Larry Hogan, Governor

Mark Belton, Secretary

A Stock Assessment of the Eastern Oyster, *Crassostrea virginica*, in the Maryland waters of Chesapeake Bay

Final Report November 2018

Maryland Department of Natural Resources Fishing and Boating Services

in consultation with

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Executive Summary

This document presents the first formal stock assessment of the Maryland oyster population and fishery as well as estimates of biological reference points for use in management of oysters in Maryland. The assessment was conducted as a means toward achieving the goal of a more scientifically managed fishery and was mandated by the Maryland General Assembly as part of the Sustainable Oyster Population and Fishery Act of 2016 (Senate Bill 937, Chapter Number 703, 2016). This legislation directs the Maryland Department of Natural Resources in consultation with the University of Maryland Center for Environmental Science to conduct a stock assessment that will provide guidance for the development of biological reference points for the management of the oyster population.

The terms of reference for this stock assessment were developed based on the Sustainable Oyster Population and Fishery Act of 2016 and were reviewed by Maryland's Oyster Advisory Commission:

1) Complete a thorough data review: survey data, reported harvest and effort data, studies and data related to population rates (growth, mortality and recruitment), available substrate, shell budgets, and sources of mortality.

> a) List, review, and evaluate the strengths and weaknesses of all available data sources for completeness and utility for stock assessment analysis, including current and historical fishery-dependent and fishery-independent data.
>
> b) Identify the relevant spatial and temporal application of data sources.
>
> c) Document changes in data collection protocols and data quality over time.
>
> d) Justify inclusion or elimination of each data source.

2) Develop stock assessment model or index based approach that estimates biological reference points and document status of the stock relative to estimated reference points. To the extent possible, quantify sources of uncertainty within model.

3) Compare estimates of stock status generated by index and model-based approaches. Justify selected approach.

4) Include sanctuaries and restoration efforts in sanctuaries in the development of stock assessment approaches.

5) Examine how hatchery plantings (aquaculture and public fishery) impact spawning potential in the fishery.

TOR 1) Complete a thorough data review: survey data, reported harvest and effort data, studies and data related to population rates (growth, mortality and recruitment), available substrate, shell budgets, and sources of mortality.

All available sources of data were evaluated for potential inclusion in the oyster stock assessment, including commercial harvest and effort, fishery independent surveys (fall dredge and patent tong surveys), habitat from the Yates Bar Survey and Maryland Bay Bottom Survey, planting of wild seed, spat on shell, and shell, and other restoration activities. In addition, a search of the peer-reviewed literature was conducted to obtain estimates for life history parameters that were not available from Maryland Department of Natural Resources. *It was determined that the available data could support a stock assessment for the 1999-2000 through 2017-2018 seasons on a NOAA code level for 36 NOAA codes.* The assessment was restricted to Maryland waters under management of the Maryland Department of Natural Resources.

Two sources of commercial harvest and effort data are collected by the Maryland Department of Natural Resources: seafood dealer buy tickets and individual harvester reports (harvest reports). Every dealer registered to buy oysters in Maryland completes a buy ticket report for every purchase made from a licensed commercial harvester. These reports are then submitted to the department. Because oysters are almost always harvested and sold to seafood dealers on the same day, buy tickets represent a record of daily oyster harvest. Harvest reports are required from all commercial license holders who paid the annual surcharge to harvest oysters, even if no oysters were harvested. Harvest reports are submitted to the department monthly and describe daily harvest, effort, and other information. Ultimately, buy tickets were used in the analyses because they represented the longest, consistent time series available. The assessment is based on a 19-year period (1999-2000 through 2017-2018 seasons) for which buy ticket data with gear type and NOAA code were available. This period also contains years of both high and low mortality as well as the years with the lowest harvest. The buy ticket data were used in depletion analyses to summarize the daily catch and effort data, which produced estimates of abundance at the start of the fishing season and the fraction of the population harvested within a season. Estimates of the fraction of the population harvested were used as a data source for the stage-structured assessment model.

Since 1939, the Maryland Department of Natural Resources and its predecessor agencies have conducted surveys to monitor the oyster population in the Maryland portion of Chesapeake Bay; however, only data since 1980 are available in useable form. The current fall dredge survey samples oysters with a 32-inch-wide (0.81 meter) dredge on natural oyster bars, seed and shell plantings, and in sanctuaries from mid-October through late November. For each sample, live oysters are sorted into spat (recently settled oysters), smalls (≥ one year old and <76 mm), and markets (≥ 76 mm). Small and market boxes (dead oysters with hinges articulated) are also counted and categorized as recent or old. This survey was designed to monitor long-term trends in the oyster population (spat density, disease, biomass and mortality) rather than to estimate abundance. In the stage-structured stock assessment, oyster abundance and mortality rates were estimated by fitting the model to standardized counts of live oysters and boxes (see Section 2.4.1 for a complete description of the model and standardization procedure). Live oysters and oyster box counts were also used in two different methods to estimate natural mortality (see Sections 2.4.2 and 2.4.3).

The Maryland Department of Natural Resources regularly conducts hydraulic patent tong surveys for a variety of purposes: 1) to evaluate the effects of power dredging, 2) to assess the effects of waterway dredging or construction on oyster populations and 3) to assess potential aquaculture lease sites. When Maryland expanded the oyster sanctuary program in 2010, the Maryland Department of Natural Resources began a study to evaluate oyster populations within sanctuaries. These sanctuary surveys use a stratified random sampling design, with the strata based on substrate type. The number of sampling points varies based on the estimated amount of potential oyster habitat within the sanctuary but ranges generally from 50 to 300. Oysters are sorted into spat (newly settled oysters), smalls (≥ one year old and < 76 mm), markets (≥ 76 mm) and boxes (dead oysters with hinges articulated). Live oysters and boxes are counted and measured. The patent tongs used in these surveys sample an area of 1 square meter and because patent tongs sample a fixed area of the bottom, oyster density can be calculated. Density estimates were used as data for fitting the stage structured assessment model (Section 3).

Several attempts have been made to estimate the amount of oyster habitat in Chesapeake Bay. The first was the Yates survey from 1906 to 1912. The purpose of this survey was to identify the boundaries of "Natural Oyster Bars" within Maryland's portion of the bay, so that areas outside of oyster bars could be used for oyster aquaculture leases. The Bay Bottom Survey was conducted from 1975-1983, generating maps that updated the Yates bars. The Bay Bottom Survey used a dragged acoustical device, patent tongs, and sonar to produce bottom classifications that included sand, mud, cultch (oyster shells), and hard-bottom. Habitat data was used in the stage structured assessment model (Section 3).

Almost every oyster bar in Maryland has been modified over time through replenishment and restoration efforts to improve oyster bar productivity. Replenishment efforts were intended to enhance the public fishery for economic benefit and occurred prior to the establishment of sanctuaries. Restoration efforts are those activities occurring after the establishment of a sanctuary with the objective to restore oyster populations for ecosystem and ecological benefits. The types of enhancements employed in both replenishment and restoration include planting fresh and dredged shell, transplanting natural, wild seed, and planting hatchery-reared spat to attempt to increase oyster populations. Records of shell and seed plantings since 1999 were used in the stage-structured assessment model (Appendix II).

TOR 2) Develop stock assessment model or index based approach that estimates biological reference points and document status of the stock relative to estimated reference points. To the extent possible, quantify sources of uncertainty within model.

A stage-structured assessment model was developed (Section 3) to estimate abundance, natural mortality rates, and fishing mortality rates of oysters. A subsequent production model was developed (Section 5) to estimate fishing level reference points. The model was stage-based using the five stages described in the fall dredge survey: spat, small, market, small box, and market box. The model year began October 1, the start date of the oyster season for all gears except power dredge (the power dredge season begins November 1). The beginning of the model year is about the same time as the fall dredge survey. The processes modeled include recruitment of spat (natural and planted), growth from small to market size, natural mortality (including disease-related mortality) of smalls and markets, the effect of fishing on smalls and markets (fishing mortality), changes to habitat over time, effects of planting substrate and oysters, and the disarticulation of small and market boxes. A single stage-structured model was developed, but run separately with common rules on 36 individual NOAA codes allowing the assessment results to reflect varying rates of reproduction, growth and mortality within the Maryland Bay. NOAA code-specific results can be combined for Maryland-wide estimates.

