

ABSTRACT

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ASSESSMENT TOOLS FOR EASTERN
OYSTER IN CHESAPEAKE BAY

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Decreasing abundance of the eastern oyster *Crassostrea virginica* in Chesapeake Bay is of concern because of its ecological, economic, and cultural importance. The objective of my study was to develop methods for conducting stock assessments of eastern oysters in Maryland waters of Chesapeake Bay that estimate abundance, recruitment, and fishing mortality at regional scales. First, I evaluated how spatial patterns in autocorrelation of recruitment and adult relative density varied over time by fitting semivariogram models to survey data for each year. This information was then used to determine appropriate scales for my second objective which was to develop a stage-based model for the lower Potomac River using data from the Maryland Department of Natural Resources fall dredge survey and fishery data from the Potomac River Fisheries Commission. Estimated abundance declined to approximately 39% of that in 1990. The analyses will provide a platform for regional management of eastern oysters.

DEVELOPING SPATIALLY-EXPLICIT ASSESSMENT TOOLS FOR EASTERN
OYSTER IN CHESAPEAKE BAY

By

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Chapter 1: Introduction

The eastern oyster (*Crassostrea virginica*) once supported an historically important fishery in North America. This was especially true in Maryland where in the late 1800's the state was the greatest oyster-producing region in the world. During this period, landings from Maryland comprised about 40% of the total U.S. oyster harvest. Maryland's oyster industry also employed 20% of the total fishermen in the U.S. making it one of the largest industries at that time (Kennedy and Breisch 1983; Rothschild et al. 1994). However, abundance of the eastern oyster (hereafter oyster) in Chesapeake Bay has declined steadily since the start of commercial fishing (Kimmel and Newell 2007). Harvest records begin around 1839 and show a peak in 1884-1885 at 15,000,000 MD bushels per year, although today's harvests remain far below these historical levels (Kennedy and Breisch 1983; Rothschild et al. 1994). Current harvests are at 1% of the levels reported 40 years ago, and spawning stock biomass is less than 0.15% of unexploited levels (Rothschild et al. 1994; Wilberg et al. *in review*).

Oysters were extremely abundant when the first European settlers colonized the Chesapeake Bay region. When the first settlers came to Chesapeake Bay, the oyster reefs were so large they created an impediment for ships sailing the bay, with some reefs even breaking the surface of the water. Concern about population decline was expressed as early as 1875 following a decline in harvest and again in 1900 when market sized oysters became depleted before the end of the fishing season (Kennedy and Breisch 1983; Rothschild et al. 1994). In 1936, a Maryland oyster commission reported overfishing, export of oyster seed to out-of-state planters, failure to return

shell to oyster bars and harvesting of small oysters as the culprits of oyster decline (Rothschild et al. 1994). Rothschild et al. (1994) also showed that overfishing, which takes place when fishing activities reduce fish stocks below an acceptable level, occurred from the early nineteenth century to the 1990s, which has had a detrimental effect on the population and was sufficiently intense to reduce the population. The other potential effects of overfishing include growth overfishing which is when oysters are harvested at an average size that is smaller than the size that would produce the maximum yield per recruit and recruitment overfishing which is when the mature adult population is depleted to a level where it no longer has the reproductive capacity to replenish itself. Both of these types of overfishing may be occurring within Maryland.

Disease is also a significant source of mortality in oysters. The two main diseases affecting the oyster population in the Chesapeake Bay are *Perkinsus marinus* (Dermo) and *Haplosporidium nelsoni* (MSX). Dermo is caused by a protozoan parasite, which was first documented in the 1940s in the Gulf of Mexico. It was later found in Chesapeake Bay in 1949 and has increased in importance since the mid 1980s. Initial infections are typically observed in July and peak prevalence (the percent proportion of infected oysters in the survey annually), intensity (averaged categorical infection intensities for all survey oysters annually), and mortality are observed in September and October (Tarnowski 2007). MSX was first documented in 1957 in Delaware Bay and the disease was found in the lower Chesapeake Bay in 1959. Oysters become infected from mid-May through October, and infections develop rapidly and result in mortalities (up to 88% in areas of high salinity in dry

years; Vølstad et al. 2008) from July through October (Gosselin and Qian 1997, Kennedy and Breisch 1983, Paynter and Burreson 1991). Higher salinities and warmer waters favor both MSX and Dermo, while lower salinities reduce the prevalence of MSX and may decrease the prevalence and intensity of Dermo infections.

Prevalence of Dermo and MSX may be decreasing in recent years (2003-2006); Maryland DNR found that the diseases remained suppressed since record high levels in 2002. Although widely distributed, oyster diseases in general have been slow to rebound despite modest streamflows and salinity increases during 2005- 2006. MSX disease was only found in two localized areas, Tangier Sound and north of Point Lookout. In contrast, Dermo was found on almost every oyster bar tested for the disease, but mostly at below average prevalences and intensities. Nevertheless, the sustained widespread distribution of Dermo, even at low to moderate intensity levels, indicates that it remains enzootic throughout most of the tidal waters of the state (Tarnowski 2007).

Recruitment of the oyster can vary spatially within the bay, and oyster recruitment in Chesapeake Bay is strongly influenced by environmental factors, such as temperature and salinity which are spatial dynamic throughout the bay (Kennedy 1991; Shumway 1996). The planktonic nature of oyster larvae combined with their sessile post settlement life history can complicate efforts to link recruitment with the spawning stock that produced them. Oysters have pelagic larvae with the capability of lateral dispersal so that separate bars are able to recruit to themselves or to nearby bars. Therefore, spat set on a bar are not necessarily the result of reproductive efforts

of the spawning stock biomass from that bar, which suggests normal stock-recruitment assessments should not be applied to individual bars, and individual bars should not be treated as separate populations. To further complicate matters, because of numerous factors affecting different population processes such as physical processes, environmental variables and habitat, it is hard to define the scale at which oyster populations operate. However, the entire bay should not be treated as one large population if local dynamics are of interest. So the question is how do we define an oyster population in the Chesapeake Bay and what spatial scale do we use? Currently, the spatial scale of recruitment variability in oysters in Maryland has yet to be clearly defined (Kimmel and Newell 2007; Mann and Powell 2007; North et al. 2010).

Management of Maryland's declining oyster population currently includes application of license limits, spatial rotational harvest, sanctuaries, and spatial and temporal restrictions on tonging, sail dredging, power dredging, and diving. The fishing season is from October to December with a minimum legal size of 76 mm from the hinge to the lip. It is estimated that about 80% of the harvest comes from areas that Maryland Department of Natural Resources has planted with seed, usually from a hatchery, and/or shell (Wieland 2007) as part of their restoration program. Reserves are areas where restoration type efforts are undertaken, and then the site is closed to fishing for five years. At the end of the five-year closure, the site is opened for a managed harvest, and then when the set amount is harvested from the site it will be closed again (Wieland 2007). Managed reserve areas are supplemented by sanctuaries, where no harvest is allowed. The MD DNR currently has 19 reserves and 31 sanctuary areas (Tarnowski 2005). Understanding the dynamics of a population is

an important for developing accurate models and making effective management decisions. A better understanding of oyster dynamics, especially at smaller spatial scales, can help guide managers in stocking juvenile oysters and creating management areas and sanctuaries in areas where restoration efforts would be most successful.

With these goals in mind, the objectives of my thesis were first to determine a spatial scale at which oyster dynamics were similar in the Maryland portion of the Chesapeake Bay and evaluate whether spatial dynamics changed over time, and once an appropriate scale was determined conduct a regional stock assessment of eastern oysters to support spatially-explicit fishery management and restoration.

In Chapter 2, I explored the temporal and spatial scale of correlations in the Maryland Department of Natural Resources fall dredge survey data from Maryland waters of Chesapeake Bay and the Potomac River to determine appropriate scales for modeling oyster population dynamics above the bar level. Specifically, I quantified the spatial scale of autocorrelation in relative density of spat and adult oysters. I also determined whether this spatial scale exhibited any temporal variability. To characterize spatial patterns in oyster recruitment and adult indices of density, I conducted semivariogram analyses for each year during 1980-2008 and used the semi-variogram models to create interpolated maps in MATLAB with ordinary kriging (Jensen et al 2006).

In Chapter 3, I developed a framework that used a stage-based model for the lower Potomac River with survey and fishery data from the Maryland Department of Natural Resources and the Potomac River Fisheries Commission. I chose the lower

Potomac River as my study area because of the numerous sources of information available as well as the historical importance of the oyster fishery within this region. To characterize the population dynamics of oysters in the lower Potomac River, I used a stage-structured model based on the three oyster size-age categories, spat (individuals less than one year old), small (individuals older than one year and less than 76 mm) and market (individuals 76 mm and greater), for live oysters and small and market size categories for dead oysters (i.e., boxes or articulated valves). The model included effects of fishing and time-varying natural mortality and estimated abundance, exploitation and natural mortality of the population during 1990-2008. The abundance in each stage changed due to growth, fishing, and natural mortality.

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Chapter 2: Spatial autocorrelation in recruitment and adult density of eastern oyster *Crassostrea virginica* in Maryland waters of Chesapeake Bay, 1990-2008

Abstract

Understanding spatial and temporal variability of population dynamics is important for determining placement of marine protected areas and spatial fishery regulations, especially for sessile species. Decreasing abundance of the eastern oyster *Crassostrea virginica* in Chesapeake Bay is of concern because of its ecological, economic, and cultural importance. However, spatial patterns of population dynamics and how these patterns have changed over time have been relatively unexplored. Using data from the Maryland Department of Natural Resources fall dredge survey; I evaluated how spatial patterns in autocorrelation of recruitment and adult relative density varied over time by fitting semivariogram models to survey catch rate data for each year. Across years, oyster bars in close proximity to one another had more similar dynamics and over time the oyster bar dynamics have become less similar. Oyster bar dynamics are similar at distances ≤ 25 -35 km and have been becoming more similar over time at this scale. This information can be used to determine appropriate scales for stock assessment models and can help guide spatial management of eastern oysters in Chesapeake Bay.

Introduction

The eastern oyster (*Crassostrea virginica*) once supported a historically important fishery in North America. This was especially true in Maryland where in the late 1800's the state was the greatest oyster-producing region in the world and comprised about 40 percent of the total U.S. oyster harvest (Kennedy and Breisch 1983). During this period, Maryland's oyster industry also employed about 20% of the fishermen in the U.S. making it one of the largest industries at that time (Kennedy and Breisch 1983; Rothschild et al. 1994). However, the abundance of the oyster in Chesapeake Bay has declined steadily since the start of commercial fishing (Rothschild et al. 1994; Kimmel and Newell 2007), and current harvests are at 1% of the levels reported 40 years ago.

Population processes, such as mortality and recruitment, of oysters can be highly variable in space and time. Mortality of oysters within the Chesapeake Bay has been attributed to disease and environmental factors which vary spatially (Ford et al. 2006; Vølstad et al. 2008). Recruitment of new individuals to the population is key to maintaining a stable and commercially-exploitable population. Causes of recruitment variability include a combination of habitat loss, reduced abundance of adults, predation, food availability and environmental factors such as temperature, salinity (Kimmel and Newell 2007). Temperature and salinity vary greatly spatially and temporally throughout the bay. Temperature is particularly known to influence oyster spawning, as well as, growth and condition. The most favorable temperature for oysters to spawn is between 20 and 26.6 °C and the most favorable temperature for

settlement is between 19 and 24 °C (Kennedy 1996) although the most favorable temperature for adult oyster survival is thought to be between 27.5 and 32.5 °C (Davis and Calabrese, 1964). Salinity also influences growth, condition and mortality (Shumway 1996). The optimum salinity ranges for larvae and juvenile growth are 15-22.5 ‰ and 12-27 ‰, respectively (Shumway 1996). Over the past few decades, recruitment of oysters in Chesapeake Bay has declined dramatically (Meritt 1977, Mann and Powell 2007; Kimmel and Newell 2007). Oysters are broadcast spawners, and their larvae are planktonic until settlement (Kennedy 1996). This type of reproductive strategy means recruitment is often sporadic because the resulting larvae are vulnerable to physical processes, changes in environmental parameters as well as stress from anthropogenic factors (Kennedy 1996). The degradation of vertical reef structure from fishing gears has also increased siltation in and around oyster bars, covering and reducing habitat for spat settlement (Powell et al. 2001).

Understanding the dynamics of a population is important for developing accurate models and making effective management decisions. Oysters have pelagic larvae with the capability of lateral dispersal so that separate bars are able to recruit to themselves or to nearby bar, combined with their sessile post-settlement life history can complicate efforts to link recruitment with the spawning stock that produced them. Therefore, spat (oysters less than one year old; i.e. young of year) set on a bar are not necessarily the result of reproductive efforts of the spawning stock of that bar, which suggests normal stock-recruitment assessments should not be applied to individual bars. Thus, it is difficult to define an oyster population in the Chesapeake Bay. It has been demonstrated that population processes of the eastern oyster vary

spatially within the bay (North et al. 2010) and eastern oyster recruitment in Chesapeake Bay is strongly influenced by environmental factors, such as temperature and salinity which are spatial dynamic throughout the bay (Kennedy 1991; Shumway 1996). Currently the spatial scale of recruitment variability in oyster population have yet to be clearly defined (Kimmel and Newell 2007; Mann and Powell 2007, North et al. 2010).

In December 2009, Maryland's governor proposed a more than doubling of the state's oyster sanctuaries, concentrating on areas with high salinity and fast growth. Also, the federal government has set a goal of restoring self-sustaining oyster populations in 20 Chesapeake tributaries by 2025 (Chesapeake Bay Foundation 2010). In order to achieve these goals managers need to think of oyster reefs as networks that depend on each other to be sustainable over time (Chesapeake Bay Foundation 2010) and determine the best areas within the bay for the type of restoration implemented (North et al. 2010). Given the new goals, a better understanding of spatial processes (e.g., interdependence of the oyster reef networks) is necessary to give managers a more accurate depiction of scale of the processes affecting the population. Changes in scale of population processes over time can be used as indicators the health of a population as well as predictors of management effectiveness.

My objective was to determine a spatial scale in which eastern oyster population dynamics were similar in the Maryland portion of the Chesapeake Bay and evaluate whether spatial dynamics changed over time. I explored the temporal and spatial scale of correlations in the fall dredge survey data from Maryland waters of

Chesapeake Bay and the Potomac River to determine appropriate scales for modeling oyster population dynamics above the bar level. Specifically, I examined whether patterns of spatial autocorrelation in relative density of spat and adult (small and market categories combined) oysters are evident and have changed over time.

Methods

Data

I used data from the Maryland Department of Natural Resources (DNR) fall dredge survey from 1980-2008. I chose this period because of the completeness of the data set. The Maryland DNR has conducted an annual fall dredge survey since 1939 in areas of known oyster habitat. Currently, the survey samples about 300 to 400 bars each fall between October and November. Sampled bars include natural oyster bars, shell and seed plantings, sanctuaries, power dredge zones, and experimental sites. The survey is conducted with a standard oyster dredge consisting of a metal rod frame 2.72 m across. The dredge is towed along the bottom once or twice at each site depending on the amount and quality of the material collected. A half bushel (a Maryland oyster bushel is approximately 46 L) sample is taken at most sites. Two half bushel samples at Key (53 bars used as a basis of an annual spatfall intensity index) and Disease Bar (43 bars established for obtaining standardized parasite prevalence and intensity data) sites. All oysters collected are classified as market (>76 mm), small (older than one year but <76 mm) and spat (less than one year old) and are reported as number per bushel of dredge material (Tarnowski 2003). I interpreted the oyster dredge survey data as an index of density per unit habitat. In order for the dredge survey to provide an index of density catchability of oysters and

catchability of clutch must be constant on average over time. This then allows the number of oysters per bushel to be proportional to the number of oysters per unit habitat, which means the catches are proportional to density per unit habitat. The index is specific to density on oyster habitat because the dredge survey actively samples in areas of known oyster habitat and collects habitat (oyster shell). Other dredge surveys have been shown to provide information on relative density (Mann et al. 2004; Powell et al. 2007). Only bars with an associated GPS location that were sampled over numerous years and were sampled in the same years were included. A total of 255 bars were used in this analysis.

Calculations

To characterize spatial patterns in oyster recruitment and adult indices of density, I conducted semivariogram analyses for each year during 1980-2008. I used linear regressions of coordinate values against the indices of density to test if the data had any north-south or east-west trends (for all years for recruitment and adult oysters). No trends were apparent, so I did not detrend the data. The adult and recruitment relative density were analyzed separately. The shortest in-water distance between the centroid of each bar was calculated with a least-cost path analysis (Jensen et al. 2006) in ArcView (ESRI Corporation, Redlands, California, v9.1). Once the distances between individual bars were determined, I used MATLAB (The Mathworks, Cambridge, MA, v7.0.1) to calculate the semi-variance for each combination of bars for each year to characterize the spatial covariance of recruitment and adult indices of density among bars. The semi-variance was half the variance of

the of indices of density between all observed points a specific distance apart, and is given by

$$\hat{\gamma}(h) = \frac{1}{2} \cdot \frac{1}{n(h)} \sum_{i=1}^{n(h)} (z(x_i + h) - z(x_i))^2,$$

where x was the location of an observation, z was relative density at a particular location, h was the distance between points, and $n(h)$ is the number of paired observations at a distance of h (Bachmaier and Backes 2008). After the semi-variances were calculated, I fitted semi-variograms for each year. A semi-variogram describes semi-variance as a function of distance between the observations. After fitting numerous models, I chose a spherical semi-variogram model because it was able to fit the most semi-variograms the best. I then fit the model to each of the semi-variograms in AD Model Builder to compare across years,

$$\gamma(h, \theta) = \begin{cases} (C_o + C_s) \left(1.5 \left(\frac{h}{a}\right) - 0.5 \left(\frac{h}{a}\right)^3\right), & h \leq a \\ C_o + C_s, & h > a \end{cases},$$

where C_o is the nugget, $C_o + C_s$ is the sill, and a is the range. I fitted the model to the empirical semi-variogram to estimate parameter values for the range, sill and nugget. To test for trends in semi-variograms over time, I fitted simple linear regressions of both nugget and range parameters for indices of density of adults and recruitment against time. In some years, parameter estimates were not uniquely identifiable.

The semi-variogram models were used to create interpolated maps in MATLAB with ordinary kriging (Jensen et al 2006). Kriging is a geostatistical

technique that interpolates the value of a random field (e.g., the density of oysters as a function of the geographic location) at an unobserved location from observations of values at nearby locations (e.g., a grid of 3000 predicted values evenly spaced one km apart over the entire study area). The interpolated values were then loaded into ArcMap, and an inverse distance weighted tool was used to create index of density maps for each year in order to visually observe spatial and temporal patterns within and between years.

Results

Semi-variogram

Semi-variance for adult and recruitment indices of density showed the expected pattern in which the semi-variance increases with distance and levels out after about 30 km in most years (Appendices 1 and 2). I was unable to estimate unique sets of parameter estimates for 1980, 1984, 1985, 1994, 1997, 2000 and 2007 for recruitment and 1980, 1982, 1987 and 1998 for the adults. These years were excluded from the regressions. The range parameter for the semi-variograms of recruitment density decreased significantly over time ($r^2=0.31$, $p = 0.007$; Fig. 2.1a). The trend for the nugget parameter was not significant ($r^2=0.13$, $p = 0.106$; Fig. 2.1b). The semi-variograms of adult index of density had significant negative trends over time for both the range and nugget parameters (range: $r^2=0.31$, $p = 0.004$; nugget: $r^2=0.44$, $p < 0.001$; Figs. 2.1c and 2.1d respectively). The sill parameter of semi-variograms decreased over time for both recruitment and adult relative density (range: $r^2=0.1653$, $p = 0.0604$; nugget: $r^2=0.4504$, $p < 0.001$; Figs. 2.1e and 2.1f respectively), which reflected an overall decrease in density during 1980-2009. The

nugget and sill parameters for recruitment and adult relative density increased in the later years of each time series.

