endl;
 exit(3);
 */
FUNCTION write_output
 //error in total biomass
 ofstream ofs("2areaerr.txt",ios::app);
  ofs << z << " " << elem_div(BT-BTtrue,BTtrue) << endl;
 //estimated biomass in both areas, not error
 ofstream bio("2areabiomass.txt",ios::app);
  bio << z << " " << B1 << " " << B2 << endl;
 //error in the estimated parameters
 ofstream res("2arearesult.txt",ios::app);
  res << z << " " << m << " " << (r-0.4)/0.4 << " " << (K-1000)/1000 << " " << (sq-
0.005)/0.005 << endl;
REPORT_SECTION
 write_output();
 report << "B1true B1 B1diff B2true B2 B2diff" << endl;
 for(i=1;i \le tmax;i++)
  report << B1true(i) << " " << B1(i) << " " << B1(i)-B1true(i) << " " << B2true(i) << "
" << B2(i) << " " << B2(i)-B2true(i) << endl;
 */
```

Spatially-Aggregate Estimating Model

//Jennifer Barkman

```
//Chapter 2 1-Area Estimation Surplus Production Model
//Created June 30, 2010
// Last edited August 4, 2010
DATA SECTION
 init_int tmax
                      //number of years of data
 init number m
                        //proportion of area that is MPA
 init_number z
                       //migration rate
 init_vector BTtrue(1,tmax) //Biomass in total area
 init_vector CTobs(1,tmax) //Catch in total area
 init_vector ST(1,tmax)
                          //survey catch from total area
 init\_vector test(1,3)
 vector STobs(1,tmax) //survey catch for total area
 vector CT(1,tmax) //Total Catch for total area
 int i
 int j
LOCAL_CALCS
 //cout << test << endl;
 //exit(2);
 for(i=1;i \le tmax;i++)
  STobs(i)=ST(i);
  CT(i)=CTobs(i);
  //cout << CTobs << endl;
  //cout << CT << endl;
  //exit(2);
END_CALCS
PARAMETER SECTION
 init_number log_sq(1) //survey catchability
 init_number log_K(1) //carrying capacity
 init_number log_r(1) //growth coefficient
 //init_number log_B0(-1) //initial biomass
 init_number log_prop_B0(1) //B0 as a proportion of K
 vector BT(1,tmax)
 vector ST_pred(1,tmax)
 vector FT(1,tmax)
```

```
number sq //survey catchability
 number K
              //carrying capacity
 number r
             //growth coefficient
 number B0
             //initial biomass
 number Bpen //penalty on negative biomass
 number SS
 objective_function_value f
LOCAL_CALCS
 \log_{q}=\log(0.005);
 log_K=log(1000.);
 \log_r = \log(0.2);
 \log_{prop_B0=\log(0.9)};
 //\log_B0 = \log(0.9 * \exp(\log_K));
PROCEDURE_SECTION
//convert all parameters back from log scale
 sq=exp(log_sq);
 K=\exp(\log_K);
 r = \exp(\log_r);
 B0=K*exp(log_prop_B0);
//cout << B0 << " " << m << endl;
//exit(2);
 //fill in first year of biomass vector
 BT(1)=B0;
 Bpen=0.;
//cout << " " << BT(1) << endl;
//exit(2);
 //fill in rest of biomass vectors
 for(i=1;i < tmax;i++)
  BT(i+1)=BT(i)+r*BT(i)*(1.-(BT(i)/K))-CT(i);
  if(BT(i+1)<0.)
   Bpen+=square(BT(i+1));
```

```
BT(i+1)=0.1;
  //cout << "B penalty" << endl;
  //exit(2);
 //fill in survey index values
 ST_pred=BT*sq;
//calculate exploitation rate
 FT=elem_div(CT,BT);
 //likelihood function
 SS=norm2(log(ST_pred)-log(STobs));
 f=double(tmax)*0.5*log(SS)+Bpen;
 /*
 cout << "BTtrue BT" << endl;</pre>
 for(i=1;i \le tmax;i++)
  cout << BTtrue(i) << " " << BT(i) << " " << BT(i)-BTtrue(i) << endl;
 cout << f << " " << SS << endl;
 exit(3);
 */
FUNCTION write_output
 ofstream ofs("lareaerr.txt",ios::app);
  ofs << z << " " << elem_div(BT-BTtrue,BTtrue) << " " << endl;
 ofstream bio("lareabiomass.txt",ios::app);
  bio << z << " " << m << " " << BT << endl:
 ofstream res("1arearesult.txt",ios::app);
  res << z << " " << m << " " << (r-0.4)/0.4 << " " << (K-1000)/1000 << " " << (sq-
0.005)/0.005 << endl;
 }
REPORT_SECTION
```

```
write\_output(); $$/*$ report << "B1true B1 B1diff B2true B2 B2diff" << endl; $$for(i=1;i<=tmax;i++)$ {    report << BTtrue(i) << " " << BT(i) << " " << BT(i)-BTtrue(i) << " " << endl; } $$} */
```

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