Maryland-wide, the estimated abundance of market-size oysters varied between approximately 600 million and 200 million individuals over the assessment period. Estimated abundance of market size oysters was highest in 1999 (note that model years start on October 1), the initial year of the time series, decreased to about 200 million individuals by 2002, and remained close to that level until 2010. After 2010 estimated market abundance increased through 2014 to more than 450 million and declined to about 300 million thereafter. In 1999, estimated market abundance was highest in the Choptank River and Eastern Bay regions, but after 2006, estimated abundance was highest in the Choptank River and Tangier Sound regions. Maryland-wide, the estimated abundance of market-size oysters was higher in 2017 than it was from 2002 through 2007 but lower than in 1999. This pattern of increase towards 1999 levels of abundance differed among regions, with some regions showing little to no increase and others showing substantial increases in market oyster abundance since 2002.

Across NOAA codes, estimated natural mortality was generally higher and more variable in the beginning of the time series (1999 to 2002) and lower and less variable during 2003-2017. Despite similar temporal patterns, the year in which natural mortality first began to be lower and less variable varied among the regions of the bay. For example, in most of the Tangier

Sound region, estimated natural mortality became lower and less variable later than in most NOAA codes in the Choptank region.

The estimated fraction of oysters harvested (i.e., harvest fraction or exploitation rate) varied over time and among NOAA codes, ranging from zero to about 80 percent per year. The fraction of oysters harvested often tracked abundance in the NOAA codes. In NOAA codes where abundance was increasing over time and there were no large sanctuaries, the fraction of oysters harvested generally increased over time during 2008-2016. The Tangier Sound region and neighboring NOAA codes had the highest harvest fraction on average. In NOAA codes with no trend or a declining trend in abundance, the fraction of oysters harvested was usually low but showed some variability.

Abundance Reference Point and Population Status

The recommended threshold (minimum safe) abundance reference point is the minimum estimated number of market-size oysters during the period 1999 through 2017 for each NOAA code. This is based on the fact that oyster populations in most NOAA codes have been able to increase in abundance from their lowest observed levels, but it is unknown whether populations would be able to persist below those levels. Market-size oysters were chosen because they represent the fished population and because they produce more eggs per individual than small oysters. If abundance falls below the threshold, the oyster population within that NOAA code would be considered depleted. Given the current low abundance of oysters relative to historic periods and significant changes in the ecosystem (e.g., habitat loss, disease), it was not possible to develop a suitable method for calculating an abundance target.

Because the threshold abundance level is proposed as the lowest value within the assessment time frame, no areas were found to be depleted, although a few areas were close or equal to the time-series minimum in the final year of the assessment (2017). In these areas, any future declines occurring without an interim increase in abundance, would place them in the depleted category. This was true of NOAA codes in the Chester River (NOAA codes 131, 231, 331) and one in the middle Chesapeake mainstem (NOAA code 127). The southern portion of Tangier Sound and the southeastern mainstem of the Chesapeake (NOAA codes 192 and 129 respectively) had their lowest abundance values in 2016. The majority of NOAA codes had an estimated market abundance well above the limit abundance reference point in 2017.

Fishing Reference Points and Status

Maryland law states that fishery management plans “Shall prevent overfishing while attempting to achieve the best and most efficient utilization of the State's fishery resources” (Natural Resources Article §4-215). As such, fishery management plans should contain an upper limit reference point for fishing mortality to identify overfishing. Fishing mortality in this document is expressed as the proportion of market oysters in a NOAA code harvested in a given year (i.e., harvest fraction or exploitation rate). Furthermore, the statute states that target reference points should be identified to achieve the best utilization of the resource. The recommended target harvest fraction (U) is that which provides maximum sustainable yield (MSY). If U_{MSY} is achieved annually, it is expected to result in the maximum harvest over time and a stable or increasing oyster population (given current abundances of oysters in Maryland). As an upper limit reference point, the recommended value is an estimate of U_{crash}, which represents the absolute maximum exploitation rate that would allow sustainable harvest. If U_{crash} is consistently exceeded over time, it is expected to result in eventual disappearance of the population. The limiting rate for oyster population growth is likely their ability to produce shell. Therefore, shell production is an important process to include in sustainable harvest reference point calculations for oysters. The target (U_{MSY}) and upper limit (U_{crash}) reference points were estimated using a harvest fraction reference point model that describes population growth as a logistic function of abundance with carrying capacity determined by the amount of habitat. The amount of habitat depended on habitat production from living oysters, habitat loss, and a maximum amount of potential oyster habitat in the system (Section 5).

Estimates of the proposed upper limit reference point ranged from zero to 0.45 per year and estimates of the proposed target ranged from zero to 0.22 per year among NOAA codes. Estimates of the target and upper limit reference point were highest, on average, in the southernmost NOAA Codes, Tangier Sound and the Potomac Tributaries, and were lower in the more northerly regions. In the most recent fishing season (2017-2018), 19 NOAA codes had exploitation rates above the limit reference point, three were between the target and limit reference points, and 14 were at or below the target reference point.

It is important to note that the value for harvest fraction can be calculated in two ways and for each NOAA code the correct harvest fraction to use for comparison to the reference points depends on the management objective for the planted oysters. If oysters were planted with an objective of supplementing the fishery, then the harvest fraction that accounts for planted oysters should be the most appropriate for comparison with the reference points. If, however, the oysters were planted as part of restoration efforts to increase population size, then the harvest fraction that does not include planted oysters should be used. For the purposes of this report, all estimates of harvest fraction are corrected for the number of planted oysters. However, annual estimates of harvest fraction estimated using both methods are presented in the body of the report.

TOR 3) Compare estimates of stock status generated by index and model-based approaches. Justify selected approach.

Analyses were conducted to explore whether index-based approaches can be used in lieu of the full stage-structured model for assessing stock status relative to reference points. The harvest fraction estimates from the depletion analyses were considered as an alternative to harvest fractions estimated from the stage structured model, and indices of market oyster density from the fall dredge survey were considered as an alternative to estimated market abundance from the stage-structured model.

Harvest fractions were estimated by the depletion analyses using only the commercial harvest and effort data (i.e., the index-based approach) and also by the stage-structured stock assessment model (i.e., the model-based approach). The estimates from both methods (calculated as log F) are compared in the model fit plots in Section 4.1. Estimated harvest fractions from the stage-structured model were lower than estimates from the depletion analyses in most NOAA Codes and years. It was determined that this lack of agreement was acceptable because of perceived issues with the estimates from the depletion analyses (see Section 8.1). The main issues include:

1) Depletion analysis can only be used in areas with enough harvest to produce a measurable decline in catch per unit effort (CPUE). Potential issues with using the depletion method include changes in fishing locations during the course of the season, inaccuracies in reported harvest or effort or the inability of our chosen CPUE metric to track changes in abundance. In addition, in areas with large sanctuaries, the depletion method likely overestimates the harvest fraction because it reflects only the change in abundance in the fished areas.

2) From a practical perspective, in many years it was not possible to obtain estimates of harvest fraction using only the depletion method. This was caused either by a lack of harvest in a NOAA code or by infeasible estimates from the depletion model (a positive relationship between cumulative catch and CPUE). Given the perceived issues, the depletion method does not appear to be practical for use in monitoring the status of the stock relative to the harvest fraction reference points in many NOAA codes. Depletion analyses may be useful in NOAA codes that have consistently high harvest, particularly if more accurate harvest data become available.