For all three parameters, relationships for adult relative density had more significant p-values than for recruitment. The changes in the parameters of the semi-variograms over time indicated that adult and recruitment relative density has become more similar throughout the Bay and that the distance over which adult and recruitment density is highly autocorrelated decreased during 1980-2009. Oyster bars had similar recruitment and adult dynamics at distances ≤ 25 -35 km. The average range for recruitment was 27.6 km and the average range for adults was 34.4 km.

Spatial Patterns

The recruitment relative density maps showed a large amount of spatial and temporal variability (Fig. 2.2.). Oyster recruitment decreased from 1980 to 2008, except for a large spike in recruitment relative density in 1997 (Fig. 2.3). The early 1980s had the highest mean density of recruits and the mid 1990s and early 2000s had the lowest mean relative density of recruits (Figure 2.4). Mean relative density was below 50 recruits per bushel from 1989 to 1991 and then again in 1993 (Figure 2.4a). Mean relative density was below 10 recruits per bushel during 1995–2006; there was a slight increase at the end of the time series to just over 20 recruits per bushel. Throughout most of time series, the bulk of the recruitment was concentrated in the southern part of the study area in Tangier Sound and the mouth of the Potomac River. The areas of high relative density were more evenly dispersed throughout Chesapeake Bay in the 1980s than in later years (Figure.2.5a).

Adult relative density was also spatially and temporally variable, although less so than recruitment. Like recruitment, adult relative density decreased substantially over time (Fig. 2.5). The earlier years (1980-1990) had the highest relative density and the high relative density areas were more evenly distributed than in later years (Fig. 2.5b). The mid 1990s and early 2000s had the largest decrease in mean relative density. The mean relative density was below 50 adults per bushel during 1993-2006, and there was a slight increase at the end of the time series to over 70 adults per bushel. The year with the highest mean relative density was 1983 with a density of 168 adults per bushel versus 2005, which had the lowest mean relative density of 2 adults per bushel. Adult relative density did not show the same pattern of concentrated density in the lower portion of the bay but instead was more evenly distributed throughout the bay than for recruitment with high density in Tangier Sound, the mouth of the Potomac River, and the Choptank River.

Discussion

Recruitment and adult relative densities varied substantially over time and among areas within the bay. Both had a distinct decrease in oyster recruitment and adult relative density during 1980-2008. Earlier years in the time series had the highest maximum densities and the high density areas were more dispersed throughout the study area than the later years. The maps illustrated a large decline in recruitment relative density from the upper, middle and tributaries of the bay starting in 1980s and continuing to retreat down bay in the early 1990s. Recruitment relative density has been concentrated in the lower portion of the Maryland portion of the bay in since the late 1990s. The adult relative density maps also exhibit a similar pattern.

The decrease of oyster abundance in Chesapeake Bay has been attributed to overfishing and disease (Kennedy and Breisch 1983; Rothschild et al. 1994). Wilberg et al. (in review) found a more than 92% decline in estimated abundance between 1980 and 2008 under the stresses of fishing and disease. This pattern agrees with the large decrease in oyster density showed by the maps in the mid 1990s and early 2000s. The main causes of the temporal decline may be overfishing and disease, but density declined at different rates in different regions.

The negative trend in recruitment and adult relative density could be due to spatial changes in environmental conditions throughout the bay. The bay has numerous spatial regions that differ in salinity, dissolved oxygen, and temperature. Kimmel and Newell (2007) found recruitment was positively related to increases in salinity and temperature. Southworth and Mann (2004) found similar results relating the importance of salinity and temperature to recruitment success. They suggest that historically, before high rates of fishing mortality, habitat degradation, and parasitic disease, a large portion of the recruits were spawned in more saline, lower river environments (favorable habitat conditions), which were then for a source of larvae for oyster bars farther upstream (less favorable habitat conditions). The high rates of fishing mortality, habitat degradation, and parasitic disease seem to be limiting oysters to these productive areas down the bay where recruitment is sustainable and oysters can survive and mature and this is reflected in the density maps as well as the negative trends in relative density

Based on the averaged semi-variance across all years oyster bars seem to have similar recruitment and adult dynamics at distances ≤ 25 -35 km, which is consistent

with evidence that oysters do not disperse over great distances, but rather recruit within a relatively close radius from their bar of origin (Strathmann 1974; Mann and Evans 1998). The simulated retention of released larval oysters in the Upper James River also suggests oysters do not disperse over great distances (Mann and Evans 1998). Mann and Evans (1998) found that most of the larvae from existing bars do not extend in significant numbers downstream in typical summer flow conditions, but spread out in both up and downstream directions remaining in the approximate region of their production. Similarly, North and Wazniak (2009) found self-recruitment of bars was less than 2.0% on 85% of the bars in Maryland and Virginia portions of the bay and most recruitment occurred in surrounding areas. Areas with the highest self-recruitment were the upper reaches of the tributaries and Tangier and Pocomoke Sounds. This range in which the dynamics are similar could also be reflective of the decreasing amount of available habitat, environmental factors, and the overall decline of adult oysters.

Looking at the relative density of oysters within this region one may come to conclusion that the population is beginning to recover. However, if we consider habitat loss and what its effects on abundance are, we then obtain a more accurate depiction of the overall trend of the population. Rothschild (1994) found a 36% decline in habitat area between the late 1970s and 1989-1990 and Smith et al. (2005) found a 63% decline from the late 1970s to 1999-2001. With less available, quality habitat it seems reasonable that oysters would be settling on the few remaining patches and therefore would have similar dynamics at smaller spatial scales. The decline in adult abundance also would have a similar effect. Wilberg et al. (in review)

estimated that the oyster population in the Maryland portion of the bay has declined to only 0.15% of its virgin abundance. Such a dramatic decline in oysters means there are less adult oysters to produce new recruits to bars as well as fewer adults to provide habitat for the future recruits to settle on.

The years the semi-variogram model parameters were not uniquely estimable corresponded to years with high freshwater flows and low salinity. High freshwater flow, such as freshets, and low salinity increase mortality in oysters (Thompson et al. 2006) which can cause relative density to become more similar throughout the bay, which in turn causes the semi-variogram model to be unable to estimate unique parameters. Significant freshets occurred in 1993, 1994, 1996 and 1998 and correspond with the years of the lowest recruitment density and some of the lowest years of adult density (Tarnowski 2003). Recruitment and adult relative densities also may have been affected by the high freshwater flow in 2003 and 2004 (Tarnowski 2005). The maps also show a coinciding decrease in relative density with the expansion of disease in low salinity areas as well as the 1999-2002 droughts (Tarnowski 2003). Disease became a significant source of mortality throughout much of upper Chesapeake Bay in 1986-1987 with an outbreak of Dermo causing widespread mortality in Maryland waters of Chesapeake Bay. Relative density of recruitment and adults decreased noticeably after these years.

Conclusions

The eastern oyster in the Maryland portion of the Chesapeake Bay has suffered a substantial decline since the beginning of commercial fishing. I found that the spatial patterns in recruitment and adult dynamics did change over time. The

changes in the parameters of the semi-variograms over time indicate that oyster density has become more similar throughout the Bay and that the distance over which oyster density is highly autocorrelated contracted during 1980-2009. In both cases, relationships for adult life stages were stronger than for the new recruits. I also found the recruitment and adult density showed a large amount of spatial and temporal variability, and periods of rapid change corresponded to disease outbreaks and drought periods. Recruitment decreased substantially from the beginning of the time series to the end, particularly in upper Chesapeake Bay. This study can help guide managers in stocking juvenile oysters and creating management areas.

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Figures

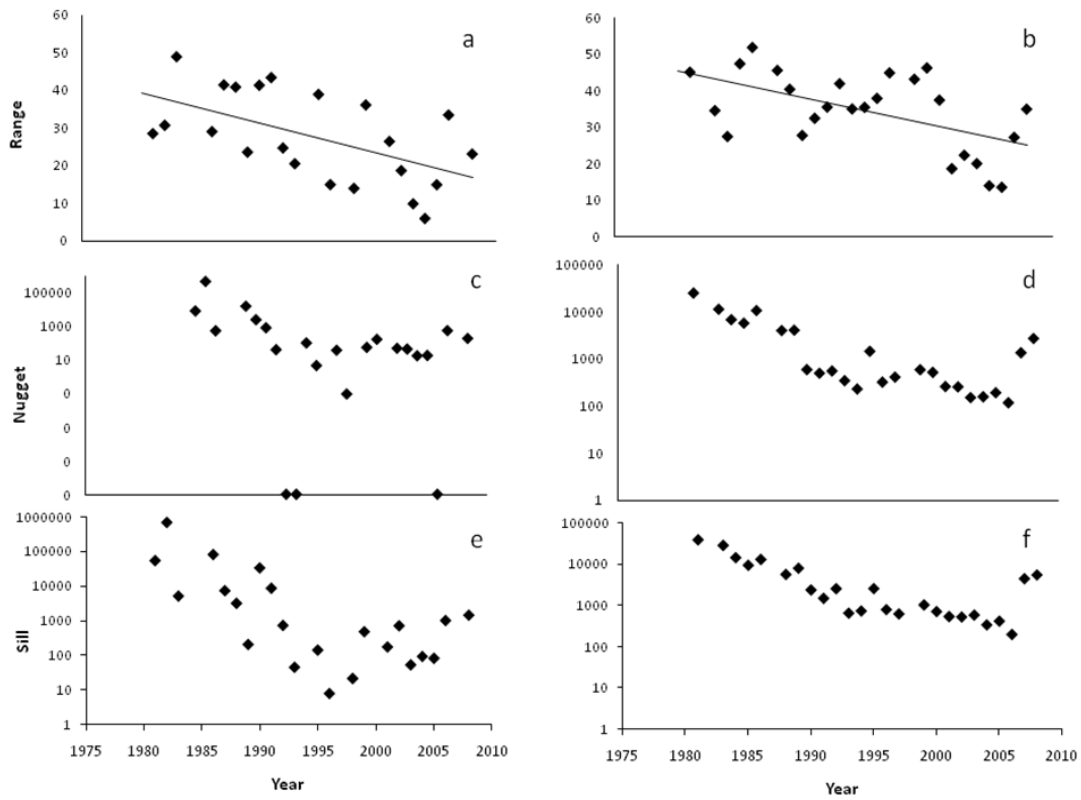


Figure 2.1. The top two panels are the estimated range parameters for recruitment (a) and adult (b) semi-variograms (points) over time and the best linear fit (line). The middle two panels are the estimated nugget parameters for recruitment (c) and adult (d) semi-variograms over time on a log scale. The bottom two panels are the estimated sill parameters for recruitment (e) and adult (f) semi-variograms over time on a log scale.

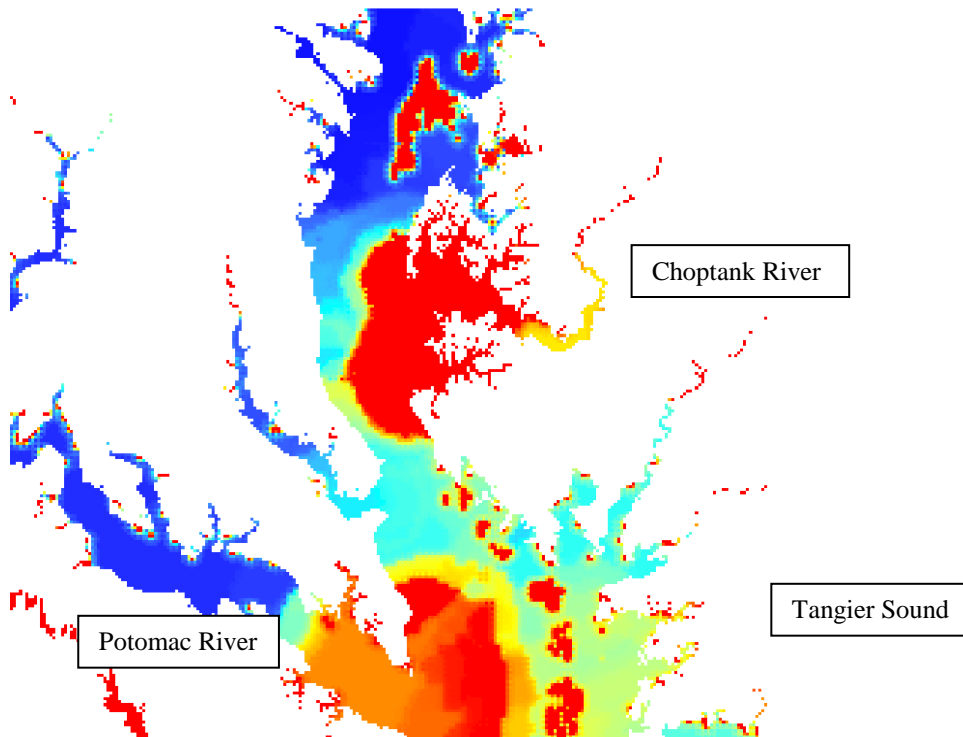


Figure 2.2. An example of a kriged map of recruitment density with areas of interest mentioned in the paper highlighted.

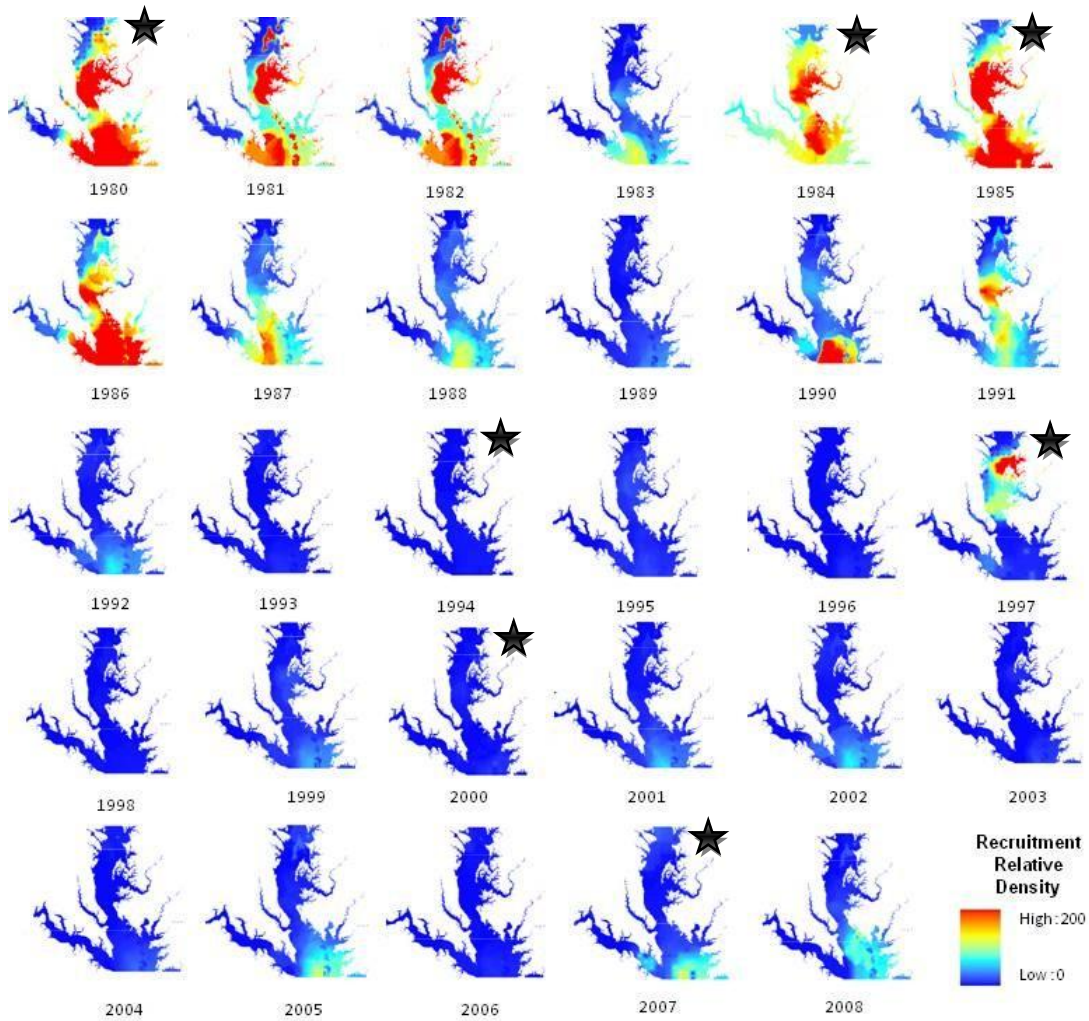


Figure 2.3. Kriged maps of recruitment density, years (from right to left, top to bottom). Stars indicate years that did not have unique parameter values.

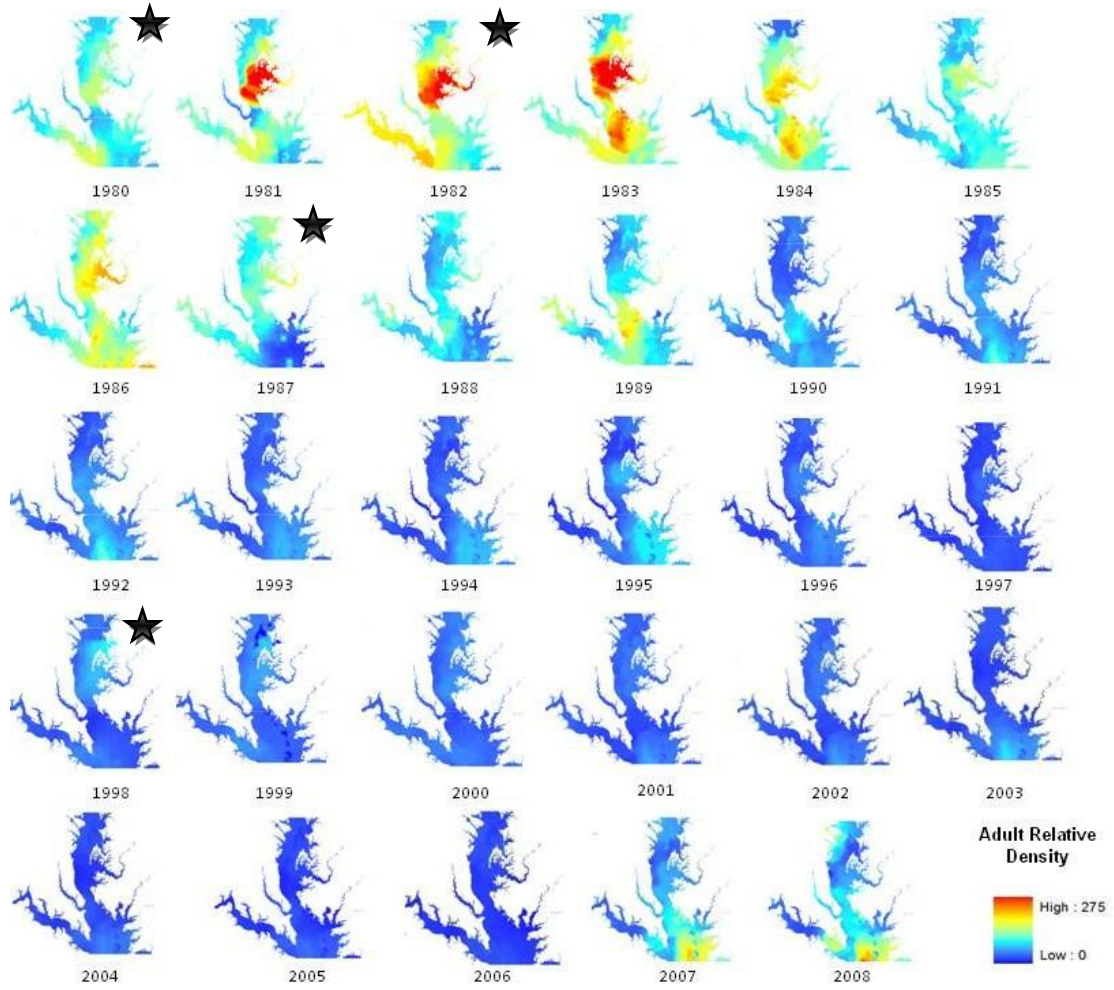


Figure 2.4. Kriged maps of adult density, years (from right to left, top to bottom). Stars indicate years that did not have unique parameter values.

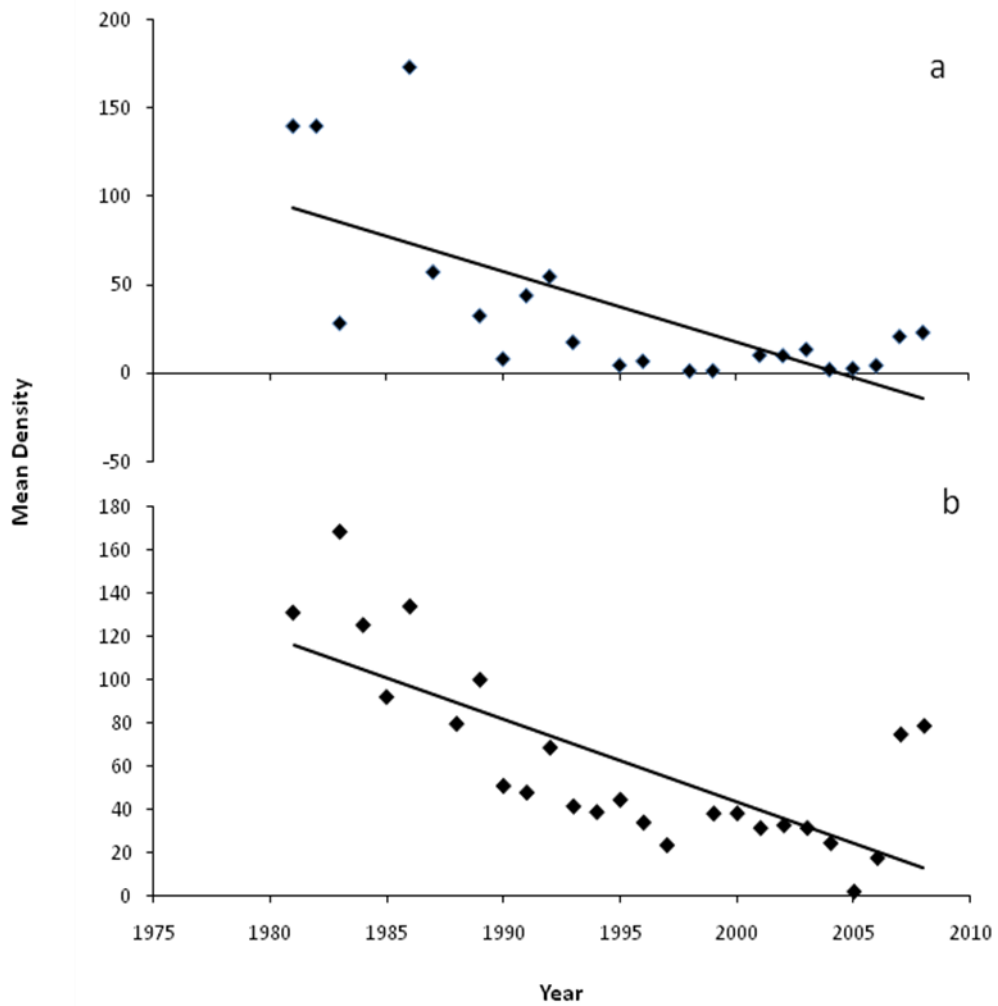


Figure 2.5. Estimated mean relative density (number per bushel) for recruitment (a) and adult (b) (points) over time and the best linear fit (line).

Chapter 3: An assessment of eastern oyster in the lower Potomac River during 1990-2008

Abstract

The decreasing abundance of the eastern oyster *Crassostrea virginica* in Chesapeake Bay is of concern because of its ecological, economic, and cultural importance. Currently eastern oysters are managed as a single population throughout Maryland except for areas that are closed to fishing. However, environmental conditions change spatially across a north-south gradient throughout the bay and have been shown to affect recruitment and mortality. Because of this gradient, eastern oysters should be managed at a scale in which population dynamics are similar. The objective of our study was to develop and evaluate methods for conducting stock assessments of eastern oysters in Maryland waters of Chesapeake Bay that estimate abundance, recruitment, and fishing mortality at regional scales. I developed a stage-based model for the lower Potomac River using data from the Maryland Department of Natural Resources annual fall dredge survey and fishery data from the Potomac River Fisheries Commission. To characterize the population dynamics of oysters in the lower Potomac River, I used three oyster size-age categories, spat (individuals less than one year old), small (individuals older than one year and less than 76 mm) and market (individuals 76 mm and greater), for live oysters and small and market size categories for dead oysters (i.e., boxes or articulated valves). The model included effects of fishing and time-varying natural mortality and estimated abundance, exploitation and natural mortality of the population during 1990-2008. Estimated abundance showed a substantial decrease over the modeled period, and abundance declined to approximately 39% of that in 1990. The analyses will provide a platform for regional management of eastern oysters.

Introduction

Decreasing abundance of the eastern oyster *Crassostrea virginica* in Chesapeake Bay is of current concern because of its ecological, economic, and cultural importance. Oysters were extremely abundant when the first European settlers colonized the Chesapeake Bay region. At this time, oyster reefs were so large they created an impediment for ships traveling the bay (Wennersten 2007). In Maryland, harvest records begin around 1839 and Maryland's peak harvest was in the 1884-1885 season at 15,000,000 bushels (1 bushel ~ 46 L) (Kennedy and Breisch 1983; Rothschild et al. 1994). Concern about population decline was expressed as early as 1875 following a decline in harvest and again in 1900 when oyster bars were fished out before the end of the fishing season (Kennedy and Breisch 1983). In 1936, the Maryland Oyster Commission reported that the decline was caused by a high rate of fishing, export of oyster seed to out-of-state planters, failure to return shell to oyster bars, and harvesting of small oysters. Rothschild et al. (1994) estimated that overfishing occurred from the early nineteenth century to 1990. Wilberg et al. (in review) found an exploitation rate around 20% from 1990 to 2008 and that the oyster population within the Maryland portion of the bay has declined to 0.15% of their virgin levels.

Disease has also played a large role in oyster decline in the Chesapeake Bay. The two main diseases affecting the oyster population in the Chesapeake Bay are caused by protozoan parasites *Perkinsus marinus* (Dermo) and *Haplosporidium nelsoni* (MSX). Dermo was first documented in the 1940s in the Gulf of Mexico and was found in Chesapeake Bay in 1949 (Ford and Tripp 1996). Initial infections in

Chesapeake Bay are typically observed in July, and peak prevalence (the percent proportion of infected oysters in the survey annually), intensity (averaged categorical infection intensities for all survey oysters annually), and disease related mortality are observed in September and October. MSX was first documented in 1957 in Delaware Bay, and the disease was found in the lower Chesapeake Bay in 1959 (Ford and Tripp 1996). Before the mid-1980s, these diseases were found only in the southern portion of Chesapeake Bay. Oysters become infected from mid-May through October and infections develop rapidly and result in mortalities from July through October (Gosselin and Qian 1997, Kennedy and Breisch 1983, Paynter and Burreson 1991). During 1986-1987, the diseases, especially Dermo, spread into the low salinity regions of the Maryland portion of the Bay and caused widespread mortality (Andrews 1988, Burreson and Ragone Calvo 1996). Higher salinities and temperatures favor both MSX and Dermo, while lower salinities reduce the prevalence of MSX disease and may decrease, but not entirely eliminate the prevalence and/or intensity of Dermo disease (Ford and Tripp 1996).

Vølstad et al (2008) examined the effect of including disease intensity and salinity when estimating natural mortality from box count (counts of articulated shells of dead oysters) data. They found that estimated mortality rate increases consistently with increases in disease intensity and salinity. Ford et al. (2006) also found an increase in natural mortality with increasing disease in moderate to high salinity areas in Delaware Bay.

Wilberg et al. (in review) estimated a doubling in natural mortality in years corresponding with the disease outbreak in the mid-1980s and again in the late 1990s

and early 2000s. Recently, the Maryland DNR found that the disease prevalence remained suppressed during 2003-2006 following record high levels in 2002 (Tarnowski 2007). MSX disease was only found in two localized areas in 2006, Tangier Sound and north of Point Lookout. In contrast, Dermo disease was found on almost every oyster bar tested for the disease, but below the average prevalence and intensity from 1990-2006. Nevertheless, the sustained widespread distribution of *P. marinus* organisms, even at low to moderate intensity levels, indicates that Dermo disease remains enzootic throughout most of the tidal waters of the state (Tarnowski 2007).

The current management of oysters in Maryland relies on a combination of restoration and fishery management efforts. Restoration efforts include repletion, reserves and sanctuaries, and bar cleaning. The repletion program has consisted of planting oyster shell, both dredged (fossilized) and fresh (shell tax) and moving or planting seed oysters from areas of high recruitment to areas with low recruitment to supplement the populations in different areas (Kennedy and Breisch 1983). Seed oysters have historically come from the wild and oysters spawned in hatcheries. Today, most seed used in restoration efforts is produced at hatcheries. It is estimated that about 80% of the harvest comes from areas that MD DNR has planted with seed and/or shell (Wieland 2007). Reserves are areas where restoration type efforts are undertaken, and then the site is closed like a sanctuary for a period of five years. To protect the oysters, restoration sites are sometimes made into sanctuaries, where no shellfish harvest is allowed. Maryland currently has 19 reserves and 31 sanctuary areas (Tarnowski 2005). Bar cleaning also started in the 1980s and is the practice of

removing older, infected oysters from an oyster bar prior to rehabilitation in an effort to maximize the survival rates of the newly planted oyster spat by reducing their exposure to Dermo. Fishery restrictions currently includes a minimum size of 76 mm for harvest and a mix of sanctuaries and spatial and temporal restrictions on tonging, sail dredging, power dredging, and diving.

Oyster management is moving toward a more spatially-explicit framework (MDNR 2009) because of oysters' sessile juvenile and adult life stages. The proposed changes in management include increasing oyster sanctuaries to about 25 percent of the productive bottom (MD DNR 2009). Additionally, environmental conditions, such as water temperature and salinity, vary spatially across a north-south gradient throughout Chesapeake Bay and have been shown to affect recruitment, mortality and growth. Because of this gradient, eastern oysters should be managed at a scale in which population dynamics are similar. In contrast, most studies of oyster dynamics in Maryland have modeled the population without spatial structure (e.g., Rothschild et al. 1994; Wilberg et al. in review).

My objective was to conduct a regional stock assessment of eastern oysters to support spatially explicit fishery management and restoration. I developed a framework that used a stage-based model for the lower Potomac River with survey and fishery data from the Maryland Department of Natural Resources and the Potomac River Fisheries Commission. The model estimated abundance, fishing mortality and natural mortality from 1990-2008.

Methods

Study Area

The study area was the main stem of Potomac River from Ragged Point to the mouth of the River (Figure 3.1). The Potomac River is the fourth largest river on the east coast of the United States. The river is approximately 616 km long, with a drainage area of about 38,000 km² and flows into the Chesapeake Bay. Fisheries in the Potomac River are managed by the Potomac River Fisheries Commission (PRFC). The PRFC is a multi-jurisdictional compact that reflects the interests of Maryland, Virginia, and Washington, D.C. It was established in 1958 and has been the fisheries regulatory authority in the Potomac River since 1962. The PRFC is responsible for approving and implementing the rules, regulations, and licenses for the recreational and commercial fishing in the Potomac River.

Data

The data used in this study are a portion of the Maryland Department of Natural Resources fall dredge survey from 1990 to 2008 (Tarnowski 2007). The survey is conducted with a standard oyster dredge with a metal rod frame 2.72 m across. The dredge is dragged along the bottom once or twice at each site depending on the amount and quality of the material collected. A half bushel sample is taken, and the oysters are classified as market (>76 mm), small (older than one year but <76 mm) and spat (less than one year old). Two half bushel samples are taken at "disease bars" for collection of additional information, such as disease prevalence and intensity and size structure of the population (Tarnowski 2007). Dredge survey catches provide an index of density (i.e., catches are proportional to density) rather

than a direct estimates of density (Mann et al. 2004; Powell et al. 2007).). I interpreted the oyster dredge survey data as an index of density per unit habitat. In order for the dredge survey to provide an index of density catchability of oysters and catchability of clutch must be constant on average over time. This then allows the number of oysters per bushel to be proportional to the number of oysters per unit habitat, which means the catches are proportional to density per unit habitat. The index is specific to density on oyster habitat because the dredge survey actively samples in areas of known oyster habitat and collects habitat (oyster shell). Other dredge surveys have been shown to provide information on relative density (Mann et al. 2004; Powell et al. 2007).

A total of 12 bars were used in this analysis including 2 disease bars. The survey bars include Bonums, Cornfield Harbor, Currioman, Hog Island, Jones, Great Neck, Kitts, Piney Point, St. George Island, Thicket Point, Ragged Point, and Tall Timbers. Drum Point was excluded because it lacked GPS coordinates. The two disease bars were Ragged Point and Cornfield Harbor. These bars were chosen because of the amount of detailed size information available and the similarity of the surrounding environment. The selected bars each have an associated bar location and have been sampled over numerous years.

Bar-specific harvest data are reported by oystermen and oyster dealers. The PRFC requires oystermen and buyers to keep weekly catch and purchase records. The information included in the catch and purchase reports includes fishery season, date, bar name, bushels of oysters harvested or purchased, and gear type.

Standardizing Indices of Density

I developed standardized indices of density from the catch of spat, small, and market-sized live oysters and small and market boxes in Maryland DNR's fall dredge survey on all bars that were sampled more than once during 1990-2008 (Wilberg et al. in review). To correct for changes in sampling sites among years and catchability among sites I used a generalized linear model (McCullagh and Nelder 1989), with a negative binomial distribution and a log link function. The negative binomial distribution is commonly used for over-dispersed count data, and a log link function is commonly recommended for this type of model (McCullagh and Nelder 1989). Indices of density were developed separately for each stage for both live oysters and boxes (i.e., boxes or articulated valves, shown in figure 3.2). The model included effects for site and year (treated as class variables; all variables are defended in Table 1),

$$E(\log_e(C_{y,site})) = \alpha + \beta_y + \gamma_{site}.$$

Population Model

To characterize the population dynamics of oysters in the lower Potomac River, I used a stage-structured model based on the three oyster size-age categories, spat (individuals less than one year old), small (individuals older than one year and less than 76 cm) and market (individuals 76 cm and greater), for live oysters and small and market size categories for dead oysters, which was modified from Wilberg et al. (in review; see appendix 4 for the model code). Boxes are often used as a measure of observed natural mortality (Southworth et al. 2005, Ford et al. 2006). The model included effects of fishing and time-varying natural mortality and estimated

abundance, exploitation and natural mortality of the population during 1990-2008. The abundance in each stage changed due to growth, fishing, and natural mortality. Natural mortality includes all non-fishing sources of mortality (e.g., disease, predation). The model used annual time steps, included years 1990-2008, and included a population submodel, an observation submodel and the likelihood functions. Abundance in spat, small and market categories represented abundance in the fall just prior to the beginning of the fishing season. The model was fitted to oyster relative density data from the MDNR fall dredge survey and harvest estimates.

Population Submodel

Annual recruitment each year was estimated as model parameters. The number of small oysters was the sum of spat that survived the year and the number of small that survived but remained small,

$$N_{Y+1,1} = N_{y,0}e^{-M_0} + (1 - G)N_{y,1}e^{-M_{y,1}} .$$

The instantaneous natural mortality rate for spat was assumed to be 0.7 per year based on estimates from sanctuaries and managed reserves in Maryland (Paynter 2007) and was assumed to be constant on average over time because spat are thought to be rarely affected by Dermo disease, which is thought to be the primary source of disease mortality in Maryland waters of Chesapeake Bay (Burreson and Ragone Calvo 1996).

The number of market-sized oysters was the sum of small oysters that grew to market size and market-sized oysters that survived natural mortality and harvest,

$$N_{y+1,2} = GN_{y,1}e^{-M_{y,1}} + N_{y,2}e^{-M_{y,2}} - H_y .$$

Natural mortality was estimated annually for market-sized and small oysters by allowing annual deviations from median M for all years. Market and small oysters were affected by the same natural mortality rate in each year. The abundance for first year of the model was estimated for each stage. The model specified that natural mortality occurred before growth, and all natural mortality and growth occurred after the fishing season because growth and most mortality from disease occur during summer and early autumn (Andrews 1988; Vølstad et al. 2008) whereas harvest occurs from October to March. The model estimated the transition probability between the market and small size categories.

The model tracked the number of boxes in small and market categories. The number of boxes for each size category was calculated as the sum of new boxes from natural mortality in the population and old boxes that still remain after natural decay and destruction by fishing,

$$B_{y+1,s} = N_{y,s}(1 - e^{-M_{y,s}}) + B_{y,s}e^{-D_s}(1 - u_Y) .$$

The instantaneous decay rate of boxes was assumed to be 1.03 year^{-1} (Ford et al. 2006). These decay rates are higher than those found by Christmas et al. (1997) and better reflect the environmental conditions within the study area because salinity is higher in the lower Potomac River than the sites used in the Christmas et al. (1997)

study. I conducted sensitivity analyses of the decay rate for boxes by applying the values from Christmas et al. (1997) of 0.52 for smalls and 0.45 for markets.

The exploitation rate was defined as the proportion of the market-sized population available at the beginning of the fishing season that was harvested annually,

$$u_y = \frac{H_y}{N_{y,2}}.$$

Observation Submodel

Predicted indices of abundance were estimated for all sizes categories for both live and dead oysters in the model as the product of catchability and abundance,

$$\hat{X}_{N,y,s} = q_{N,s} N_{y,s}.$$

Catchability was calculated using the maximum likelihood estimate,

$$\log_e q_{X,s} = \frac{\sum_y \log_e \left(\frac{X_{y,s}}{N_{y,s}} \right)}{n}.$$

Likelihood Functions

The objective function contained lognormal likelihood components for indices of density for market, small, and spat size-category live oysters and market and small boxes,

$$L_{X,s} = n \log_e(\sigma_X) + \frac{1}{2\sigma_X^2} \sum_{y=1980}^{2008} \left(\log_e(X_{y,s}) - \log_e(\hat{X}_{y,s}) \right)^2.$$

The constants in the likelihood function and priors were ignored for simplicity. The assumed fixed standard deviations on the \log_e scale for these data sources were 1.0

for spat, 0.4 for small, 0.3 for market, 0.5 for small articulated shells, and 0.4 for market articulated valves. These values were chosen because they represent the selectivity of the sampling gear and the ability for individuals to be identified within the samples. They are also consistent with the residual variance of the model fits to the data series. Available habitat was assumed constant during 1990-2008, so observed indices of density are also indices of abundance.

Lognormal penalties were specified for the median natural mortality rate parameter (Table 2),

$$P_d = \log_s(\sigma_d) + \frac{1}{2\sigma_d^2} (\log_s(\mu_d) - \log_s(M_d))^2.$$

I assumed the annual deviations in natural mortality for small and market-sized oysters followed a lognormal distribution with a log-scale standard deviation of 0.5. The model contained a lognormal penalty on the transition probability from small to market size class, with a median of 0.45 based on growth in sanctuaries in Maryland waters of Chesapeake Bay and a log-scale standard deviation of 0.3 (Paynter et al. 2010). The overall objective function was the sum of the log likelihood components for each data source and the priors.