As an index method for monitoring the abundance of market-size oysters relative to the proposed threshold, abundance estimates of market-size oysters from the stage-structured model were compared to the time series minima of the fall dredge survey standardized indices (index approach, Section 2.4.1). The index- and model-based approaches for abundance produced very similar results for some NOAA codes, but were substantially different for others. There was a close correspondence in the year of minimum abundance and density in the Tangier Sound and Choptank River regions with no NOAA codes having more than a one-year difference in the year of the minimum. Similarly, there was a close correspondence in the trends over time relative to the reference points in these two regions. The other regions had larger differences in both the year of the minimum abundance and the pattern over time between the index- and model-based approaches. In the Eastern Bay Region, patterns in estimated abundance and indices of market density were similar for NOAA codes in the Chester River. However, for other NOAA Codes in this region and most other regions (i.e., Mainstem, Patuxent and Potomac, and the Western Shore) the index of density was farther above its minimum value in the most recent years compared to results from the stage-structured model. Many of the NOAA codes in these regions had large differences in the year of the minimum value between the index- and model-based approaches, with ten of 20 NOAA codes having differences of at least three years.

Differences among the index- and model-based approaches for abundance arise because the stage-structured model estimates abundance whereas indices from the fall dredge survey reflect density (number per area). Therefore, if habitat (i.e., shell material) has declined substantially, abundance could decrease while densities remain relatively stable over time. The stage-structured model includes changes in oyster habitat over time, whereas the fall dredge survey time series does not include any adjustments for changes in habitat. Given the substantial declines in oyster habitat that have been documented in Maryland and the disagreement in results between the index- and model based approaches for abundance, the estimated market abundance from the stage-structured model is more appropriate than the indices of density from the fall dredge survey for comparison to the reference points.

It is recommended that estimates generated by the stage-structured model be used for the evaluation of the status of the oyster population and fishery relative to the reference points because these can be readily compared to both the harvest fraction and abundance reference points. The stage-structured assessment model integrates more available data than the index-based methods; therefore, estimates of harvest fraction and market abundance from this model are likely more accurate than the index based approaches. There is potential to use the depletion analysis in limited NOAA codes that have consistently high harvest, particularly if more accurate harvest data become available.

TOR 4) Include sanctuaries and restoration efforts in sanctuaries in the development of stock assessment approaches.

This TOR was addressed by including substrate and spat plantings (i.e., restoration efforts) explicitly in the stage-structured assessment model and conducting the assessment at the NOAA code level. Substrate additions (shell and alternative) increase habitat in the stage-structured model. Plantings of spat and wild seed also increase abundance of spat and small oysters, respectively. For the limit abundance reference point, oysters in sanctuaries count towards the limit within a NOAA code.

Fishing mortality (harvest fraction) on oysters in Maryland varies spatially. Sanctuaries represent one end of the fishing mortality continuum by mandating locations from which harvest is not permitted. A few NOAA codes are complete or nearly complete sanctuaries (e.g., Severn, upper Chester, upper Choptank and Nanticoke Rivers), and conducting the assessment at the NOAA code level explicitly accounts for sanctuary status on the population dynamics. However, for most other NOAA codes, sanctuaries and public harvest areas are both present. We were not able conduct our modeling efforts at a spatial scale smaller than the NOAA code level, because reported harvest at smaller spatial scales is not thought to be accurate.

In the methods employed in this analysis, oysters in sanctuaries count towards the abundance reference point within a NOAA code. However, it was not possible to address how sanctuaries affect harvest fraction reference points for several reasons outlined below.

1) The potential for increased productivity in areas outside of sanctuaries due to larval export from sanctuaries relies on larvae being the limiting factor for oyster abundance in a region. If the limiting factor for productivity outside of sanctuaries is not larvae, but something else such as available habitat, then an increase in larval supply will not result in increased numbers of spat. In most areas, the amount of available habitat is highly uncertain and has not been surveyed since the late 1970s-early 1980s. Without knowing what the limiting factor is for oyster populations in a NOAA code, it is difficult to determine if larval export from a sanctuary would increase productivity in neighboring areas outside of the sanctuary.

2) The connectivity among sanctuary and non-sanctuary areas would have to be known to modify exploitation rate reference points for the effects of sanctuaries. While progress is being made in understanding larval dispersal, larval transport models have yet to be validated for oysters in Maryland. Due to the limited understanding of larval oyster dispersal in Maryland, trying to fine tune reference points for these effects seems premature.

3) If abundance of adult oysters does not increase in a sanctuary, there will not be additional production within the sanctuary available to increase harvest rates outside the sanctuary. For example, oyster abundance in NOAA code 331 (upper Chester River) has not increased despite being a sanctuary, and therefore there is no increased production in this sanctuary to allocate to nearby public fishery areas.

4) If oyster abundance increases because of larval export from sanctuaries to surrounding areas, then the number of bushels allowed for sustainable harvest will increase even if the target fishing mortality reference point remains unchanged. For example, if the target is 0.1 (i.e., 10% of the population can be harvested) and there are 10 million market oysters in a NOAA code, then the target level of harvest would be 1 million oysters. If the number of oysters increased to 15 million because of increased spat sets caused by larval supply from a

sanctuary, then the target level of harvest would increase to 1.5 million oysters (10% of 15 million).

Overall, substantial improvements in information are needed to quantify the effect of sanctuaries on oysters in areas outside of sanctuaries. If oyster abundance increases in areas outside of sanctuaries because of larval supply from sanctuaries, then the currently proposed reference points would allow for a subsequent increase in sustainable harvest.

TOR 5) Examine how hatchery plantings (aquaculture and public fishery) impact spawning potential in the fishery.

This is a challenging TOR to address because once oysters are planted on public bottom or in sanctuaries they cannot always be readily distinguished from wild oysters. Also, aquaculture uses both diploid and triploid oysters, the latter of which are specifically bred not to spawn. Cultured oysters may also be harvested year-round and sometimes at a smaller size than wild-harvested oysters, which complicates determination of whether they are harvested before or after they spawn.

The approach used to address this term of reference was to make a broad comparison among 1) the estimated abundance of market-sized oysters from the stage-structured assessment model, 2) the estimated number of market-sized oysters generated by hatchery plantings using two different values for the assumed planted spat survival during their first two months (15% - base model, 5% - sensitivity analysis), and 3) the number of market-sized oysters harvested from leased grounds. While this simple comparison provides a perspective on the relative importance of planted oysters relative to wild oysters, there are several important caveats to the analysis: 1) the harvest of oysters from lease grounds is used as a proxy value for the number of market-size oysters that may be on lease grounds, 2) a mortality rate is applied to hatchery spat to project the number of market-sized oysters present in the population and this rate may vary spatially and temporally, 3) the reproductive output per individual is similar among wild and planted oysters, and 4) aquaculture data are not currently available on a NOAA code scale so this comparison must be done in aggregate for the entire Maryland portion of Chesapeake Bay. This aggregation will mask important spatial variation in the contribution of planted and aquaculture oysters because areas with plantings often receive higher fishing pressure than neighboring areas. Data on aquaculture planting numbers and harvest were summarized from leaseholder reports. The data included the bushels planted on leases, the number of individuals planted on leases by ploidy (diploid or triploid) and the bushels of oysters harvested.

The stage-structured assessment models were used to estimate the number of market-size oysters from plantings outside of leases each year. The number of market oysters from plantings outside of leases were then subtracted from overall market abundance to estimate the number of market oysters from wild production. These calculations assume that planted oysters experience the same mortality rates as wild oysters after October 1 of the year in which they were planted.

The number of oysters planted on leases in the Maryland portion of Chesapeake Bay increased by 30% from 231.7 million in 2012 to 301.3 million in 2016. Additionally, the percentage of planted oysters that are triploid more than doubled to 34% in 2016 from 15% in 2012 as the number of triploid oysters planted increased while diploid oyster plantings remained relatively constant. The number of oysters harvested from commercial shellfish leases in the Maryland portion of Chesapeake Bay increased from approximately 1.0 million in 2012 to 22.2 million in 2017.