The standard deviations of the residuals for the fits to the indices of density were:

$$\hat{\sigma}_x = \sqrt{(1/n^i) \sum_y (\log_s I_y^i - \log_s q^i B_y^i)^2}$$

where n^i is the number of data points for abundance series i .

The overall objective function was the sum of the individual likelihood components and penalties.

Model Evaluation

I evaluated the quality of the model's fit to the data by comparing the values estimated in the model to the actual survey and catch data as well as comparing the residuals for patterns and evaluating the model's biological accuracy. I regressed the observed index of density with the estimate from the model to quantify the model fit.

Natural Mortality

I tested whether natural mortality was related to prevalence of Dermo and MSX diseases or environmental variables such as temperature and salinity. The disease prevalence and intensity data were from the Maryland DNR fall survey, where prevalence was the percent of infected oysters in the survey annually and intensity the averaged categorical infection severity (severity scored on a 7 point scale (see Tarnowski 2007 for details)). Environmental data were from the Chesapeake Bay Program's water quality database (Chesapeake Bay Program 2010). I used data from two monitoring stations within the Potomac River, LE1.2 and LE1.3, to obtain average yearly temperature and salinity values. I chose these stations because they are directly upstream and downstream of the modeled region. I conducted a multiple linear regression to test if annual natural mortality was related to prevalence of MSX and Dermo, temperature, or salinity. I transformed natural mortality using an arcsine square root transformation to normalize the residuals (McDonald 2009).

Results

The estimated indices of density matched the observed survey catch data fairly well (Figures 3.2 and 3.3) and a model that used faster rates of box decay was better than one that used slower rates of decay (Table 2). The model, however, had trouble estimating the density at the beginning of the time series for both live and dead oysters in all the size categories. The model underestimated density in the first couple years, especially for the live and dead small oysters and the live market oysters. The residuals for both live and dead size categories appear to be normally distributed (on the log scale) however there are patterns in some of the fits (Appendix 3).

The model estimates of total abundance declined during 1990-2008 (Figure 3.4). Abundance at the beginning of the time series was 269 million oysters and was reduced to 142 million oysters by the end of the time series, a 39% decline. The change in abundance over time seems to be driven by low recruitment. Abundance of spat and small oysters exhibited very different levels of declines in total abundance during the time series 80% and 9%, respectively. However, abundance was highly variable for these size categories, ranging from 120 thousand to 127 million oysters for spat and 20 million to 88 million for the small size category (Figure 3.5a and b). The estimates of abundance for the market-sized oysters exhibited an intermitted amount decline in abundance over time when compared to spat and small oysters (23%; Figure 5c). The decline starts after a peak in abundance in 1995 of 113 million market-sized oysters, and abundance is reduced to 21 million in 2002 before a slight rebound at the end of the time series.

Estimated natural mortality averaged 0.34 year^{-1} during 1990-2008, and fluctuated between 0.12 and 0.71 per year (Figure 3.6). The average natural mortality pre 1997 was 0.25 year^{-1} . There was a sharp increase in 1997 followed by a peak in 1999. Estimated natural mortality then declined and leveled off around 0.25 from 2002 to 2008. The average exploitation rate for the time series was very low at only 1% per year (Figure 3.7). The estimates are fairly constant over time with the exception of a large peak in 1996-1998, during which the exploitation rate increased to 11% per year. The estimated transition probability from small to market size classes was 0.5 year^{-1} .

Dermo prevalence steadily declined throughout most of the time series spiking in 1990 and 2002 and averaged 55% prevalence over the time series (Figure 3.8a). MSX prevalence was highly variable with a large spike in prevalence between 1999 and 2002. The average MSX prevalence was 10% over the time series (Figure 3.8b). Temperature and salinity were variable ranging from $15 \text{ }^{\circ}\text{C}$ to $17 \text{ }^{\circ}\text{C}$ and 10 ppt to 17 ppt, respectively (Figure 3.8c and d). Natural mortality was not significantly related to disease prevalence ($P=0.20$; $R^2=0.1824$), temperature ($P=0.73$; $R^2=0.0074$) or salinity ($P=0.12$; $R^2=0.1428$).

Discussion

I developed a spatially explicit stock assessment of oysters in the Chesapeake Bay using a stage-based model for the lower Potomac River. The model estimated the initial abundance to be 239 million oyster, natural mortality ranged from 0.12 to 0.71 year^{-1} and exploitation varied between .01% and 11% during 1990-2008. Overall the model seems to reflect the dynamics of the oysters within the region during the time

series. Converting the abundance to density with habitat estimates from the Maryland Bay Bottom Survey, the density seems similar to other studies with low density (Wilberg et al. in review). Densities ranged from 5 individuals/m² in 1990 to 0.33 individual/m² in 2008 for spat, 3 individuals/m² in 1990 to 2.75 individual/m² in 2008 for small, to 3 individuals/m² in 1990 to 2.38 individual/m² in 2008 for markets. The model estimate of total abundance shows a 39% decline in abundance for this region during this time series. The estimated decline was substantially less than decline in oyster abundance (56%) throughout the Maryland portion of the Bay from 1990 to 2008 found by Wilberg et al. (in review). The decline in abundance in Wilberg et al. (in review) may be greater than the decline found in this study because the smaller spatial extent of this work along with the assumption that the dredge survey was an index of abundance. By using the dredge survey as an index of abundance, I assumed that habitat did not decrease after 1990. Preliminary versions of the model did estimate habitat decline, as in Wilberg et al. (in review), but the estimate was zero. The absence of habitat decline in this region could be due to little to no fishing within this area and more consistent recruitment as demonstrated in Chapter 2.

Although the estimated exploitation rate is very low compared with other studies of fishing mortality in Maryland (Rothschild et al. 1994; Wilberg et al. in review), it seems to be an accurate reflection of fishing mortality within this region. Little fishing currently occurs in this region because of low oyster abundance (A.C. Carpenter, PRFC, personal communication). Reported effort concurs with the low estimated exploitation rate (Figure 3.9). Harvest was also low in this region except between 1997 and 1999 (Figure 3.10). The spike between 1997 and 1999 in reported

effort and harvest, is mirrored in the exploitation rate and can be explained by the fact that Jones Shore bar was added to the "open" areas for hand scraping (i.e., use of a small oyster dredge) and accounted for 27,083 bushels of the 39,547 bushel total hand scrape harvest for the 1996-1997 season (PRFC unpublished data). Fishing by hand scrape appears to be the main source of fishing mortality in this region.

The model was able to estimate the time-varying natural mortality. It is important to include time-varying natural mortality when modeling oysters in the Chesapeake Bay because of the large fluctuations in oyster natural mortality due to disease and environmental factors (Ford et al. 2006, Vølstad et al. 2008). The average natural mortality rate was 0.34 year^{-1} although the rate was highly variable. This is similar to the natural mortality rates found by Wilberg et al. (in review) who estimated an average natural mortality rate of 0.37 for small oysters and about 0.30 for market oysters from 1990 to 2008.

The decline in abundance of the eastern oyster in the Chesapeake Bay is often attributed to high exploitation and disease (Rothschild 1994). Conversely, in this region exploitation is very low, averaging 0.01 from 1990-2008 and disease does not appear to explain annual variation in natural mortality within this region. I did not find significant relationships between natural mortality and disease prevalence, temperature, or salinity contrary to Ford et al. (2006) and Vølstad et al. (2008). This finding is contrary to the popular belief that disease is the main cause of natural mortality within the Bay (Andrews 1988, Burreson and Ragone Calvo 1996, Ford and Tripp 1996). Dermo related mortality is thought to be extremely high in the lower Potomac (Tarnowski 2005). Tarnowski (2007) has also suggested that the spike

present in the estimated natural mortality between 1998 and 2002 is thought to correspond with high disease prevalence, particularly high prevalence of MSX.

I did not find any significant relationships between natural mortality and disease prevalence, temperature, and salinity. The lack of significant relationships may be because they are potentially non-linear or factors affecting natural mortality may interact with other factors not included in this analysis. In particular natural mortality may also be affected by low dissolved oxygen. Alternatively, the timing of surveys and time averages of environmental variables may not match up with critical periods for oysters in this region. There is also the potential for a change in virulence of the diseases over time. Fishing may interact with estimated natural mortality by injuring oysters that are not caught by the gear, but subsequently die (Lenihan and Peterson 2004). The spike in 1997 exploitation seems to precede the spike in 1999 natural mortality suggesting a potential connection between the destructiveness of the fishing gear and natural mortality.

The limitations of this model include not being able to estimate natural mortality for spat, and also not included is a length based growth model for the region. In addition, the model includes numerous assumptions such as constant catchability of the survey, that harvest was known without error, constant growth over time, that habitat did not decline, that natural mortality was the same for small and market size individuals, and that the rate of decay was known and the same for small and market boxes. These limitations and assumptions provide areas of focus for future work to improve this model including sensitivity analyses of parameters that

were assumed known and constant such as the natural mortality rate for spat and the degradation rate for boxes.

Management Implications

The model developed in this study can provide a basis for regional management of eastern oysters in upper Chesapeake Bay. The model can provide information on abundance, exploitation rate and natural mortality in sanctuaries and areas for future sanctuaries. These estimates along with the spatial analysis presented in my 1st chapter are useful in managing a species with different patterns in growth and can help managers determine regions where restoration efforts would be most successful. The findings of this model also suggest a link between exploitation and natural mortality; more so the consequences of allowing destructive fishing gears in areas where they were previously not allowed and the associated raise in natural mortality.

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Tables

Table 1. Parameters, data and variables for Maryland regional oyster stock assessment model.

<i>Variables</i>	<i>Description</i>
C	Catch
y	Year
$site$	Index for site effect
α	Intercept
β	Categorical year effect
γ	Site effect
N	Abundance
M	Natural Mortality
G	Probability of transition between small and market size classes
H	Harvest
B	Number of boxes
D	Natural Decay
u	exploitation rate
s	Stage (spat, oysters less than one year old; small, oysters older than one year and less than 76 cm; or market, oyster 76 cm and greater)
q	Catchability
X	Observed index of density ($\hat{}$ indicates an estimated value)
n	Number of years
σ	Log-scale standard deviation
P	Prior for natural mortality and transition probability
d	Instantaneous rate of habitat decline
μ	Median of prior for natural mortality

Table 2. Comparison of negative log likelihood values for different specifications of rates of decay for boxes and habitat. Parameters specified in the model are indicated in the table.

Model	Small box decay rate	Market box decay rate	Habitat decay rate	Negative log likelihood
Base	1.03	1.03	1.07*	-68.02
2	0.52	0.45	1.07*	-62.65
3	1.03	1.03	1	-26.22

* indicates the parameter was estimated.

Figures

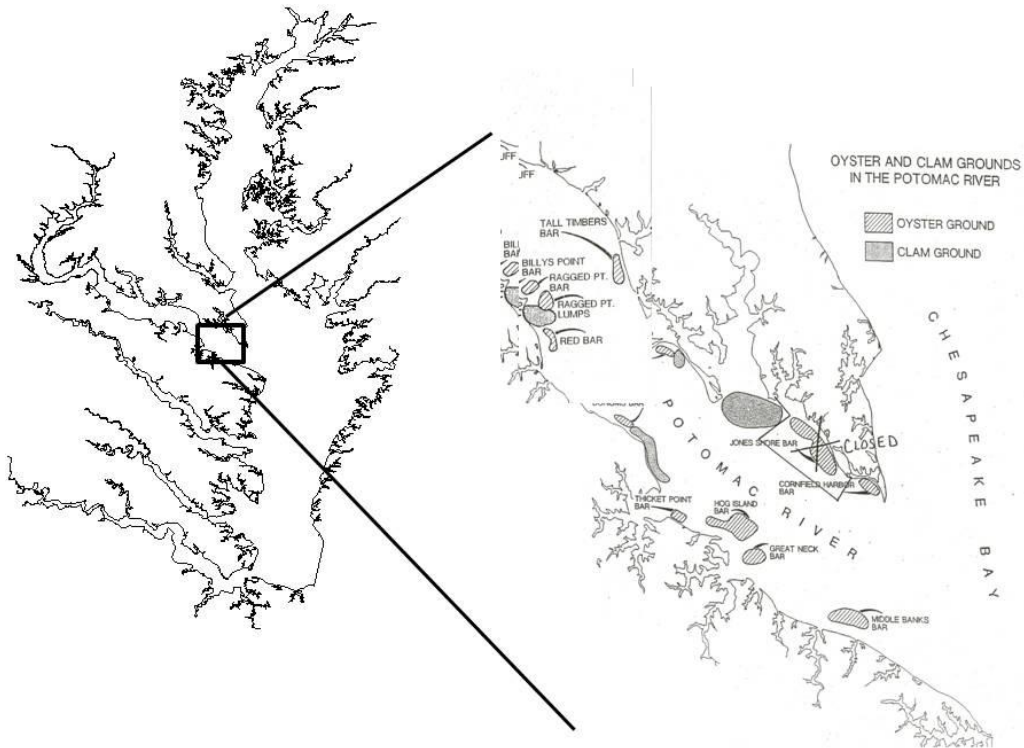


Figure 3.1. The study area in the lower Potomac River in the Chesapeake Bay and the locations of the bars included in this study.

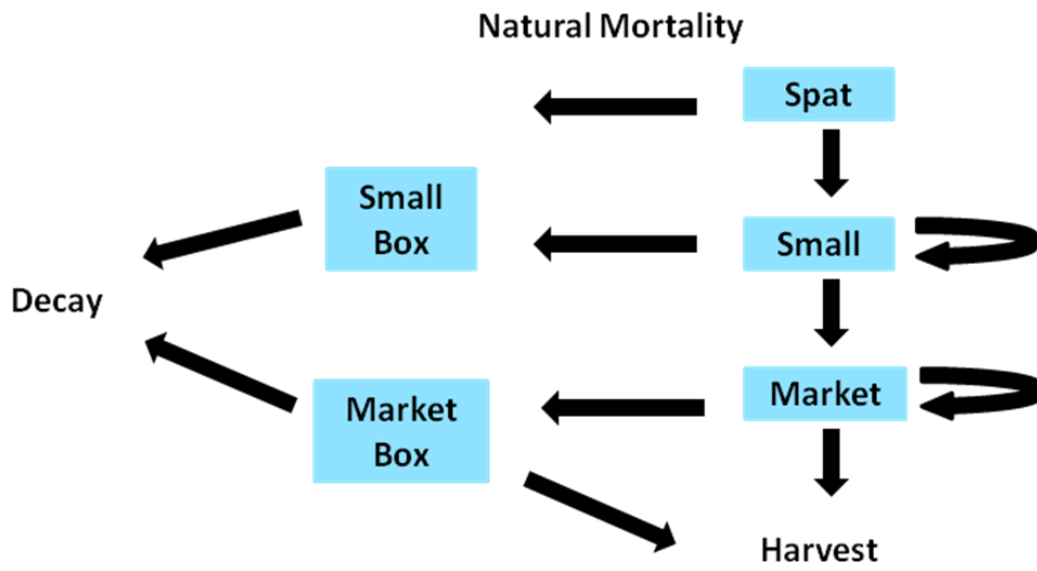


Figure 3.1. Conceptual diagram of the stage-structured assessment model.

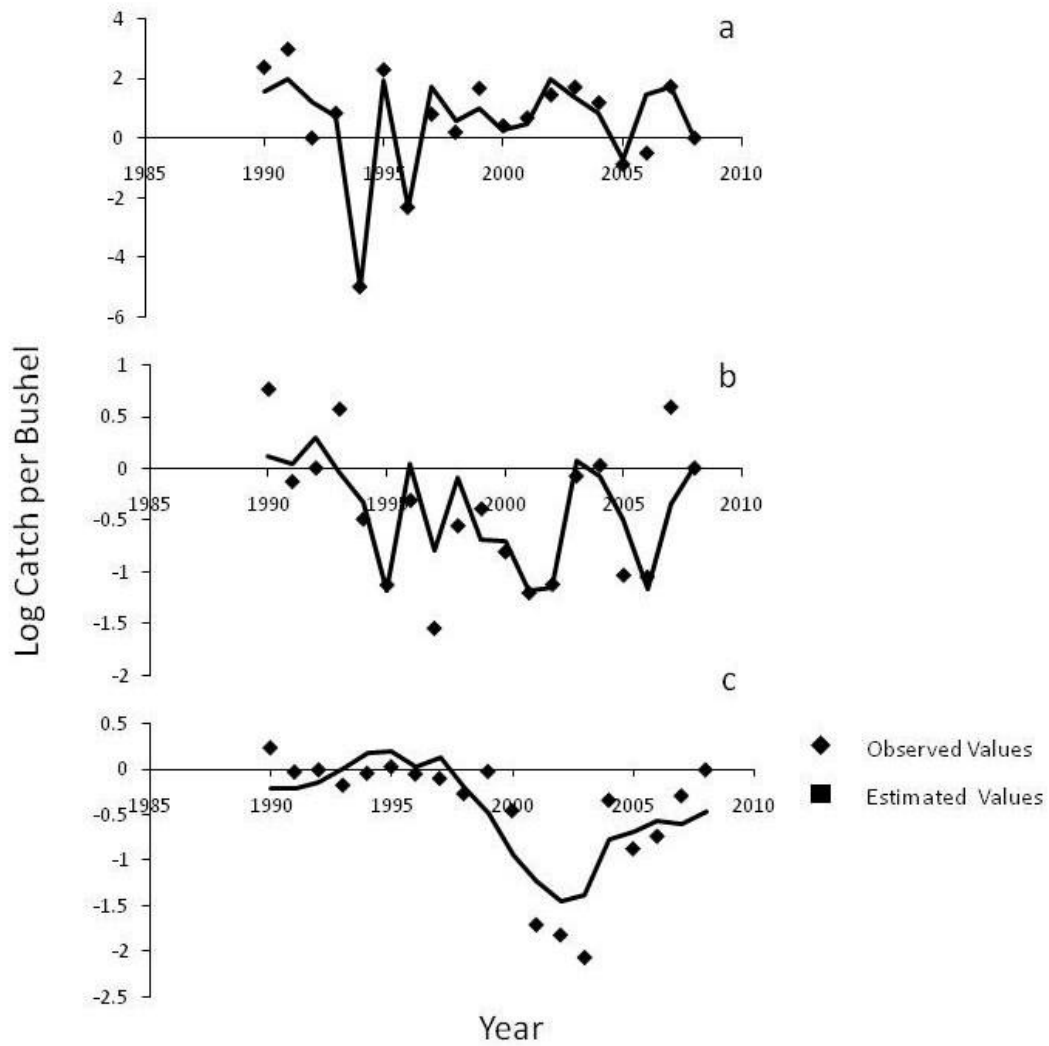


Figure 3.2. Comparison of observed and estimated indices of density over time for spat (a), small (b) and market (c) category oysters.