The number of market-size oysters estimated from the stage-structured model as 'wild origin' was, on average, 18 times greater than the number harvested from commercial shellfish leases during 2012-2017. The estimated number of market-sized oysters generated from hatchery and wild plantings in non-lease areas was substantially greater than the number of oysters that were reported as being harvested from commercial shellfish leases.

The magnitude of lease harvest is small relative to the estimated abundance of oysters of wild origin, indicating that the spawning potential of oysters on leases is likely small relative to the population outside of leases at the Maryland-wide scale. In addition, any potential shift in the proportion of triploid oysters planted on leases would further erode the contribution of these animals to the total spawning potential.

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1.0 Background and Introduction

1.1 Distribution and Biology

The Eastern oyster, *Crassostrea virginica*, is native to coastal waters from the Gulf of St. Lawrence in Canada to the Atlantic coast of Argentina (Carriker and Gaffney, 1996). It is common in estuaries and coastal areas of reduced salinity and can occur as extensive reefs or 'bars' on hard to firm bottoms in both the intertidal and subtidal zones (Carriker and Gaffney, 1996). As is typical of animals that have evolved to inhabit the environmentally variable estuarine environment*, C. vir*ginica can tolerate a broad range of both temperatures and salinities (Shumway, 1996). In Maryland, sub-freezing temperatures and ice scouring restrict oyster bars to the subtidal zone (Galtsoff, 1964).

In the Maryland portion of Chesapeake Bay variable salinity and temperature regimes are primary environmental determinants of oyster population dynamics, given their influence on reproduction, growth, and mortality (Shumway, 1996). Mortality rates are interrelated with temperature and salinity because of the presence of two oyster protozoan parasites, *Perkinsus marinus* (Dermo disease) and *Haplosporidium nelsoni* (MSX). Dermo disease was identified in Chesapeake Bay oysters in 1949 but did not become a major problem until the mid-1980s (Ford and Tripp, 1996). MSX appeared in the Bay in 1959 and by the 1970s had dramatically reduced oyster densities in Virginia's high salinity oyster grounds (National Research Council, 2004). MSX is active at temperatures above 10°C although it is intolerant of salinities below 10 parts per thousand (ppt) (Ford and Tripp, 1996). The highly lethal Dermo disease proliferates most rapidly at temperatures between 25° and 30°C and salinities greater than 15 ppt, but survives at much lower temperatures and salinities (Ford and Tripp, 1996). During the latter part of the 20th century, these diseases had a devastating impact on oyster populations in Chesapeake Bay, although they acted on a population that was already compromised by poor water quality, fishing and habitat loss (National Research Council, 2004). In any case, the presence of these two pathogens adds complexity to oyster population dynamics in Chesapeake Bay because mortality rates may vary substantially among years and also spatially within the same year depending on where the oysters are located within the Bay.

All oyster bars in Maryland are located in mesohaline salinities (5-18 ppt). Within this salinity range, Maryland oyster bars are further classified into three zones whose boundaries, especially in the mid ranges, shift with varying climatic conditions. Zone one has an average salinity between five and < 12 ppt, Zone two has an average salinity between 12 and 14 ppt and Zone three salinities are greater than 14 ppt (Maryland Department of Natural Resources, 2004). In general, disease pressure intensifies during dry years as a result of the northward intrusion of the salt wedge and the resulting elevated salinities. In these years, Zone one can serve as a refuge from disease so that oysters in these areas may have lower mortality rates relative to the other zones. However, the influx of oyster larvae is intermittent and settlement rates are low in these less saline areas. Oysters in Zone one can also be subject to episodic freshets that result in substantial mortality (Maryland Department of Natural Resources, 2004). Zone two represents a transition area and oysters in these areas may have fluctuating rates of reproduction, growth and mortality based on the salinity variation between wet and dry years (Maryland Department of Natural Resources, 2004). In the Maryland portion of Chesapeake Bay, Zone three salinities are equal to or above 14 ppt and generally fall within what is thought to be the optimal salinity range (14 - 28 ppt) for *C. virginica* (Shumway, 1996). Although disease pressure can be persistent and mortality rates high in Zone three, reproductive capability is maximized so that there is likely to be consistent recruitment of new oysters.

Gametogenesis and spawning in oysters are directly correlated with water temperature (Shumway, 1996). In the Chesapeake, oysters begin gametogenesis in the spring and spawning can occur from late May to late September and generally peaks in late June or early July (Shumway, 1996; Thompson et al., 1996). The larval stage lasts for about 2 to 3 weeks, depending on food availability and temperature. Larval growth rates increase rapidly with increasing temperature; the fastest rates occur near 30°C. Larvae appear to migrate vertically, particularly at later stages, tending to concentrate near the bottom during the outgoing tide and rising in the water column during the incoming tide, thus increasing their chance of being retained in the estuary (Kennedy, 1996; Shumway, 1996)

C. virginica are either male or female (the reported incidence of simultaneous hermaphroditism is less than 0.5%) but may change sex over the winter when they are reproductively inactive. Generally, *C. virginica* function as males when they first mature which can happen as early as 6 weeks post settlement (Thompson et al., 1996). As the individuals grow, the proportion of functional females in each size class increases, with an excess of females occurring among larger (and presumably older) animals (Galtsoff, 1964).

The assessment team could find no definitive study of the longevity of *C. virginica*. Several ages have been proposed, the most common being 20 years (Sieling, ca. 1972; Buroker, 1983; Mann et al., 2009; NOAA-CBO, 2018), but the statements are either unsupported or make questionable inferences from other sources. Sieling (ca. 1972) comments “Oysters may live as long as 20 years, at least if undisturbed, as records of oysters kept in laboratories for that long are well known”, but with no supporting references. Powell and Cummins (1985) are cited in two papers for *C. virginica* lifespans of 10 to 15 years and 10 to 20 years, even though this species is never mentioned by them. Likewise, Lavoie and Bryan (1981) are cited for a longevity estimate of at least 15 years, although the only suggestion of longevity in their paper is a von Bertalanffy curve that extends to 14 years but with observed data only up to age eight. The longest estimate, 30 years, was made by Lockwood (1882). He based it on very old-appearing oysters that were supposedly planted 30 years earlier. He supported this assertion by counting 30 bands in the hinge area of both the upper and lower valves of a single oyster, a technique that subsequently has not gained widespread acceptance. *C. virginica* from plantings in Maryland have been reported to survive at least 9 years (assuming no natural reproduction in these areas; Paynter et al., 2010).

1.2 The Importance of Substrate

Larvae of *C. virginica* require a firm, sediment-free surface upon which to settle and metamorphose (Kennedy 1996), and this substrate is typically provided by oyster shell. The larvae's gregarious settlement response produces dense aggregations of oysters coexisting in communities, often called bars, reefs, or rocks (Smith et al., 2005). Oysters are unique in that they create the habitat they require for population growth. In the absence of fishing and other anthropogenic effects, the rate of shell accretion through recruitment, growth and mortality exceeds by some small amount the rate of shell loss (Mann and Powell, 2007). Fishing not only removes adult animals but also potentially decreases productivity of the population by altering and diminishing necessary habitat (Lenihan and Peterson, 1998). Reefs with higher profiles above the seafloor appear to promote enhanced oyster productivity. Low-profile reefs, are subject to sediment deposition on the reef surface (DeAlteris, 1988; Seliger and Boggs, 1988). Increased sedimentation reduces the nutritional value of material that oysters ingest, leading to reduced growth and reproduction and heightened physiological stress from clogging of the oyster's filtering mechanism (MacKenzie, 1983). Siltation on reefs also impairs habitat quantity and quality for settling larvae and attached juveniles (Bahr, 1976). Smith et al. (2005) concluded that, regardless of the cause, high rates of oyster mortality in the Maryland portion of Chesapeake Bay have reduced the ability of natural oyster bottom to accrete more shell, thereby rendering the remaining shell more susceptible to being covered by sediment.

1.3 Description and History of Fisheries

At the peak of its production in the late 1800s, the Chesapeake Bay was the greatest oyster-producing region of the world, with an oyster harvest twice that of the rest of the (non-US) world (Kennedy and Breisch, 1983). However, commercial landings in Maryland plummeted in the last part of the 19th century, with annual harvests decreasing by more than half between the late 1800s and the 1930s (Table 1, Figure 1). Over the following 50 years, harvests remained fairly stable, fluctuating around 2 million bushels annually until another decline occurred in the late 1980s primarily due to the oyster diseases MSX and Dermo (Maryland Department of Natural Resources, 1987). Since that time, commercial yields have remained at less than 400,000 bushels with a low of 19,028 bushels occurring in the 2003-2004 oyster season due to drought conditions and resulting elevated disease-related mortality (Maryland Department of Natural Resources, 2016). Although the department has harvest records back to the latter part of the 19th century, this stock assessment is conducted on an 19-year time series beginning with the 1999-2000 harvest season. This represents the time period when the most comprehensive and consistent harvest reports are available along with corresponding survey indices.

Maryland's commercial oyster fishery remains an important cultural and economic driver within Bay-side communities. Over the years since the 1999-2000 harvest season, the average annual ex-vessel value of the Maryland oyster fishery is estimated to be $6,888,960.

Oyster bars throughout the Maryland portion of Chesapeake Bay vary widely in their habitat quality and level of productivity. The patchiness of oyster habitat combined with the regional management of the harvest gears and the activities of the County Oyster Committees (see section 1.4) results in an oyster population and fishery that is spatially complex. During the time series covered by this assessment (1999-2000 through 2016-2017 seasons), the bulk (75 percent) of the harvest was generated by a small percentage of harvest reporting areas, known as NOAA codes and the fishery is generally consolidated in the lower Eastern regions of the Maryland portion of the Chesapeake.

1.4 Management

The Maryland oyster fishery is currently managed using a variety of laws and regulations that are mainly targeted at controlling effort:

Licensing and limited entry: Maryland regulation limits the number of commercial licenses for the harvest of oysters to 737. In addition to their annual license renewal fee, these licensees must pay an annual surcharge of $300(US) in order to activate their license to harvest oysters prior to each season. Maryland also has a cap of 2,091 commercial fishing licenses which enable the licensee to participate in a wide variety of fisheries including oysters. Individuals possessing this 'umbrella' license must also pay the annual surcharge to harvest oysters, which allows the department to identify what subset of these licensees are active in an oyster season. As such, there are 2,828 individuals who have the potential to harvest oysters in any given year (Code of Maryland Regulations [COMAR] 08.02.01.05, Natural Resources Article §4-10). Since the 1999-2000 oyster season, an average of 803 individuals paid the annual surcharge for oyster harvest. However, this number can fluctuate dramatically with changes in oyster abundance. For example, the number of surcharges rose from 599 in the 2011-2012 season to 1,134 in the 2014-2015 season, likely fueled by above average spat sets occurring in 2010 and 2012 which increased the availability of oysters for harvest.

Gear: There is a variety of permissible gears for the commercial harvest of oysters. Gears are restricted both in terms of when and where they can be used as well as in their dimensions (Code of Maryland Regulations [COMAR] 08.02.04, Natural Resources Article §4-10). The primary gears are hand tongs, patent tongs, diver, power dredge, and sail dredge. Hand tongs are typically constructed of two wooden shafts ranging from 16 to 30 feet long and attached to each other with a pin, similar to scissors, with rakes at the ends to harvest oysters. Patent tongs are similar to hand tongs, except the patent tongs are suspended from a cable, the rakes are larger and heavier and the tongs are opened and closed with hydraulic power. Divers use a surface-supply air hose or, in some cases, SCUBA to collect oysters, cull them, and then send them to the surface. A power dredge is a chain-mesh bag attached to a frame that is lowered to the bottom using a winch. The dredge is pulled along the bottom using a motorized vessel to collect oysters and then retrieved. A sail dredge, operated from a sailboat or skipjack, is typically a chain-mesh bag attached to a frame and pulled across the bottom using a boat under sail power. Sail dredges are allowed to use an auxiliary yawl boat to push the skipjack two days per week, which renders them similar to power dredges.

Season and time limits: The harvest of wild oysters in Maryland is restricted to the months of October through March (power dredging is conducted November-March). The department does have the authority to extend the season into April in the event of significant weather events such as icing that impede harvest during the normal season. Harvesting is allowed Monday through Friday from sunrise to 3 p.m., and the hours are extended to sunset in November and December. Because oyster harvest seasons straddle the calendar year, this report refers to 'seasons' rather than years. In cases where a year is used, it refers to the beginning year of the season.

Bushel limits: Daily catch limits have remained basically unchanged since the 1980s and depend on gear types. Currently, all gear types except power and sail dredge are allowed 15 bushels/license/day, not to exceed 30 bushels/vessel. Power dredges are allowed 12 bushels/license/day, not to exceed 24 bushels/vessel. Sail dredges are allowed 150 bushels/vessel/day.

Size limits: In 1927 the minimum size limit for oysters harvested from public grounds was increased from 2.5 to 3 inches, and this size limit remains in place to the present day (Kennedy and Breisch, 1983).

In addition to the traditional use of effort and size limit controls described above, the Maryland wild oyster fishery has been historically managed on a fine spatial scale (bar level) in cooperation with the oystermen of the State. In 1947 legislation created county oyster committees whose charge is to interact with management and to advise on closing and opening bars; and on shell and seed planting activities (Kennedy and Breisch, 1983). The county oyster committees remain in place to the present day and are closely involved in the management of harvest bars (Natural Resources Article §4-1106). Funding for county efforts to improve certain bars through the planting of hatchery spat on shell, wild spat on shell, or just cultch (shell) is generated from the $300 license surcharge paid by each oysterman, by a $1 tax levied on each bushel of oysters harvested, an oyster export tax, (Natural Resources Article §4-1020, §4-701) and since 1996, by a grant from the Maryland Department of Transportation, Port Authority.

The active management of the wild oyster fishery has historically focused on bolstering the productivity of individual bars through the placement of shell and oysters in order to maintain some level of harvest, rather than on population level parameters related to overall stock sustainability.

In 2010 the Maryland Department of Natural Resources amended its management plan for oysters to include a 10-point plan for the restoration of the oyster population and fishery in the Maryland portion of Chesapeake Bay (Maryland Department of Natural Resources, 2010). To implement the amended plan, the Maryland Department of Natural Resources overhauled its regulations for managing oysters; expanding the scale of oyster sanctuaries, creating new opportunities for oyster aquaculture, and designating areas to be maintained for the public fishery. Several objectives were laid out within the preamble to the regulations including to "*Implement a more targeted and scientifically managed wild oyster fishery*" (Maryland Register, 2010).

1.5 Call for Stock Assessment

This represents the first formal stock assessment of the Maryland oyster population and fishery. It is the first attempt to estimate biological reference points for use in management. This assessment is being conducted as a means toward achieving the goal of a more scientifically managed fishery and was mandated by the Maryland General Assembly as part of the Sustainable Oyster Population and Fishery Act of 2016 (Senate Bill 937, Chapter Number 703, 2016). This legislation directs the department to conduct a stock assessment that will provide guidance for the development of biological reference points for the management of the oyster population. A full report of assessment results will be submitted to the Maryland Oyster Advisory Commission and the Maryland General Assembly on or before December 1, 2018.

1.6 Terms of Reference

The terms of reference for this stock assessment were developed by the stock assessment team based on the Sustainable Oyster Population and Fishery Act of 2016 and were reviewed by Maryland's Oyster Advisory Commission:

> 1) Complete a thorough data review: survey data, reported harvest and effort data, studies and data related to population rates (growth, mortality and recruitment), available substrate, shell budgets, and sources of mortality.

a) List, review, and evaluate the strengths and weaknesses of all available data sources for completeness and utility for stock assessment analysis, including current and historical fishery-dependent and fishery-independent data.

b) Identify the relevant spatial and temporal application of data sources.

c) Document changes in data collection protocols and data quality over time.

d) Justify inclusion or elimination of each data source.