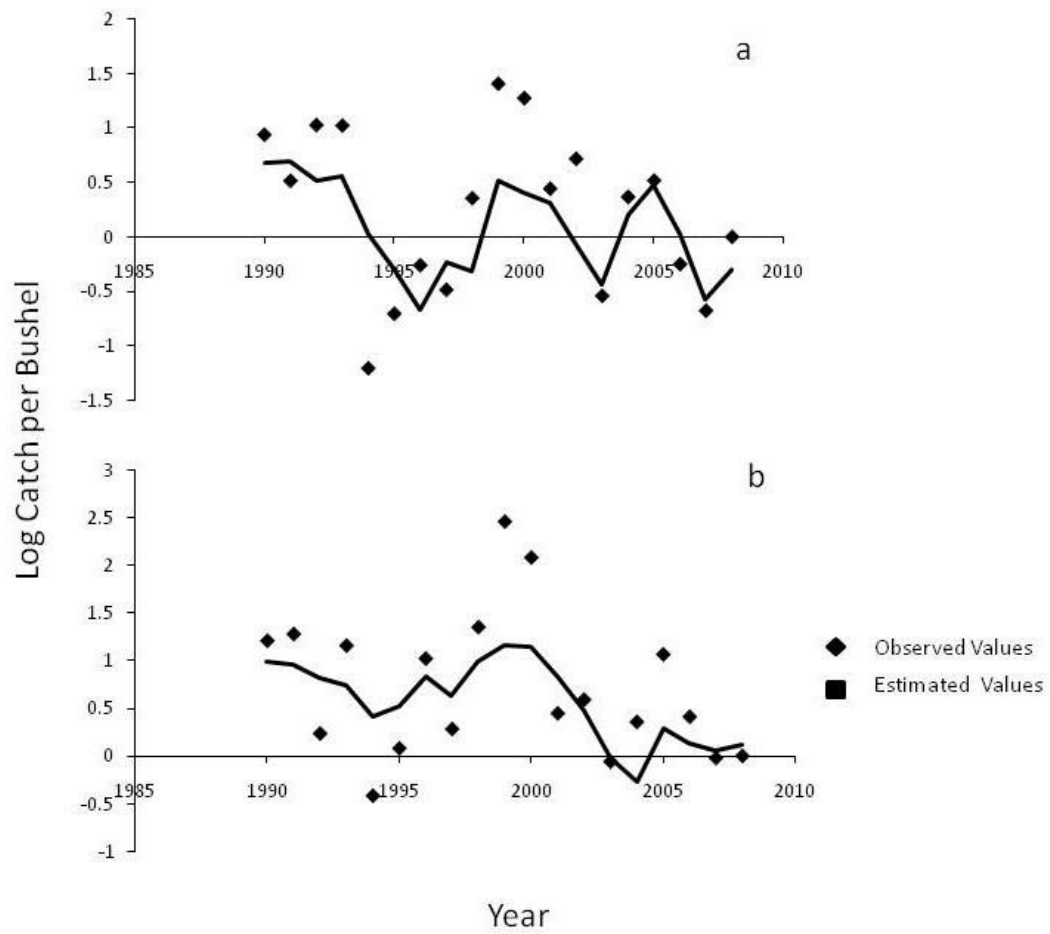


Figure 3.3. Comparison of the observed box data from the Maryland DNR fall dredge survey and estimated values over time for small (a) and market (b) sized oysters.

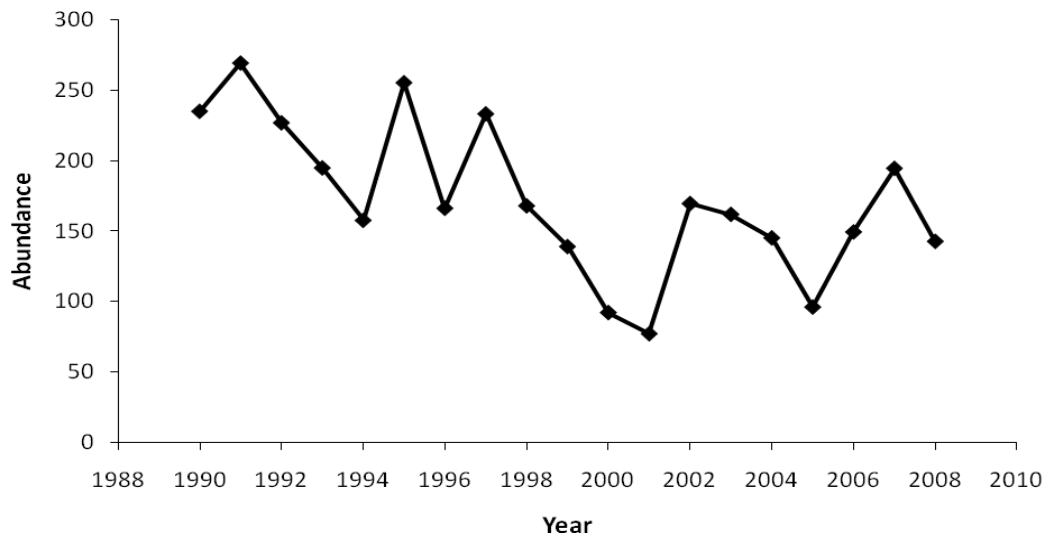


Figure 3.4. Estimated total abundance (in millions) of oysters for the lower Potomac River from 1990 to 2008.

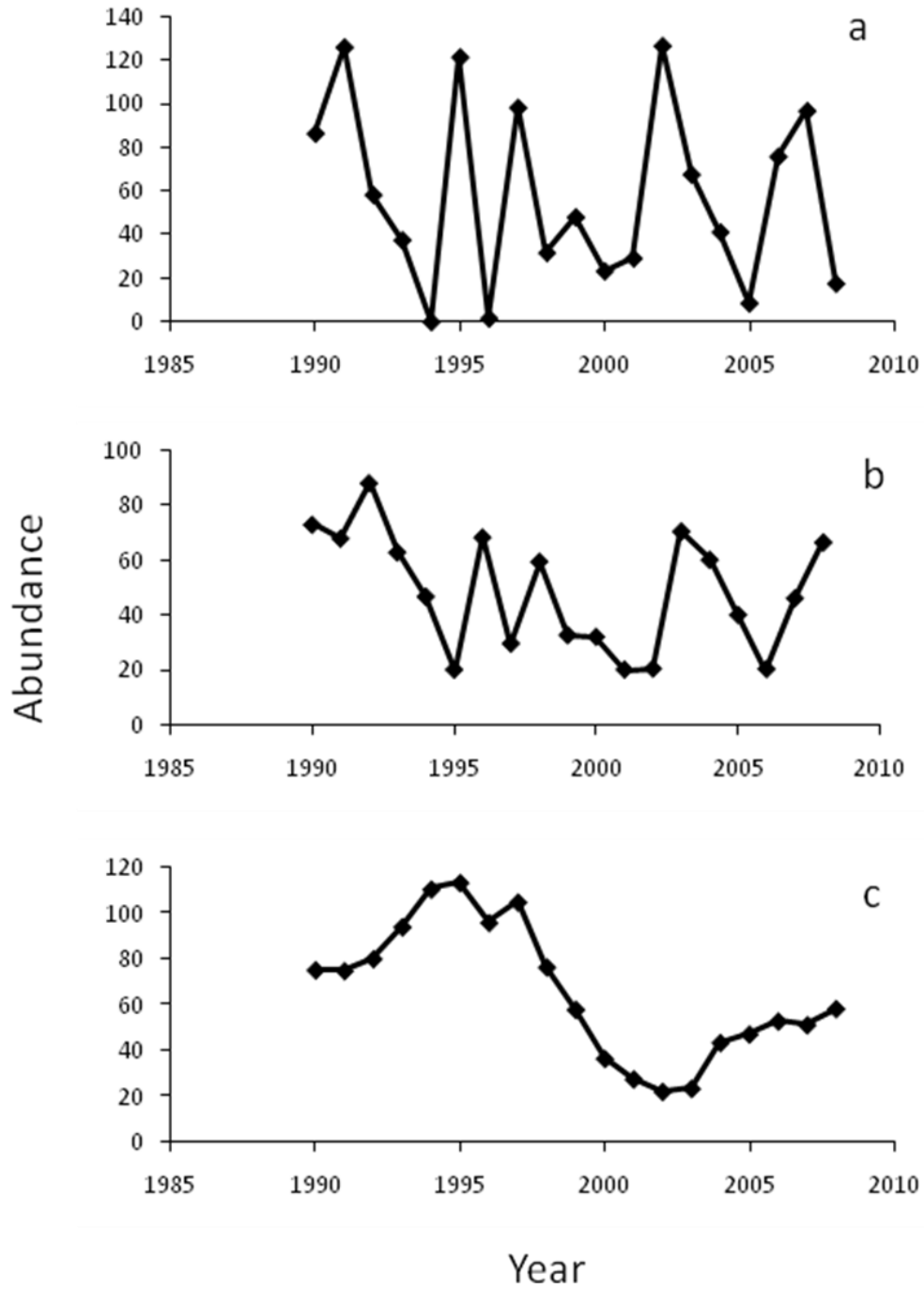


Figure 3.5. Estimated oyster abundance (in millions) for spat (a), small (b) and market (c) size categories in the lower Potomac River during 1990-2008.

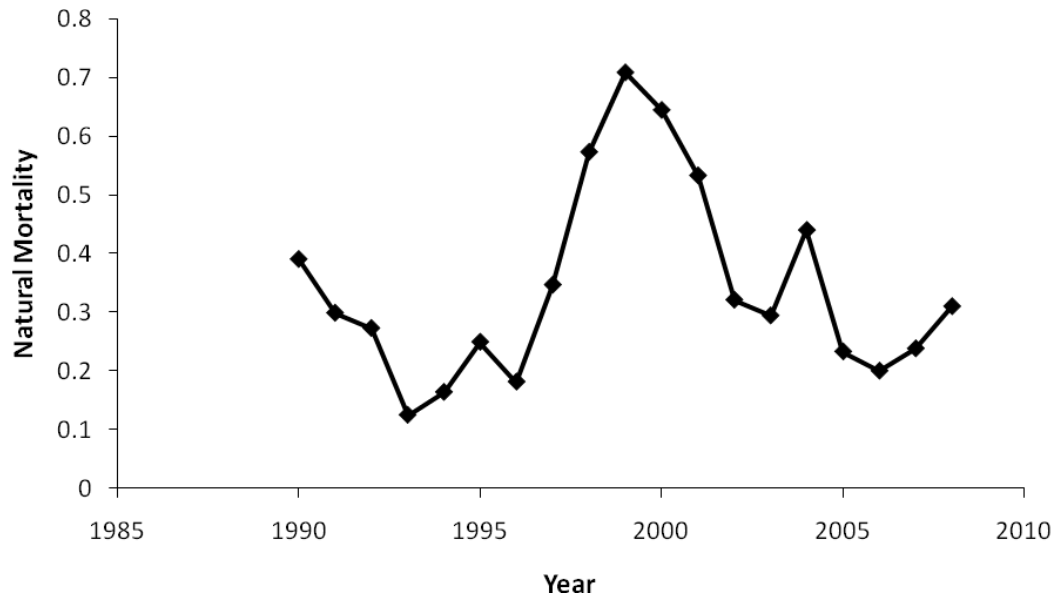


Figure 3.6. Estimated instantaneous natural mortality of oysters (in millions), for the lower Potomac River during 1990-2008.

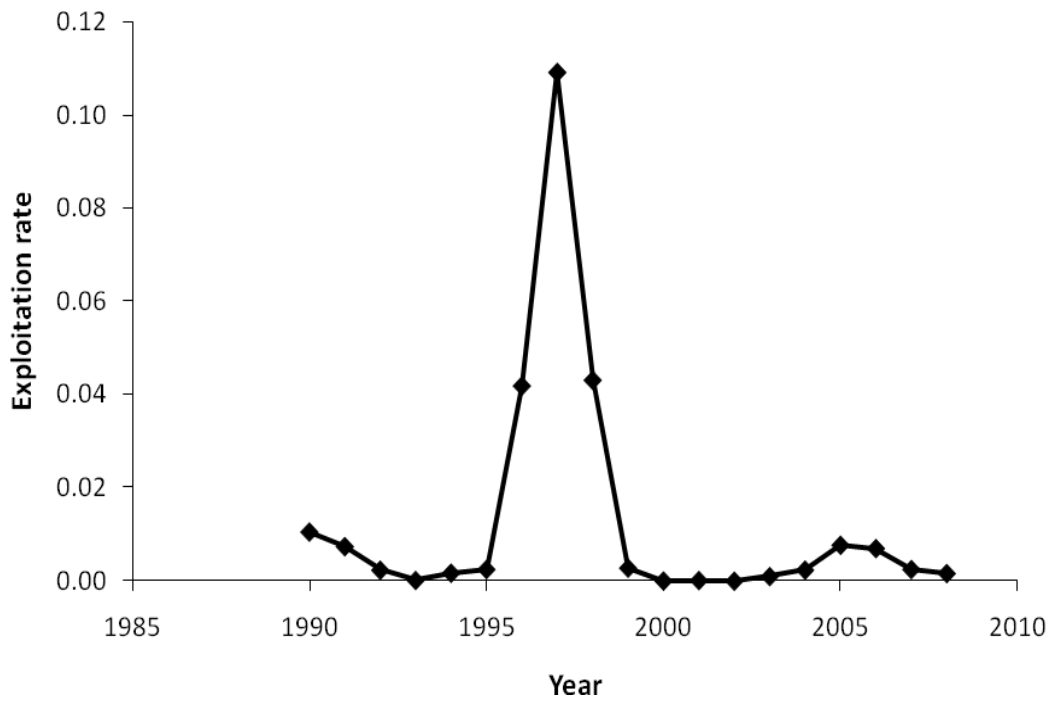


Figure 3.7. Estimated exploitation rate of oysters for the lower Potomac River during 1990-2008

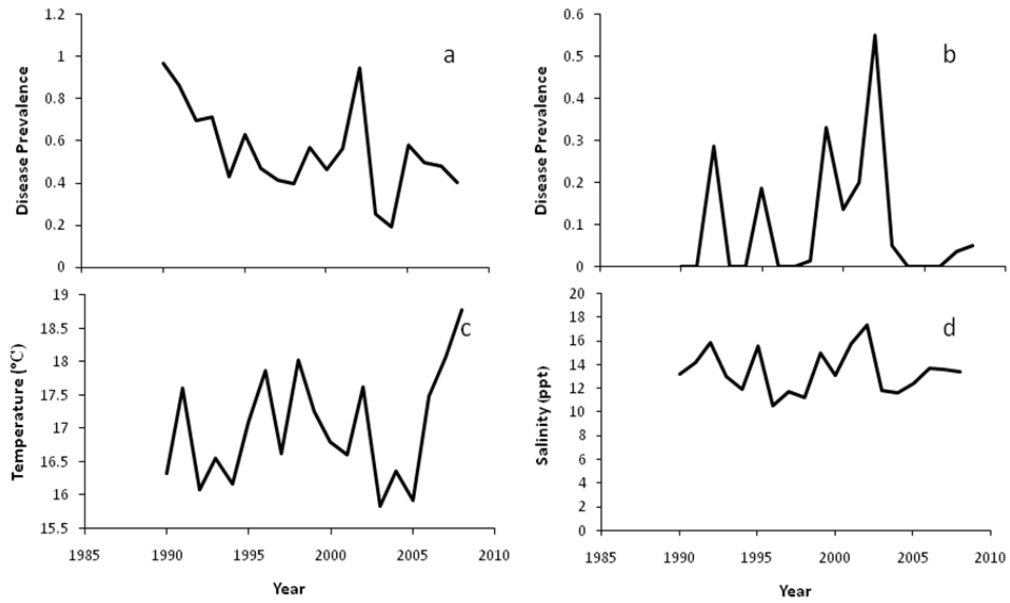


Figure 3.8. Disease prevalence for Dermo (a) and MSX (b) and average annual temperature (c) and salinity (d) for the lower Potomac River during 1990-2008.

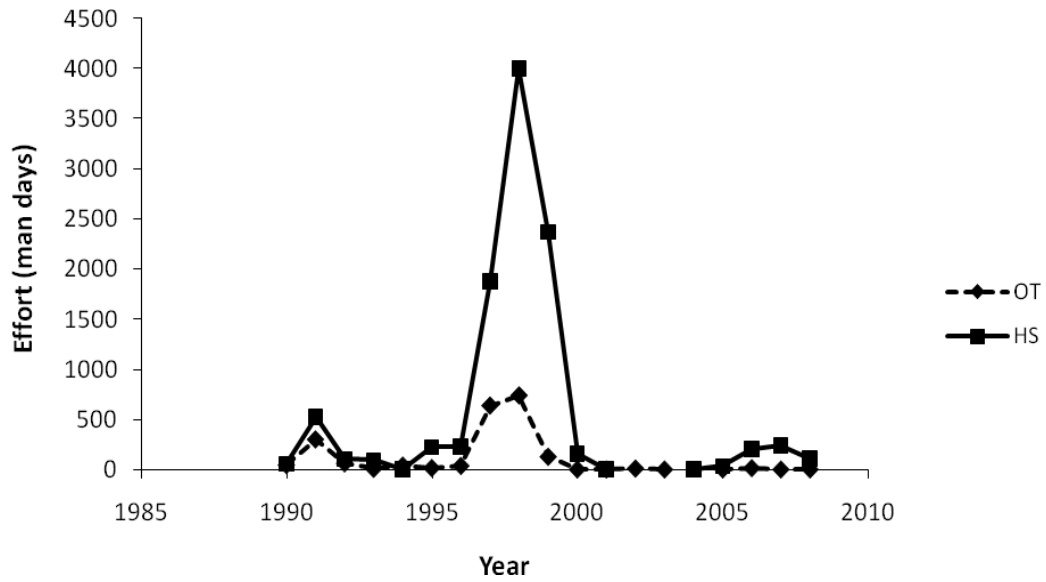


Figure 3.9. Reported effort in man days from the PRFC for hand tongs (OT) and hand scrapes (HS), for the lower Potomac study area from 1990-2008.

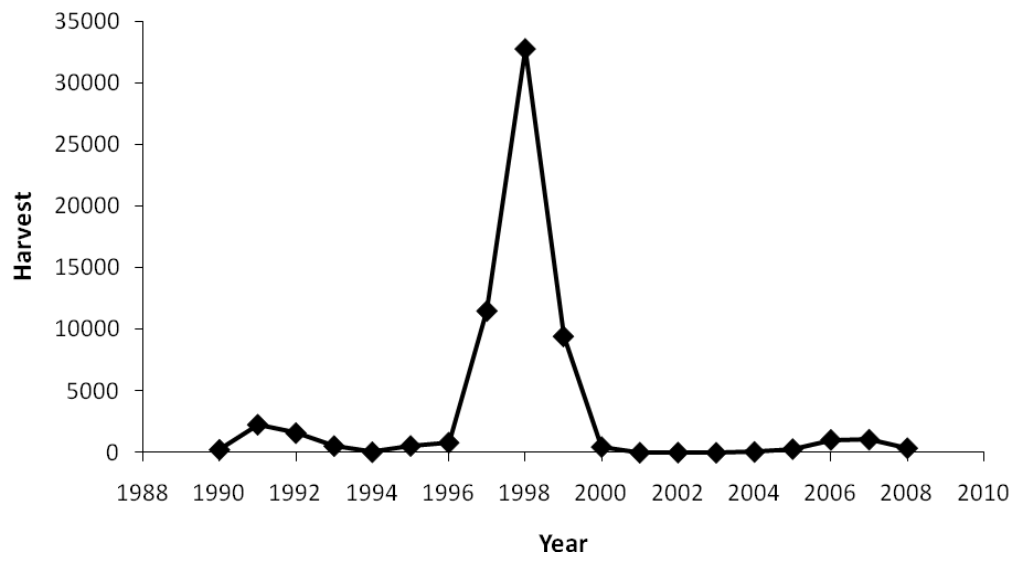


Figure 3.10. Reported harvest (bushels) from the lower Potomac River during 1990-2008.