2) Develop stock assessment model or index based approach that estimates biological reference points and document status of the stock relative to estimated reference points. To the extent possible, quantify sources of uncertainty within model.

3) Compare estimates of stock status generated by index and model-based approaches. Justify selected approach.

4) Include sanctuaries and restoration efforts in sanctuaries in the development of stock assessment approaches.

5) Examine how hatchery plantings (aquaculture and public fishery) impact spawning potential in the fishery.

2.0 Description of Data Sources

2.1 Fishery Dependent Data

2.1.1 Harvest Data

Two sources of commercial harvest and effort data are collected by the Maryland Department of Natural Resources (the department): seafood dealer buy tickets (buy tickets) and individual harvester reports (harvest reports). Every dealer registered to buy oysters in Maryland completes a buy ticket report for every purchase made from a licensed commercial harvester. These reports are then submitted to the department (Appendix I). Because oysters are almost always harvested and sold to seafood dealers on the same day, buy tickets represent a record of daily oyster harvest. Harvest reports are required from all commercial license holders who paid the annual surcharge to harvest oysters, even if no oysters were harvested. Harvest reports are submitted to the department monthly and describe daily harvest, effort, and other information for that month (Appendix I).

Buy tickets and harvest reports both include useful information for estimating effort and harvest as they include trip-level data on total bushels harvested, gear used, location of harvest, and hours spent harvesting. The primary difference between the two data sources is that buy tickets indicate whether there were one or two licensees aboard the same vessel whereas harvester reports are submitted for each individual and it cannot be determined if two harvesters were working from the same boat. Therefore, buy tickets have important additional information because two licensees aboard a vessel each may harvest a full bushel limit so that vessels with two licensees have effectively twice the bushel limit of a vessel with only one licensed harvester aboard. The other major difference between the two data sources is the length of time for which the data are available. Buy tickets have been collected by the department since the 1970s and are available in an electronic database since 1988. The department did not require harvest reports until the 2009-2010 season, and these data are available through 2017.

This assessment is based on a 19-year time period (1999-2000 through 2017-2018 seasons) for which buy ticket data with gear type and NOAA code were available. This period also contains years of both high and low mortality as well as the years with the lowest harvest. While the assessment includes preliminary harvest data from the most recent season (2017-2018), the exploratory and ancillary analyses done for this assessment do not include 2017-2018 harvest data. This is due to timing of the analyses and the availability of the most recent year's harvest data.

This assessment is conducted on the scale of NOAA code. Harvest location is reported by the name of the oyster bar and by NOAA code (Maryland Department of Natural Resources, 2016). Individual oyster bars were delineated in surveys conducted between 1906 and 1912 (Yates,

1913) and these delineations were amended until the 1980s. There are 1,105 Yates bars and amendments with areas ranging from 1.2 to 4,988 acres with a mean size of 299 acres. NOAA codes are statistical reporting areas that were created for the purpose of reporting fishery harvest. There are currently 47 NOAA codes used by the department for shellfish harvest reporting but only 39 were considered for use in this stock assessment (Figure 2). The NOAA codes range in size from 868 to 236,874 acres with a mean size of 35,707 acres. A single NOAA code may contain multiple oyster bars. For convenience of presentation, individual NOAA codes are grouped into six geographical regions: Tangier Sound, Choptank River, Eastern Bay, Chesapeake Mainstem, Patuxent and Potomac Rivers, and the Western Shore. Table 2 presents summary details for each NOAA code.

Trip-level NOAA code information is included in buy ticket data for the entire time series, whereas bar-level information is not available before 2000, many bars have multiple common names, and official names are not universally applied within the oystering community. Eight NOAA codes were excluded from this analysis either because they were outside of the department's management jurisdiction (i.e., Potomac River NOAA codes 177, 277, and 377) or because the area is outside Chesapeake Bay (Maryland coastal bays NOAA codes 12, 212, 312, and 412) or because no oyster bars are located in the NOAA code based on historic surveys (NOAA code 14).

2.1.2 Description of Harvest and Effort

Harvest, effort and the annual number of participants show very similar patterns over the time series (Figure 3). Effort is calculated as the number of person (licensee) days per year, which is also used in the calculation of CPUE (section 2.2.1). The number of participants varies over time and is equal to the number of oyster license surcharges purchased each year. Effort is likely a primary determinant of harvest. Under current management, the fishery may be self-regulating in that effort diminishes when oyster density drops to a point where it is no longer commercially profitable to fish resulting in a boom and bust dynamic.

Over the 18-season time period (1999-2000 through 2016-2017), a total of 3.73 million bushels was reported harvested. This time series captures high harvest at the onset of the four-year drought (1999-2002). Harvest then fell to a time-series low of 19,028 bushels in the 2003-2004 as the persistent drought resulted in increased disease-related mortality. Harvest was low and stable during the period of 2004-2005 to 2011-2012 with an average of about 102,000 bushels per year. The reported harvest rose sharply in the 2012-2013 season to 330,664 bushels, following the strong spat sets of 2010 and 2012, and continued at this higher level through the 2015-2016 harvest season (Figure 4).

2.1.3 Patterns of Harvest by NOAA Code

No particular gear is used exclusively in any NOAA code but the harvest from most NOAA codes is dominated by a single gear (Figure 5).

Over 50 percent of the 3.73 million bushels harvested during the 1999-2000 to 2016-2017 seasons was reported from five NOAA codes, all located in southern and eastern regions of the Maryland portion of Chesapeake Bay (Figure 6). All other NOAA codes were negligible contributors to the overall harvest. Over this 18-season time series, 75 percent of the harvest was taken from 12 of 39 NOAA codes (Figure 7).

The top five NOAA codes with the greatest harvest are (in order from highest to lowest), Broad Creek (537), Eastern Bay (39), Upper and Lower Tangier Sound (292 and 192), and Fishing Bay (43). Harvest was reported from these NOAA codes for at least 15 seasons of the time series. These NOAA highly productive NOAA codes are located in three major regions: Tangier Sound, the Choptank River, and Eastern Bay/Chester River. All major gear types are represented in this harvest. It should be noted that the high harvest reported from Eastern Bay is due to extremely high harvests in the first two seasons of the time series (1999-2000 and 2000-2001) and this area is not currently a highly productive area.

A number of NOAA codes were inconsistently harvested, resulting in zero-harvest for many seasons (Table 3).

2.1.4 Patterns of Harvest by Gear

During the 1999-2000 to 2016-2017 seasons, 63 percent of the total harvest was from hand tong and power dredge in approximately equal proportion (32 percent and 31 percent). Patent tong and diver provided another 30 percent of the harvest (18 and 12 percent, respectively; Figure 8). Harvest by gear has shifted through the times series with power dredge harvest becoming more prevalent and then declining somewhat in the 2015-2016 and 2016-2017 seasons (Figure 9). This reflects the expansion of allowable power dredge areas in the 2002-2003 season. The shift to power dredge became more pronounced beginning in the 2008-2009 season. Prior to the 2002-2003 season, hand tong accounted for the majority of harvest (approximately 2.5 times the power dredge harvest). Patent tong harvest ranks third and has generally varied without trend to 2012-2013 season after which there is a slight increase (Table 4).

The gears used in the most productive NOAA codes differed (Figure 5; Table 5). Broad Creek (537) had separate hand tong and power dredge areas. The Little Choptank (053) was dominated by hand tong (88 percent of reported time series harvest). Although there was a small area designated for hand tong-only harvesting, Fishing Bay (043) was dominated by power dredge (88 percent of reported time-series harvest). Tangier Sound was the only one of the five most productive NOAA codes with a large proportion of patent tong harvest. Upper Tangier Sound reported harvest (292) was dominated by patent tong (47 percent) and Power Dredging (31 percent). Lower Tangier Sound (192) showed the opposite pattern with 67 percent of reported harvest from power dredge and 24 percent from patent tong. The shift in gear usage over time from hand tong to power dredge and a recent increase in patent tongs was a consistent Bay wide pattern.

2.1.5 Harvest Data Assumptions

Reported harvest, whether on buy tickets or harvester reports, is not expected to be a precise accounting of harvest as under-reporting and reporting errors are known to occur. An additional means to estimate harvest is through records of a tax ($1.00 per bushel) that is collected by the department from dealers for every bushel purchased from harvesters. These and other funds are used to maintain and enhance oyster bars through the additions of oyster shell, seed (smalls), and hatchery-reared spat. The pattern of harvest was similar between the three report types (Figure 10).

The three different harvest reporting methods provided the opportunity to estimate a reporting rate which can be applied to the time series of harvest used in the assessment model. Harvester reports were required for the first time in the 2009-2010 oyster season. During the first two years these were required, catch reported by individual harvesters was greater than that reported via buy tickets. In these first two years, harvester reporting was not enforced and it is assumed that this catch represents 'true reporting behavior' of the harvesters and therefore is a reasonable estimate of a scaling factor to for buy ticket data to correct for under reporting. The average difference between the two harvest estimates for these two years was about ten percent (90 percent of the harvest reported on harvester reports was reported on buy tickets). As such, ten percent was applied as a scalar to adjust the annual harvest used in the assessment upward.

The buy ticket records within the assessment time period were not all complete and there was no means to independently verify the reported catch. Many records did not have gear type or NOAA code recorded. Gear codes are used on the form to facilitate data entry but caused confusion among some dealers, especially during the period covered by this assessment. This was likely due to the co-occurrence of power dredging and traditional skipjack dredging, also known as “dredge boat” or “sail dredge.” For example, there was apparently no reported sail dredge harvest from 1999-2009 through buy tickets although it is known that skipjacks were harvesting during this period. While sail dredge harvest was not used for calculating catch per unit effort (section 2.2.1), some portion of this harvest may have been erroneously coded to power dredge. Some of the smaller NOAA codes may have also had a disproportionate amount of error due to the difficulty for harvesters and dealers to ascertain the proper boundaries on the maps provided to them. Nevertheless, the general trend of annual harvest estimates was very similar among the three sources of information which provides additional justification for use of the buy ticket data for the stock assessment.

2.2 Fishery Dependent Data - Calculations for Model Inputs and Verification

2.2.1 Catch per Unit Effort

The calculation of catch per unit effort (CPUE) was used in a depletion analysis to develop season-specific estimates of initial abundance and fishing mortality rates (F) by NOAA code. The resultant time series of F was used as an input to the assessment model. A complete description of the depletion analyses is provided in section 6.1 of this report.

Four different estimates of CPUE were considered:

1) bushels per license per day, 2) bushels per license per hour, 3) bushels per vessel per hour and 4) bushels per vessel per day.

Ultimately, bushels per license per day was chosen. Of the four CPUE calculations considered, bushels per license per hour had the greatest potential to accurately reflect effort expended for a given amount of catch. However, the number of hours spent harvesting was missing from many records (especially at the beginning of the time series), and the overall reliability of the reported values for hours was questionable.

Bushels per vessel per day would have provided the largest sample size because almost every record in both the buy tickets and the harvest reports has this information. However, the harvest reported on buy tickets is, in part, a function of the number of license holders on the vessel, since Maryland's daily oyster catch limit is defined as 'per licensee'. All but sail dredge vessels are allowed two licensees on board and each may catch their full limit. Therefore, vessels with two licensees may harvest more oysters than a vessel with a single licensee.

The chosen CPUE metric of bushels per license per day accounts for the presence of more than one license holder on a vessel and can be developed from both buy tickets and harvester reports. Buy ticket data were used in the depletion analyses because they provide a longer time series than the harvester report data. However, a comparison of results from both data sources indicated that initial abundance and fishing mortality rate (F) estimates were similar on average.

Before conducting depletion analyses with the buy ticket data, it was necessary to exclude six percent of the observations due to missing information or apparent mistakes either in the original physical buy ticket or in the data entry. Specific reasons for data exclusion included missing buy date, harvest season, or number of bushels; buy dates outside of the oyster season;

illegal gear for the time or area; gear type not permitted for commercial harvest; and reported daily bushel harvest above the legal limit.

2.2.2 Exploitation Fraction and Fishing Mortality Rate

The depletion method used was developed by Leslie and Davis (1939). The following description is modified from Ricker (1975). CPUE can be defined as,

$$CPUE_t = qN_t,$$

where the CPUE at time t is equal to the catchability (q) multiplied by mean abundance during time t (N_t). The abundance at time t is calculated as the difference between the starting abundance (N_0) and the cumulative harvest to time t (K_t),

$$N_t = N_0 - K_t.$$

Substituting the right hand side of the first equation into the second equation results in CPUE at time t as a function of the starting abundance, cumulative harvest to time t, and the catchability,

$$CPUE_t = qN_0 - qK_t.$$

This last equation is a linear function with CPUE at time t plotted against cumulative catch, which should result in a straight line with the slope (q) being an estimate of catchability. The y-intercept is the product of the catchability (q) and initial population size (N_0). The value of cumulative catch when CPUE is zero (i.e., the x-intercept) is an estimate of the initial population size.

The primary assumptions of the Leslie depletion method are:

1) removals are large enough to cause a decrease in abundance and CPUE,
2) cumulative harvest is known without error,
3) the removals represent random samples from the population,
4) the population is closed (i.e., no net immigration, emigration, non-harvest mortality, or recruitment) and
5) catchability is constant within a season (Cabraal and Wheaton 1981; Krebs, 1999).

Most of these assumptions have been discussed in detail as they apply to the oyster population in the Maryland portion of Chesapeake Bay (Cabraal and Wheaton, 1981).

Harvest exists in most NOAA codes, but these analyses were restricted to NOAA codes and years with at least 50 harvest records for a specific gear to ensure capturing the signal of decreasing CPUE and oyster abundance. The cumulative harvest data are thought to be a reasonably accurate representation of harvest patterns over time. Although the harvest data may be biased, there is no reason to believe the reporting rate changes during the harvest season which could cause bias in the estimated exploitation rate.

Oysters are sessile and therefore are not able to migrate. Most natural mortality and growth occur outside the harvest season (Albright et al., 2007; Liddel, 2008; Vølstad et. al., 2008). Some areas within a NOAA code receive more harvest pressure than others so removals are not random samples from the population, which means the depletion analysis reflects abundance and exploitation rates only in harvested areas and potentially not for an entire NOAA code.

The catchability assumption is the most difficult to ascertain as met. It has been postulated that catchability increases with increased harvest activity (Powell et al., 2006) which would cause estimates of exploitation rates to be biased low and initial abundance to be biased high.

Overall, it was determined that the assumptions are sufficiently satisfied to justify application of the Leslie depletion analysis techniques to these data.

When daily harvest limits exist, a substantial number of observations occur at the maximum legal daily harvest, especially early in the season when oysters are most abundant. Therefore, values for the CPUE metric (bushels per license per day) that were above the maximum daily limit were 'censored' and considered errors. To account for the upper limit on the CPUE metric, a censored regression was used (Tobin, 1958), in which the data are modeled separately for censored observations and non-censored observations. The R package VGAM (Yee, 2017) was used to conduct censored regression analyses.

After obtaining y-intercept and slope estimates from the censored regressions, initial population size (N_0) was estimated by setting y = 0 and solving for x in the following equation:

$$y = mx + b$$

where y is the CPUE, x is cumulative catch, m is the slope, and b is the y-intercept. This results in the following estimate of initial population size (N_0):

$$N_0 = -\frac{b}{m}$$

Because different gears are used within the same NOAA code, initial abundance was estimated using two different methods provided there were multiple gear types with at least 50 records for a season. The first approach assumes spatial overlap of the gears within a NOAA code and was applied to 34 of the 39 NOAA codes. In this method, total cumulative harvest from all gear types over the season and gear-specific CPUE data were used to estimate separate slopes and y-intercepts for each gear type, which assumes that the gear types were spatially intermixed or overlapping one another while harvesting. Each of the separate slope and y-intercepts were then used to estimate initial abundance, which could result in multiple estimates (one from each gear) for a season and NOAA code. When multiple estimates for a season were available the estimate from the gear type that had the most estimates in the 18-season time series was chosen.