Chapter 4: Conclusion

The eastern oyster (*Crassostrea virginica*) was once an historically important fishery in Maryland, but fishing and disease has dramatically reduced the population. Current harvests are at 1% of the levels reported 40 years ago, and spawning stock biomass is less than 0.15% of unexploited levels (Rothschild et al. 1994; Wilberg et al. *in review*). Previous management of Maryland's declining oyster population has had little to no success throughout the Bay. In December 2009, Maryland's governor proposed a more than doubling of the state's oyster sanctuaries, concentrating on areas with high salinity and fast growth. Also, the federal government has set a goal of restoring self-sustaining oyster populations in 20 Chesapeake tributaries by 2025 (Chesapeake Bay Foundation 2010). In order to achieve these goals managers need to think of oyster reefs as networks that depend on each other to be sustainable over time (Chesapeake Bay Foundation 2010) and determine the best areas within the bay for the type of restoration implemented (North et al. 2010). Given the new goals, a better understanding of spatial processes (e.g., interdependence of the oyster reef networks) is necessary to give managers a more accurate depiction of scale of the processes affecting the population.

The objectives of my thesis were to determine a spatial scale in which eastern oyster population dynamics were similar in the Maryland portion of the Chesapeake Bay and evaluate whether spatial dynamics changed over time and once an appropriate scale was determined, to conduct a regional stock assessment of eastern

oysters to support spatially explicit fishery management and restoration. In Chapter 2, I explored the temporal and spatial scale of correlations in the Maryland Department of Natural Resources fall dredge survey data from Maryland waters of Chesapeake Bay and the Potomac River to determine appropriate scales for modeling oyster population dynamics above the bar level. Specifically, I examined whether patterns of spatial autocorrelation in relative density of spat and adult oysters are evident and have changed over time. To characterize spatial patterns in oyster recruitment and adult indices of density, I conducted semivariogram analyses for each year during 1980-2008 and used the semi-variogram models to create interpolated maps in MATLAB with ordinary kriging (Jensen et al 2006).

In Chapter 3, I developed a framework that used a stage-based model for the lower Potomac River with survey and fishery data from the Maryland Department of Natural Resources and the Potomac River Fisheries Commission. I chose the lower Potomac River as my study area because of the numerous sources of information available as well as the historical importance of the oyster fishery within this region. To characterize the population dynamics of oysters in the lower Potomac River, I used a stage-structured model based on the three oyster size-age categories, spat (individuals less than one year old), small (individuals older than one year and less than 76 cm) and market (individuals 76 cm and greater), for live oysters and small and market size categories for dead oysters (i.e., boxes or articulated valves). The model included effects of fishing and time-varying natural mortality and estimated abundance, exploitation and natural mortality of the population during 1990-2008. The abundance in each stage changed due to growth, fishing, and natural mortality.

Key findings from these analyses were that eastern oyster in the Maryland portion of the Chesapeake Bay has suffered a substantial decline since the early 1980s. In Chapter 2, I found that the spatial patterns in recruitment and adult dynamics did change over time. The changes in the parameters of the semi-variograms over time indicate that oyster density has become more similar throughout the Bay and that the distance over which oyster density is highly autocorrelated contracted during 1980-2009. Oyster bars seem to be similar at distances ≤ 25 -35 km. I also found the recruitment and adult density showed a large amount of spatial and temporal variability, and periods of rapid change corresponded to disease outbreaks and drought periods. Recruitment decreased substantially from the beginning of the time series to the end, particularly in upper Chesapeake Bay.

In Chapter 3, estimated total abundance of oysters declined 39% in the lower Potomac River during 1990-2008. The average natural mortality rate for adult oysters during this period was 0.34 year^{-1} . The estimated exploitation rate was very low in this region, averaging 0.1% from 1990 to 2008, and disease prevalence did not explain annual variation in natural mortality within this region. I also did not find significant relationships between natural mortality and average annual temperature or salinity.

However, I discovered an interesting relationship between the exploitation rate and natural mortality. The spike in 1997 exploitation does seem to precede the spike in 1999 natural mortality suggesting a relation between the destructiveness of the fishing gear and natural mortality. This has serious implications for managers. It

speaks to the consequences of allowing destructive fishing gears in areas where they were previously not allowed and the associated raise in natural mortality.

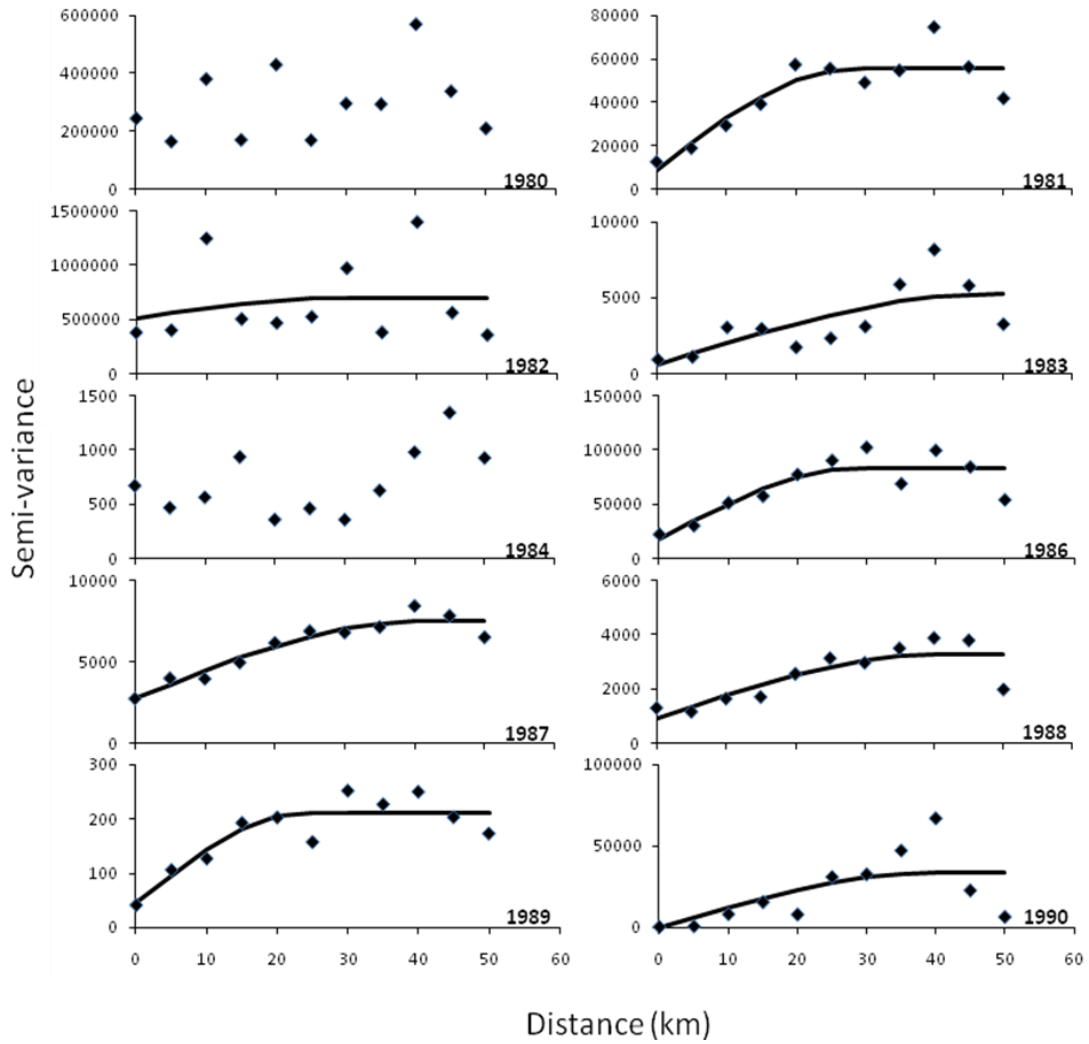
The spatial scale at which oyster dynamics were similar from Chapter 2 and model developed in Chapter 3 can provide a basis for regional management of eastern oysters in upper Chesapeake Bay. The spatial scale from the semi-variogram analysis in Chapter 2 can be used to determine the area of focus for the assessment model developed in Chapter 3. The model can provide information on abundance, exploitation rate and natural mortality in sanctuaries and areas for future sanctuaries. These estimates along with the spatial analysis presented in my 1st chapter are useful in managing a species with different patterns in growth and can help managers determine regions where restoration efforts would be most successful. The model would also be useful in a rotational harvest management strategy similar to the strategy suggested in Wilberg et al. (in review). Future work that would build upon my research includes looking for potential non-linear relationship between disease prevalence and natural mortality and potential interactions with other factors not included in this analysis, such as low dissolved oxygen. In addition, alternative time averages of environmental variables may better match up with critical periods for oysters in this region.

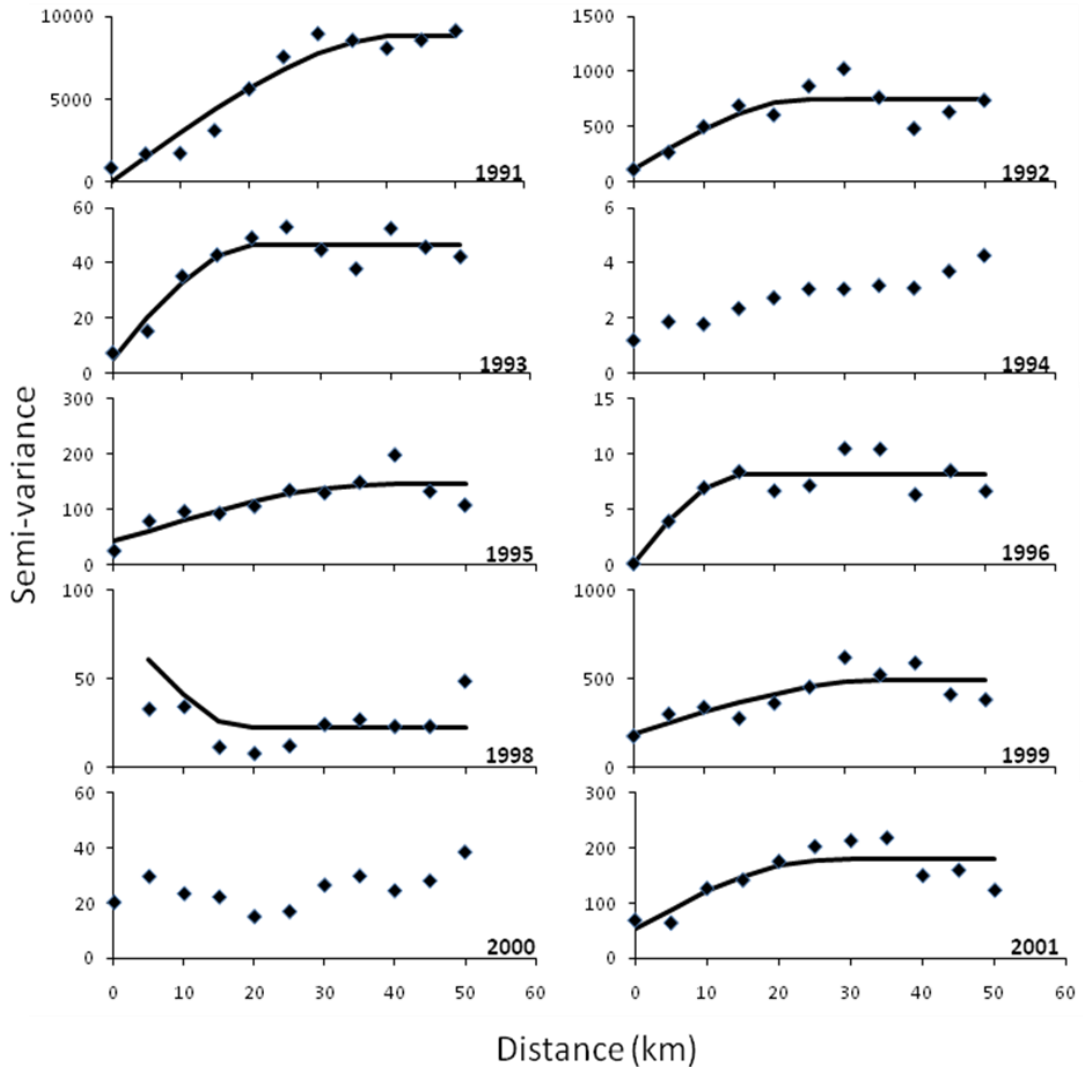
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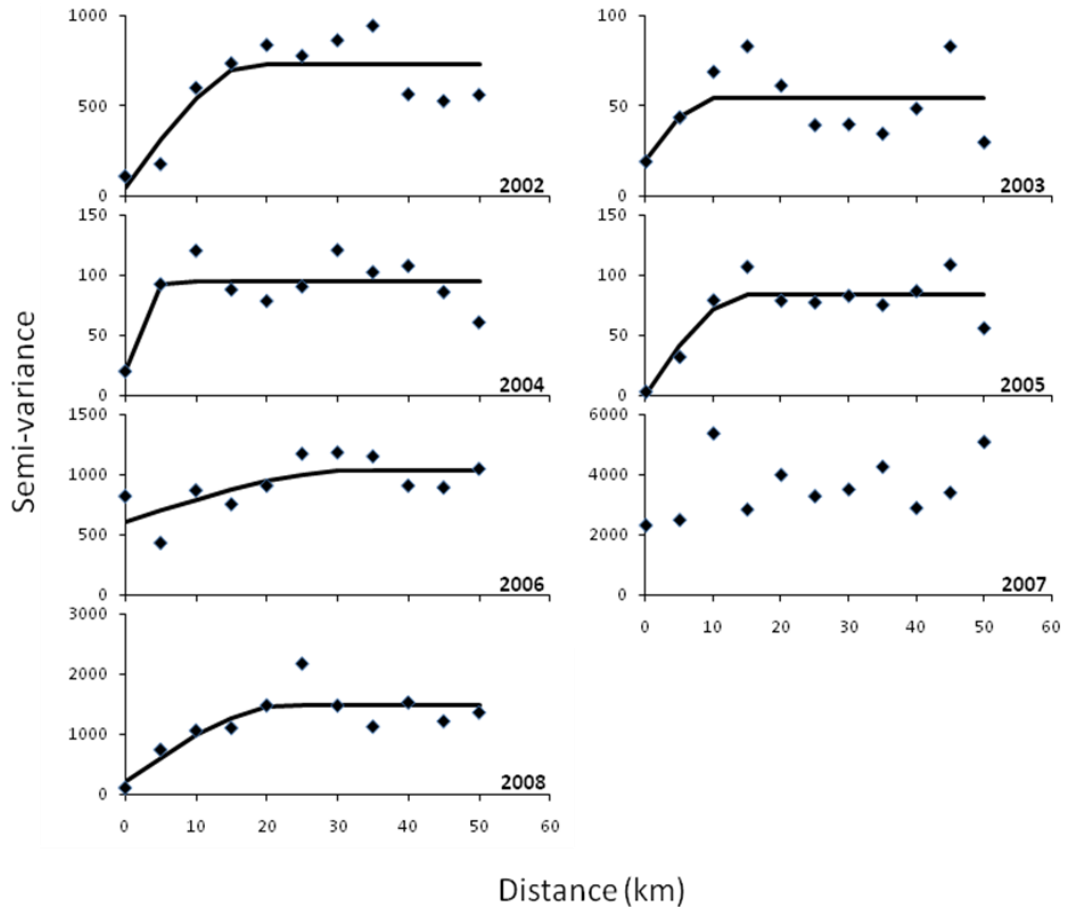
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Appendices

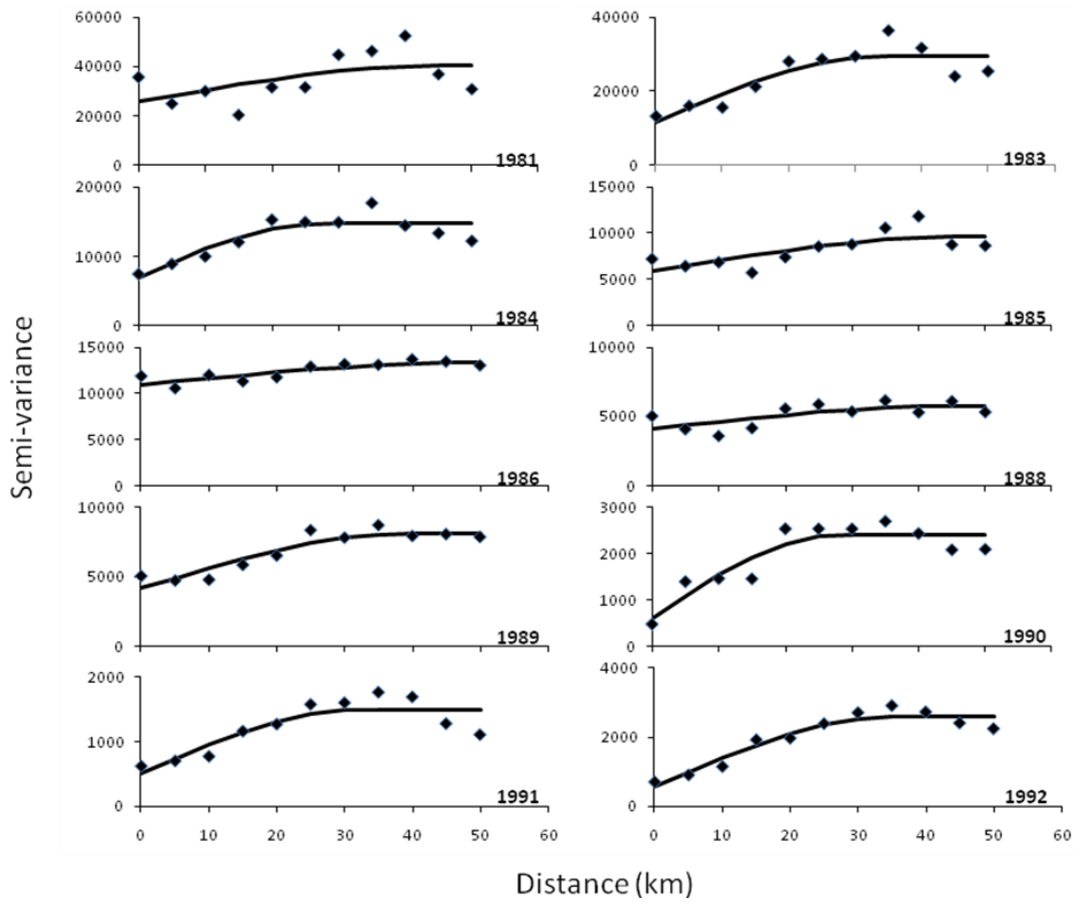
Appendix 1. Year-specific semi-variance plots with fitted spherical model for recruitment density from 1980-2008.

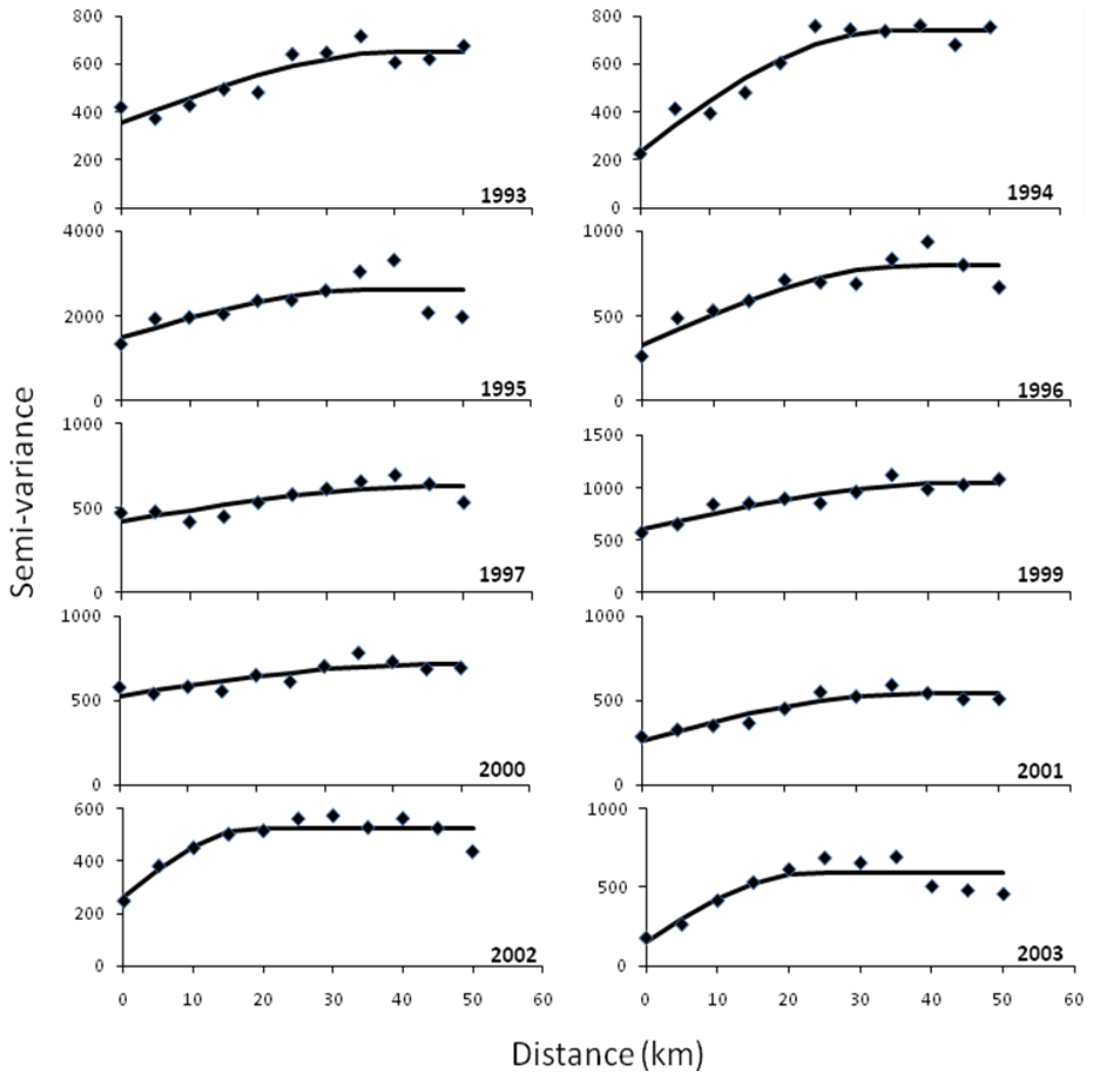


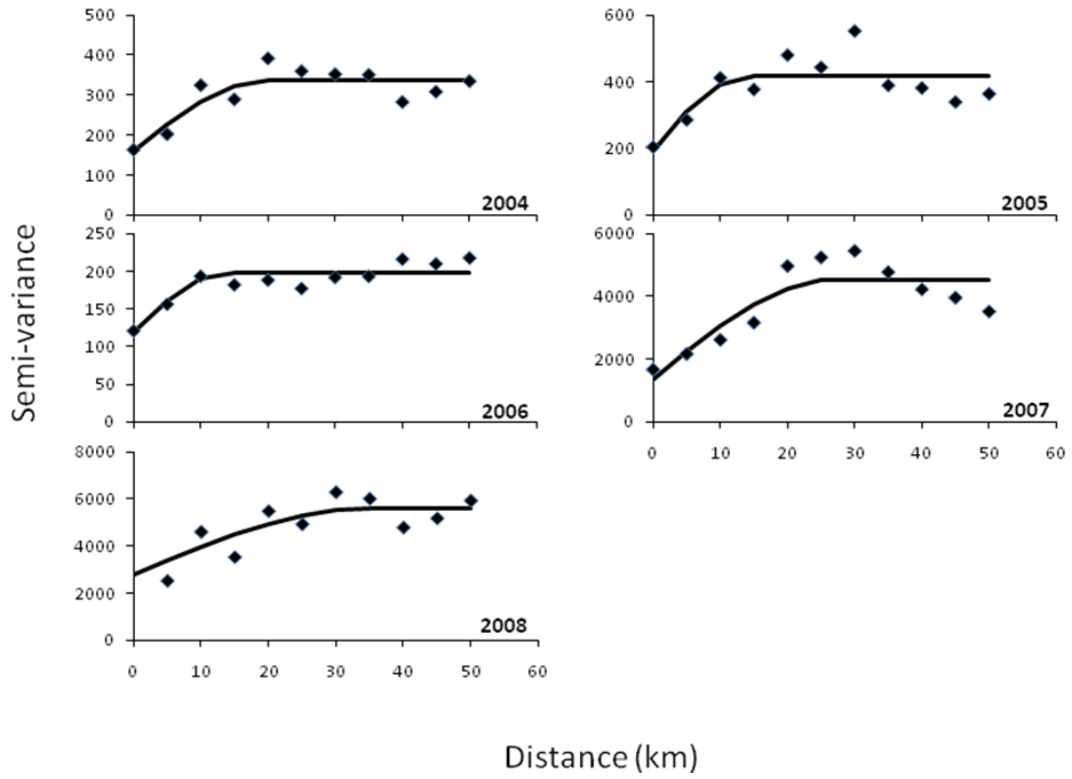




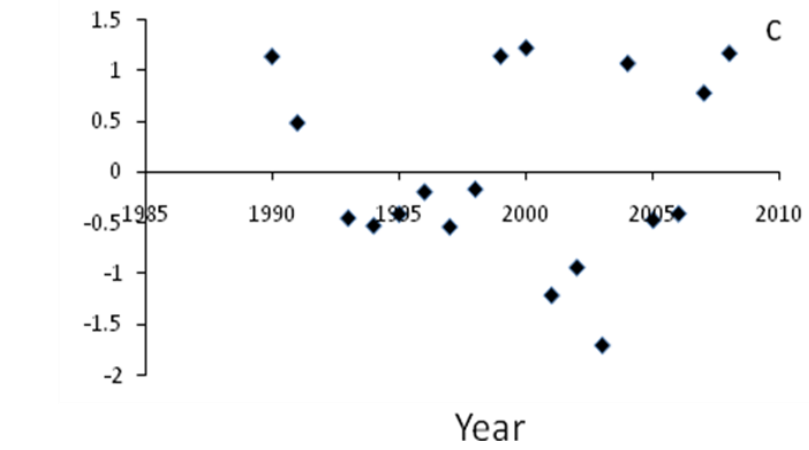
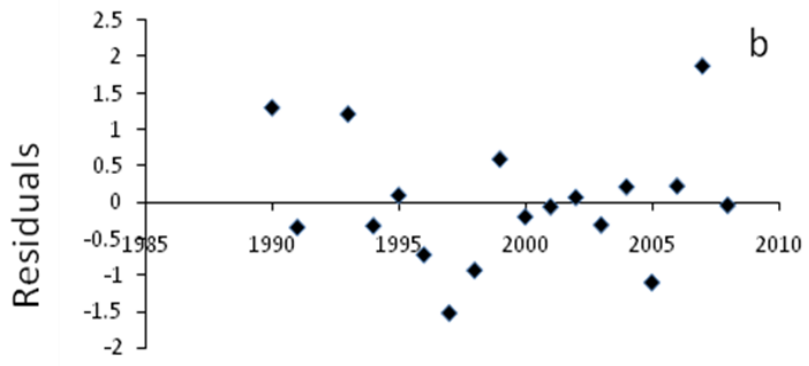
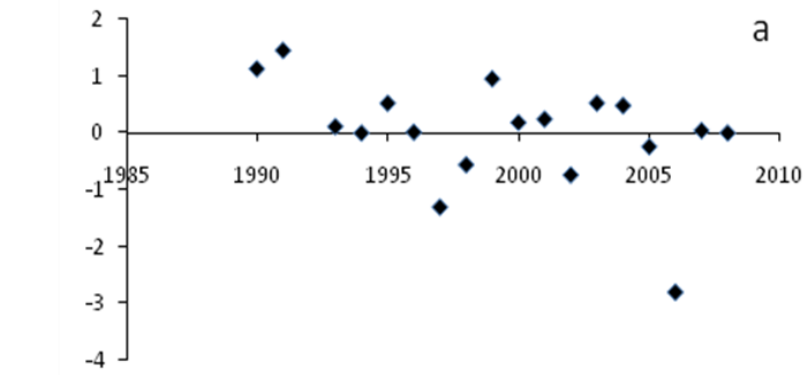
Appendix 2. Year-specific semi-variance plots with fitted spherical model for adults from 1980-2008.

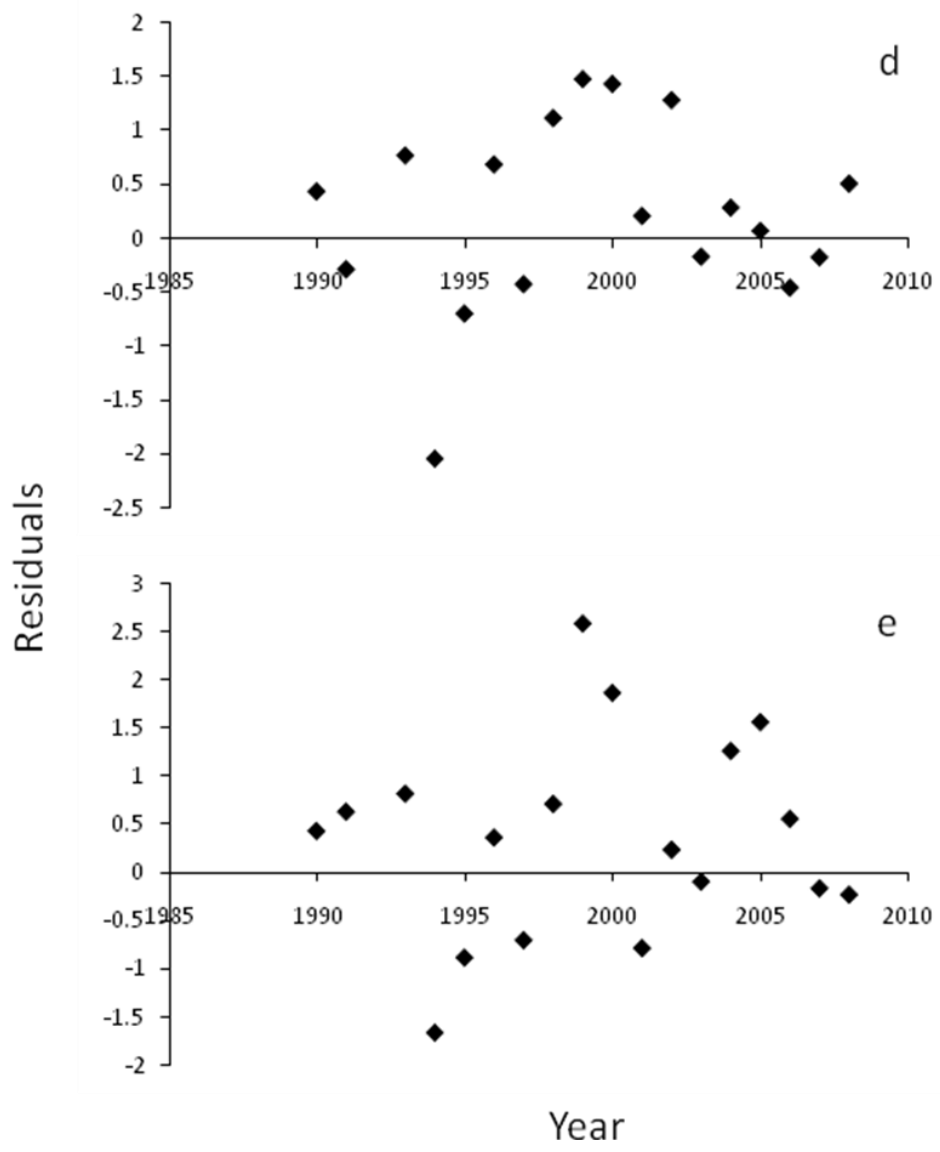






Appendix 3. Residuals for live oysters and boxes in each size category, spat (a), small (b) and market (c), small box (d) and market box (e) during 1990-2008.





Appendix 4. Model Code for the stage-structured model.

```
//Oyster model for MD portion of Ches. Bay
```

```
//Version for lower Potomac River
```

```
//12-15-2010
```

```
//M. Livings
```

DATA_SECTION

```
///ad_comm::change_datafile_name("mdoyst_rev_4-6.dat");
```

```
init_int fyear
```

```
init_int lyear
```

```
init_int fstage
```

```
init_int lstage
```

```
//init_int freyear
```

```
//init_int lreyear
```

```
init_vector Catch(fyear,lyear)
```

```
init_matrix obs_log_CPUE_den(fyear,lyear,fstage,lstage)
```

```
init_vector obs_log_spat_CPUE_den_7079(1980,1989)
```

```
init_matrix in_M(fyear,lyear,fstage,lstage)
```

```
init_vector Habitat(fyear,lyear)
```

```
init_vector stock(fyear,lyear) //numbers stocked
```

```
init_vector s_box_den_obs(fyear,lyear) //index of small boxes
```

```
init_vector m_box_den_obs(fyear,lyear) //index of market boxes
```

```
init_vector box_M_r(1,2)
```

```
init_vector sd_box_M(1,2)
```

```
init_number nperbushel
```

```
init_number sex_rS
```

```
init_number sex_rM
```

```
init_number fec_S
```

```
init_number fec_M
```

```
init_number sd_spat
```

```
init_number sd_small
```

```
init_number sd_mark
```

```
init_number sd_small_box
```

```
init_number sd_mark_box
```

```
init_vector sM_prior_mean(1,2)
```

```
init_vector mM_prior_mean(1,2)
```

```
init_vector sd_sM_mean(1,2)
```

```
init_vector sd_mM_mean(1,2)
```

```
init_number sd_sM
```

```
init_number sd_mM
```

```
init_number transit_prior_mean
```

```
init_number sd_transit
```

```
init_int non_rep_year
```

```

init_int non_rep_type
init_number non_rep_prop //amount of non-reporting 1986-2005
init_number non_rep_amt
init_int non_eq_yr1 //use equilibrium or non-eq method for estimating initial
stage structure
init_number stock_early_mort //additonal spat mortality due to stocking at a smaller
size
init_int stock_mort_change //year stocking practices changed
init_number hab_M
init_number test

```

```

vector adj_catch(fyear,lyear) //catch adjusted for non-reporting
vector CatchN(fyear,lyear)
number var_spat
number var_small
number var_mark
number var_small_box
number var_mark_box
vector var_sM_mean(1,2)
vector var_mM_mean(1,2)
number var_sM
number var_mM
number var_box_sM
number var_box_mM
number var_transit

```

```

number nyears
int i
int j

```

LOCAL_CALCS

```

/*
cout << "fyear " << fyear << " lyear " << lyear << " fstage " << fstage << " lstage "
<< lstage << endl;
cout <<"Catch"<<endl<<Catch<<endl;
cout << endl;
cout<<"obs_log_CPUE_den"<<endl<<obs_log_CPUE_den<<endl;

cout<<"obs_log_spat_CPUE_den_7079"<<endl<<obs_log_spat_CPUE_den_7079<<
endl;

cout << endl;
cout << "in_M"<<endl<<in_M<<endl;

```

```

cout << endl;
cout<<"Habitat"<<endl<<Habitat<<endl;
cout<<"stock"<<endl<<stock<<endl;
cout<<"s_box_den_obs"<<endl<<s_box_den_obs<<endl;
cout<<"m_box_den_obs"<<endl<<m_box_den_obs<<endl;
cout<<"box_M_r"<<endl<<box_M_r<<endl;
cout<<"sd_box_M"<<endl<<sd_box_M<<endl;
cout <<"nperbushel"<<endl<<nperbushel<<endl;
cout <<"sex_rS"<<endl<<sex_rS<<endl;
cout <<"sex_rM"<<endl<<sex_rM<<endl;
cout <<"fec_S"<<endl<<fec_S<< endl;
cout <<"fec_M"<<endl<<fec_M<<endl;
cout << test << endl;
*/

if (test!=123)
{
  cout << "data not reading properly" << endl;
  exit(1);
}

//convert SDs to variances
var_spat=square(sd_spat);
var_small=square(sd_small);
var_mark=square(sd_mark);
var_small_box=square(sd_small_box);
var_mark_box=square(sd_mark_box);
var_sM_mean=square(sd_sM_mean);
var_mM_mean=square(sd_mM_mean);
var_sM=square(sd_sM);
var_mM=square(sd_mM);
var_box_sM=square(sd_box_M(1));
var_box_mM=square(sd_box_M(2));
var_transit=square(sd_transit);

nyears=double(lyear-fyear+1);

//cout << var_mark_box << " " << var_small_box << endl;

//calculate catch in numbers
for (i=fyear;i<=lyear;i++)
{
  if (i<non_rep_year)

  {
    if (non_rep_type==0)

```

```

    {
      adj_catch(i)=Catch(i)/(1.-non_rep_prop);
    }
    else
    {
      adj_catch(i)=Catch(i)+non_rep_amt;
    }
  }
  else
  {
    adj_catch(i)=Catch(i)/.75;
  }
}

```

```
CatchN=adj_catch*nperbushel/1000000.;
```

```
//cout << r_catchN << endl;
```

```
//cout << CatchN << endl;
```

```
//adjust number stocked for changes in stocking practice
```

```
//no stocking is included in this model
```

```
for (i=fyear;i<=lyear;i++)
```

```

{
  if(i>=stock_mort_change) stock(i)*=(1.-stock_early_mort);
}

```

END_CALCS

PARAMETER_SECTION

```
//Phase 1 parameters
```

```
init_bounded_number log_init_R(0.,20.,1)
```

```
init_bounded_number log_eq_R(0.,20.,-1)
```

```
init_bounded_number log_N1(0.,20.,1)
```

```
init_bounded_number log_B1(0.,20.,1)
```

```
init_bounded_dev_vector log_N1_dev(1,2,-10.,10.,1)
```

```
init_bounded_dev_vector log_B1_dev(1,2,-10.,10.,1)
```

```
//Phase 2 parameters
```

```
init_bounded_number log_u0(-10.,0.,-2) //Not estimable because of timing of
growth relative to fishing mortality and survey
```

```
init_bounded_number log_transit(-5.,0.,5)
```

```
init_bounded_dev_vector log_rec_devs(fyear,lyear,-10.,10.,2)
```

```
//Phase 3 parameters
```

```

init_bounded_vector log_sM(1,2,-5.,5.,-3)
init_bounded_number log_mM(-5.,5.,3)

//Phase 4 Parameters
init_bounded_dev_vector log_M_dev1(fyear+1,lyear,-10.,10.,-4)
init_bounded_dev_vector log_M_dev(fyear,lyear,-10.,10.,4)
//init_bounded_dev_vector log_M_dev22(1996,lyear,-10.,10.,4)

//Phase 5 parameters
init_bounded_number log_box_sM(-5.,5.,-5)
init_bounded_number log_box_mM(-5.,5.,-5)

//Phase 6 parameters
init_bounded_number log_hab_par(0.,2.,6)
init_bounded_vector log_C_e(fyear,lyear,-5,5,-6)

//Calculated quantites
vector box_M(1,2)
vector Hab(fyear,lyear)
matrix obs_log_CPUE(fyear,lyear,fstage,lstage)
vector s_box_obs(fyear,lyear) //index of small boxes
vector m_box_obs(fyear,lyear) //index of market boxes
matrix N(fyear,lyear+1,fstage,lstage)
matrix M(fyear,lyear,fstage,lstage)
matrix trans_M(fstage,lstage,fyear,lyear)
vector u(fyear,lyear)
vector est_spat_CPUE(fyear,lyear)
vector est_small_CPUE(fyear,lyear)
vector est_mark_CPUE(fyear,lyear)
number spat_q
number small_q
number mark_q
number small_box_q
number mark_box_q
vector SSB(fyear,lyear+1)
vector rec_devs(fyear,lyear)
vector M_dev1(fyear,lyear)
vector M_dev2(fyear,lyear)

number transit
number u0
number box_p
matrix pre_N(1980,1989,0,2)

```

```

//vectors of residuals
vector sp_res(fyear,lyear)
vector sm_res(fyear,lyear)
vector ma_res(fyear,lyear)
matrix box(fyear,lyear,1,2) //boxes in the population
vector s_box_est(fyear,lyear) //index of small boxes
vector m_box_est(fyear,lyear) //index of market boxes

```

```

//variable so MCMC will run
sdreport_number p
likeprof_number Blast

```

```

//SPR quantities
vector SPR(fyear,lyear)
vector SPR_0(fyear,lyear)
vector N_SPR(fyear,lyear)
vector N_SPR_0(fyear,lyear)

```

```

//output for simulations
vector outputs(1,175)
number LL1
number LL2
number LL3
number LL4 //catch penalty
number LL6 //small box index
number LL7 //market box index
number LL8 //penalty on M variation
number prior_sm_box_q
number prior_ma_box_q
number prior_sM
number prior_mM
number prior_box_M
number prior_transit
number q_pen

```

```

matrix trans_N(fstage,lstage,fyear,lyear+1)
matrix L(fstage,lstage,fstage,lstage)
vector cat(fyear,lyear+1)
vector Exp_S(fyear,lyear)
objective_function_value negLL

```

LOCAL_CALC

```
log_init_R=log(28.);
```

```
//log_init_R= 8.1603;
```

```
log_eq_R=log(28.);
```



```

log_u0=log(0.1);
log_transit=log(0.4);
//log_rec_devs=log(Habitat)+.725;
log_sM=log(in_M(fyear,1));
log_mM=log(in_M(fyear,2));
//log_mM(2)=log(in_M(fyear,2));
log_box_sM=log(box_M_r(1));
log_box_mM=log(box_M_r(2));
//log_hab_par(1)=log(.069);
//log_hab_par(2)=log(.069);
log_hab_par=hab_M;
//log_hab_par(2)=log(hab_M);
//high hab loss
//log_hab_par(1)=log(.09);
//log_hab_par(2)=log(.09);

box_p=0.0; //proportion of the year used for box mortality calcs (when do boxes
decay)

```

END_CALCS

PROCEDURE_SECTION

```

//do calculations to initialize parameters
set_initial_conditions();
//Set initial abundance and recruitment
set_initial_N_and_R();
//calculate abundance, SSB, exploitable SS, and exploitation rate
get_N();
//calculate catchability and CPUE
get_q_CPUE();
//calculate likelihood function
evaluate_likelihood();
//calculate SPR
//calc_SPR();
//code to output MCMC results
if (mceval_phase()) MCMC_report();

```

FUNCTION set_initial_conditions

```

//Calculate relative habitat
Hab(fyear)=1.0;
for (i=fyear;i<1year;i++)
{

if(i<=1990)
{
Hab(i+1)=Hab(i)*exp(-log_hab_par);

```

```

}
else
{
  Hab(i+1)=Hab(i)*exp(-log_hab_par);
}
}

//Calculate indices of abundance from habitat and indices of density
for (i=fyear;i<=lyear;i++)
{
  for(j=fstage;j<=lstage;j++)
  {
    if(obs_log_CPUE_den(i,j)>-99)
    {
      obs_log_CPUE(i,j)=obs_log_CPUE_den(i,j)+log(Hab(i));
    }
  }
  if(s_box_den_obs(i)>-99)
  {
    s_box_obs(i)=s_box_den_obs(i)+log(Hab(i));
  }
  if(m_box_den_obs(i)>-99)
  {
    m_box_obs(i)=m_box_den_obs(i)+log(Hab(i));
  }
}

//convert box_M from log scale
box_M(1)=exp(log_box_sM);
box_M(2)=exp(log_box_mM);
/*
//fill in M_dev vector
for (i=fyear;i<=lyear;i++)
{
  if(i==fyear)
  {
    M_dev1(i)=0.;
    M_dev2(i)=0.;
  }
  else if(i>fyear && i<1996)
  {
    M_dev1(i)=log_M_dev1(i);
    M_dev2(i)=log_M_dev21(i);
  }
  else
  {

```

```

    M_dev1(i)=log_M_dev1(i);
    M_dev2(i)=log_M_dev22(i);
  }
}
*/
cat=0.;

//convert transition probability
transit=exp(log_transit);
p=transit;

// calculate M matrix
for(i=fyear;i<=lyear;i++)
{
  //M for spat from Mann et al. 2009
  M(i,fstage)=in_M(fyear,fstage);
  //if (i<1996) //pre disease
  {
    M(i,1)=exp(log_mM+log_M_dev(i));
    M(i,2)=exp(log_mM+log_M_dev(i));
  }
  /*else //post disease
  {
    M(i,1)=exp(log_mM(2)+M_dev2(i));
    M(i,2)=exp(log_mM(2)+M_dev2(i));
  }
  */
}

//reconvert initial assumed exploitation rate
u0=exp(log_u0);

//Function to set initial abundance and recruitment

FUNCTION set_initial_N_and_R

//No S-R function
for (i=fyear;i<=lyear;i++)
{
  N(i,fstage)=exp(log_init_R+log_rec_devs(i));
}

//calculate spat q

```

```

//Martell method to calculate spat q as geometric mean
spat_q=0.0;
for (i=fyear;i<=lyear;i++)
{
if(obs_log_CPUE_den(i,0)>-.99)
{
spat_q+=(obs_log_CPUE(i,0)-log(N(i,0)))/double(lyear-fyear);
}
}
spat_q=exp(spat_q);

//cout << spat_q << endl;
N(fyear,1)=exp(log_N1+log_N1_dev(1));
N(fyear,2)=exp(log_N1+log_N1_dev(2));

//calculate initial number of boxes
box(fyear,1)=exp(log_B1+log_B1_dev(1));
box(fyear,2)=exp(log_B1+log_B1_dev(2));

//calculate SSB
SSB(fyear)=N(fyear,2)*fec_M*sex_rM+N(fyear,1)*fec_S*sex_rS;

FUNCTION get_N
for(i=fyear;i<=lyear;i++)
{
//Calculate numbers in later stages
//Small
N(i+1,1)=N(i,fstage)*exp(-M(i,fstage))+N(i,1)*exp(-M(i,1))*(1.-transit);
//market
N(i+1,lstage)=(N(i,lstage)-CatchN(i))*exp(-M(i,lstage))+N(i,1)*exp(-
M(i,1))*transit;
//cout << N(i,lstage)<< " " <<exp(-M(i,lstage))<< " " << N(i,1) << " " << exp(-
M(i,1))<< " " << transit << " " << CatchN(i) << endl;

//calculate exploitable stock size
Exp_S(i)=N(i,lstage);

//check to make sure N stays positive
if(N(i+1,lstage)<0)
{
cat(i)=N(i+1,lstage);
N(i+1,lstage)=1.;
}
}

```

```

//calculate exploitation rate
u(i)=CatchN(i)/Exp_S(i);

//cout << i << endl;

//calculate SSB in the fall
SSB(i+1)=N(i+1,2)*fec_M*sex_rM+N(i+1,1)*fec_S*sex_rS;

//calculate boxes
if(i<lyear)
{
  for(j=1;j<=2;j++)
  {
    box(i+1,j)=box(i,j)*exp(-box_M(j))*(1-u(i))+exp(-box_M(j)*box_p)*N(i,j)*(1.-
exp(-M(i,j)));

    //constrain boxes so they are above zero (necessary to keep likelihood function
defined)
    if (box(i+1,j)<=0.) box(i+1,j)=0.1;
  }
}
}

//set BI=SSB in the last year (for likelihood profile to get starting values for multiple
MCMC chains
Blast=SSB(lyear);

FUNCTION get_q_CPUE
  //exit(1);
  //calculate catchability
  //Martell method to calculate spat q as geometric mean
  small_q=0.;
  mark_q=0.;
  small_box_q=0.;
  mark_box_q=0.;
  for (i=fyear;i<=lyear;i++)
  {
    if(obs_log_CPUE_den(i,1)>-99) small_q+=(obs_log_CPUE(i,1)-
log(N(i,1)))/double(lyear-fyear);
    if(obs_log_CPUE_den(i,2)>-99) mark_q+=(obs_log_CPUE(i,2)-
log(N(i,2)))/double(lyear-fyear);
    if(s_box_den_obs(i)>-99) small_box_q+=(s_box_obs(i)-
log(box(i,1)))/double(lyear-fyear);
    if(m_box_den_obs(i)>-99) mark_box_q+=(m_box_obs(i)-
log(box(i,2)))/double(lyear-fyear);
  }
}

```

```

small_q=exp(small_q);
mark_q=exp(mark_q);
small_box_q=exp(small_box_q);
mark_box_q=exp(mark_box_q);

//calculate indices just before fishery
for(i=fyear;i<=lyear;i++)
{
  est_spat_CPUE(i)=spat_q*N(i,0); //stocking not included
  est_small_CPUE(i)=small_q*N(i,1);
  est_mark_CPUE(i)=mark_q*N(i,2);
  s_box_est(i)=small_box_q*box(i,1); //index of small boxes
  m_box_est(i)=mark_box_q*box(i,2); //index of market boxes
}

//cout << box << endl;
//cout << endl;

FUNCTION evaluate_likelihood
//calculate likelihood function
LL1=0;
LL2=0;
LL3=0;
LL6=0;
LL7=0;

for(i=fyear;i<=lyear;i++)
{
  if(obs_log_CPUE_den(i,0)>-.99) LL1+=square(obs_log_CPUE(i,0)-
log(est_spat_CPUE(i)));
  if(obs_log_CPUE_den(i,1)>-.99) LL2+=square(obs_log_CPUE(i,1)-
log(est_small_CPUE(i)));
  if(obs_log_CPUE_den(i,2)>-.99) LL3+=square(obs_log_CPUE(i,2)-
log(est_mark_CPUE(i)));
  if(s_box_den_obs(i)>-.99) LL6+=log(sd_small_box)+.5*square(s_box_obs(i)-
log(s_box_est(i)))/var_small_box;
  if(m_box_den_obs(i)>-.99) LL7+=log(sd_mark_box)+.5*square(m_box_obs(i)-
log(m_box_est(i)))/var_mark_box;

  //if(N(i,0)<=0. || N(i,1)<=0. || N(i,2)<=0.)
  //{
  // cout << N << endl;

```

```

// exit(1);
//}
}

LL1/=var_spat*2.;
LL2/=var_small*2.;
LL3/=var_mark*2.;
LL1+=(nyears-1)*log(sd_spat);
LL2+=(nyears-1)*log(sd_small);
LL3+=(nyears-1)*log(sd_mark);
LL4=10.*norm2(cat);

//prior for natural mortality
//prior_sM=log(sd_sM_mean(1))+.5*square(log_sM(1)-
log(sM_prior_mean(1)))/var_sM_mean(1)+log(sd_sM_mean(2))+.5*square(log_sM(
2)-log(sM_prior_mean(2)))/var_sM_mean(2);
prior_mM=log(sd_mM_mean(1))+.5*square(log_mM-
log(mM_prior_mean(1)))/var_mM_mean(1);

//normal distribution for deviations from mean M
LL8=(nyears)*log(sd_mM)+.5*norm2(log_M_dev)/var_mM;

//prior for mean box M
prior_box_M=log(sd_box_M(1))+.5*square(log_box_sM-
log(box_M_r(1)))/var_box_sM+log(sd_box_M(2))+.5*square(log_box_mM-
log(box_M_r(2)))/var_box_mM;

//prior for transition probability
prior_transit=log(sd_transit)+.5*square(log(transit)-
log(transit_prior_mean))/var_transit;

//penalty for difference between small and market catchability
//q_pen=0.5*square(log(small_q/mark_q)-log(r_q(1)/r_q(2)))/.0001

negLL=LL1+LL2+LL3+LL4+LL6+LL7+LL8+prior_box_M+prior_sM+prior_mM+
prior_transit; //+square(Hab(1990)-.64)+square(Hab(2000)-.37);

//add penalty in negative log likelihood for large abundance
if (!last_phase())
{
//negLL+=0.5*norm2(u-.5)/.04;
//cout << "1" << endl;
}

```

```

FUNCTION MCMC_report
  trans_N=trans(N);
  trans_M=trans(M);

  ofstream ofest("mcmc_results.dat", ios::app);
  {
    ofest << negLL << " " << u << " " << SSB << " " << trans_N(0) << " " <<
    trans_N(1) + trans_N(2) << " " << 1.-exp(-trans_M(2)) << " " << 1.-exp(-
    exp(log_sM)) << " " << transit << " " << log_hab_par << " " << Hab << " " <<
    trans_N(1) << " " << trans_N(2) << endl;
  }
  ofstream ofpar("mcmc_par.dat", ios::app);
  {
    ofpar << log_init_R << " " << log_transit << " " << log_rec_devs << " " <<
    log_sM << " " << log_mM << " " << log_M_dev << " " << log_hab_par << endl;
  }
  ofstream ofspr("mcmc_spr.dat", ios::app);
  {
    ofspr << SPR << " " << SPR_0 << " " << elem_prod(trans_N(0)(fyear,lyear),SPR)
    << " " << elem_prod(trans_N(0)(fyear,lyear),SPR_0) << " " << SSB << endl;
  }
  ofstream ofpreds("mcmc_pred.dat", ios::app);
  {
    ofpreds << log(elem_div(est_spat_CPUE,Hab)) << " " <<
    log(elem_div(est_small_CPUE,Hab)) << " " << log(elem_div(est_mark_CPUE,Hab))
    << endl;
  }

```

REPORT_SECTION

```

//standard output to identify run
cout << "entering report section" << endl;
report << "Run details" << endl;
report<<"nperbushel"<<endl<<nperbushel<<endl;
report<<"sex_rS"<<endl<<sex_rS<<endl;
report<<"sex_rM"<<endl<<sex_rM<<endl;
report<<"fec_S"<<endl<<fec_S<<endl;
report<<"fec_M"<<endl<<fec_M<<endl;
report<<"non_rep_year"<<endl<<non_rep_year<<endl;
report<<"non_rep_prop"<<endl<<non_rep_prop<<endl;
report<<"non_eq_yr1"<<endl<<non_eq_yr1<<endl;
report<<"sd_spat"<<endl<<sd_spat<<endl;
report<<"sd_small"<<endl<<sd_small<<endl;
report<<"sd_mark"<<endl<<sd_mark<<endl;
report<<"sd_small_box"<<endl<<sd_small_box<<endl;
report<<"sd_mark_box"<<endl<<sd_mark_box<<endl;
report<<"box_p"<<endl<<box_p<<endl;

```



```

report<<"box_M_r(1)"<<endl<<box_M_r(1)<<endl;
report<<"box_M_r(2)"<<endl<<box_M_r(2)<<endl;
report<<"sd_box_M(1)"<<endl<<sd_box_M(1)<<endl;
report<<"sd_box_M(2)"<<endl<<sd_box_M(2)<<endl;
//report<<"sM_prior_mean(1)"<<endl<<sM_prior_mean(1)<<endl;
//report<<"sM_prior_mean(2)"<<endl<<sM_prior_mean(2)<<endl;
//report<<"mM_prior_mean(1)"<<endl<<mM_prior_mean(1)<<endl;
//report<<"mM_prior_mean(2)"<<endl<<mM_prior_mean(2)<<endl;
report<<"sd_sM_mean(1)"<<endl<<sd_sM_mean(1)<<endl;
report<<"sd_sM_mean(2)"<<endl<<sd_sM_mean(2)<<endl;
report<<"sd_mM_mean(1)"<<endl<<sd_mM_mean(1)<<endl;
report<<"sd_mM_mean(2)"<<endl<<sd_mM_mean(2)<<endl;
report<<"sd_sM"<<endl<<sd_sM<<endl;
report<<"sd_mM"<<endl<<sd_mM<<endl;
//report<<"transit_prior_mean"<<endl<<transit_prior_mean<<endl;
report<<"sd_transit"<<endl<<sd_transit<<endl;
report<<"stock_early_mort"<<endl<<stock_early_mort<<endl;
report<<"stock_mort_change"<<endl<<stock_mort_change<<endl;
report<< endl;
report << "NegLL: " << negLL << endl;
report << "spat small market catpen smallbox markbox M_devs smbox_q_prior
mboxprior sM_prior mM_prior prior_box_M trans_prior" << endl;
report << LL1 << " " << LL2 << " " << LL3 << " " << LL4 << " " << LL6 << " " <<
LL7 << " " << LL8 << " " << prior_sm_box_q << " " << prior_ma_box_q << " " <<
prior_sM << " " << prior_mM << " " << prior_box_M << " " << prior_transit <<
endl;
report << endl;

//calculate residuals
for(i=fyear;i<=lyear;i++)
{
//cout << i << endl;
if(obs_log_CPUE(i,0)>-.99) sp_res(i)=obs_log_CPUE(i,0)-log(est_spat_CPUE(i));
if(obs_log_CPUE(i,1)>-.99) sm_res(i)=obs_log_CPUE(i,1)-
log(est_small_CPUE(i));
if(obs_log_CPUE(i,2)>-.99) ma_res(i)=obs_log_CPUE(i,2)-
log(est_mark_CPUE(i));
}
//cout << "1" << endl;
trans_N=trans(N);
//cout << "2" << endl;

//report column labels

```

```

report << "year habitat obs_spat obs_small obs_mark obs_small_box obs_mark_box
est_spat est_small est_mark est_small_box est_mark_box spat_res small_res
mark_res small_box_res mark_box_res small_M mark_M u num_stocked
prop_stocked SSB_ind Exp_SS spat_N small_N market_N small_box_N
mark_box_N wild_R ln(R/S) sp_A sm_A ma_A SPR SPR_0 SPR_R Tot_N" <<
endl;
for(i=fyear;i<=lyear;i++)
{
report << i << " " << Hab(i) << " " << obs_log_CPUE(i,0) << " " <<
obs_log_CPUE(i,1) << " " << obs_log_CPUE(i,2) << " " << s_box_obs(i) << " " <<
m_box_obs(i) << " " << log(est_spat_CPUE(i)) << " " << log(est_small_CPUE(i))
<< " " << log(est_mark_CPUE(i)) << " " << log(s_box_est(i)) << " " <<
log(m_box_est(i)) << " " << sp_res(i)/sd_spat << " " << sm_res(i)/sd_small << " " <<
ma_res(i)/sd_mark << " " << (s_box_obs(i)-log(s_box_est(i)))/sd_small_box << " "
<< (m_box_obs(i)-log(m_box_est(i)))/sd_mark_box << " " << M(i,1) << " " <<
M(i,2) << " " << u(i) << " " << stock(i) << " " << 1.-(N(i,0)-stock(i))/N(i,0) << " " <<
SSB(i) << " " << Exp_S(i) << " " << N(i,0) << " " << N(i,1) << " " << N(i,2) << " "
<< box(i,1) << " " << box(i,2) << " " << N(i,0)-stock(i) << " " << log((N(i,0)-
stock(i))/SSB(i)) << " " << 1.-exp(-M(i)) << " " << SPR(i) << " " << SPR_0(i) << " "
<< (N(i,0)-stock(i))*SPR_0(i) << " " << sum(N(i)) << endl;
}
report << endl;

//Output parameter values
report << "qs" << endl;
report << spat_q << " " << small_q << " " << mark_q << " " << small_box_q << " "
<< mark_box_q << endl;
report << "transition probability" << endl;
report << transit << endl;
report << "box M" << endl;
report << box_M << endl;
report << "hab_pars" << endl;
report << exp(log_hab_par) << endl;

```

RUNTIME_SECTION

```

//change the maximum number of iterations for each phase
maximum_function_evaluations 2000, 2000, 2000, 2000, 2000, 5000

```

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