The second approach was used where there was almost complete spatial separation of harvest by different gear types within a NOAA code, which included NOAA codes 78, 192, 231, 292, and 537. For this subset of NOAA codes, separate regressions were conducted for gear-specific cumulative harvest and CPUE data from each gear type with at least ≥ 50 records. The initial abundance estimates from each gear-specific regression were then summed to give a total abundance estimate. Regardless of which of the above two methods was used to estimate initial abundance, exploitation rate was estimated by dividing the total bushels harvested from all gears by the estimate of initial abundance (Ricker, 1975).

Exploitation rate estimates (u) were converted to instantaneous fishing mortality (F) using the following equation

$$F = -\log(1 - u)$$

Values for F were log-transformed before being used in the population dynamics model.

2.3 Fishery Independent Data

2.3.1 Fall Dredge Survey

Since 1939, the Maryland Department of Natural Resources and its predecessor agencies have conducted surveys to monitor the oyster population in the Maryland portion of Chesapeake Bay. Samples are collected on natural oyster bars, seed and shell plantings and in sanctuaries from mid-October through late November (Tarnowski, 2017). This survey was designed to look at long-term trends in aspects of the oyster population (spat density, disease, biomass and mortality) rather than to estimate abundance. Since 1975, 53 sites have been designated as "key bars" and are used to provide an annual index of spat settlement intensity at fixed locations. A subset of 43 bars, 31 of which are also key bars, are used to collect information on oyster parasite prevalence and intensity. From 1999-2017, the number of samples taken during the survey ranged from 310 to 385 (mean = 347) and the number of oyster bars sampled ranged from 255 to 270 (mean = 261).

The survey uses a 32-inch-wide (.81 meter) oyster dredge to obtain samples. Beginning in 2005, the distance for each tow has been recorded using a hand-held GPS unit. The total volume of dredged material is recorded prior to the sample being removed. A full dredge is 2.1 Maryland bushels (Maryland bushel = 2008.9 cubic inches or 45 liters). On key bar and disease bar sites, two one-half bushel samples are collected from replicate dredge tows, while at most other stations, a single half-bushel sample is taken. Water quality data (salinity and temperature) are collected on each bar. For each sample, live oysters are sorted into spat (recently settled oysters), smalls (≥ one year old and <76 mm), and markets (≥ 76 mm). Small and market boxes (dead oysters with hinges articulated) are also counted and the relative age of the boxes is assessed. For disease bars, key bars, and selected other samples, all live oysters and boxes are measured to the nearest millimeter. For the remainder, a range of oyster shell heights and an estimate of the mean are taken. Samples of live oysters are retained for disease testing at the 43 disease sites and selected other locations in the bay.

The oyster stock assessment incorporated data from the fall dredge survey for the years 1999 through 2017 for all NOAA codes except for the Potomac River, West and Rhode rivers, the Magothy River and Monie Bay. Potomac River samples were excluded because bars in that area are managed by the Potomac River Fisheries Commission. The other NOAA codes had no fall dredge survey samples for the time series. Figure 11 shows the sample sites for the 2016 fall dredge survey, excluding the Potomac River.

In the stock assessment, standardized counts of live oysters and boxes were used as data to which the assessment model was fitted to estimate abundance and natural mortality (see Section 2.4.1 for a complete description of the model and standardization procedure). Live oysters and oyster box counts were also used in two different methods to estimate natural mortality (see Section 2.4.2).

2.3.2 Patent Tong Surveys

The Maryland Department of Natural Resources regularly conducts patent (hydraulic) tong surveys for a variety of purposes: 1) to evaluate the effects of power dredging, 2) to assess the effects of waterway dredging or construction on oyster populations and 3) to assess potential aquaculture lease sites. When Maryland expanded the oyster sanctuary program in 2010, the department began a study to evaluate oyster populations within sanctuaries. Most sanctuaries have been sampled at least once (Maryland Department of Natural Resources, 2016).

These surveys use a stratified random sampling design, with the strata based on substrate type. The number of sampling points varies based on the estimated amount of potential oyster habitat within the sanctuary but ranges generally from 50 to 300. The patent tongs used in these surveys sample an area of 1 square meter. Any oysters in the sample are sorted into spat (newly settled oysters), smalls (≥ one year old and < 76 mm), markets (≥ 76 mm) and boxes (dead oysters with hinges articulated). Live oysters and boxes are counted and measured. The amount of total material in a sample is measured to the nearest 0.5 liter and the amount of surface material is estimated. Depth and bottom type are also recorded.

Because patent tongs sample a fixed area of the bottom, oyster density can be calculated. The average density of oysters based on all samples collected within a sanctuary was used to derive the overall density of oysters within the sanctuary.

2.3.3 Bay Bottom Surveys

Several attempts have been made to estimate the amount of oyster habitat in Chesapeake Bay. The first was the Yates survey from 1906 to 1912. The purpose of this survey was to identify the boundaries of "Natural Oyster Bars" within Maryland's portion of the bay, so that areas outside of oyster bars could be used for oyster aquaculture leases. The original Yates survey and subsequent surveys identified approximately 1,100 oyster bars and over 300,000 acres of oyster habitat. Later studies have estimated that only 36,000 acres is currently viable oyster habitat (U.S. Army Corps of Engineers, 2009).

The Bay Bottom Survey was conducted from 1975-1983, generating maps that updated the Yates bars. This survey used a dragged acoustical device, patent tongs and sonar, to produce bottom classifications that included sand, mud, cultch (oyster shells) and hard-bottom. Cultch and mixed-cultch categories are substrate types that provide habitat for oyster spat. These surveys (and other, more recent, side-scan sonar surveys conducted in sanctuaries) can be used to estimate the amount of habitat available for oysters.

2.3.4 Replenishment and Restoration Efforts

Almost every oyster bar in Maryland has been manipulated over time through replenishment and restoration efforts to improve oyster bar productivity. Replenishment efforts were intended to enhance the public fishery for economic benefit and occurred prior to the establishment of sanctuaries. Restoration efforts were those activities occurring after the establishment of a sanctuary with the objective to restore oyster populations for ecosystem and ecological benefits. The types of enhancements employed in both replenishment and restoration include planting fresh and dredged shell, transplanting natural, wild seed, and planting hatchery-reared spat in hopes of increasing oyster populations. Records of these activities date back to 1960, but shell and seed plantings only since 1999 were used in the assessment (Appendix II). All replenishment and restoration planting data are stored in an Arc GIS file. Information recorded includes planting year, planting type, planting location, and planting amount. Both the planting center point latitude and longitude is recorded along with the corner coordinates.

Since 2010, planting data has been recorded using GPS trackers and exact tracklines are provided to the department. Prior to 2010 there are issues within the data concerning both precision and completeness of records, and care must be used when trying to infer total planting volume within a given area.

2.4 Fishery Independent Data - Calculations for Model Inputs

2.4.1 Density - Standardization of Fall Dredge Survey Indices

A mixed-effects generalized linear model (GLM) was used to standardize the number of oysters per half bushel from the fall dredge survey data. This was done to account for bars that are not sampled every year so that in years when certain bars are not sampled the standardized indices would still reflect the influence of the un-sampled bars. For example, if a bar has very low numbers of live market oysters compared to other bars in the same NOAA code, then in years when that bar is not sampled the mean live market oysters for the NOAA code would be inflated because of missing data from the low density bar. Standardizing the indices accounts for the missing sample from that bar and adjusts the mean accordingly.

The mixed effects GLM was applied to each stage of oyster identified in the fall dredge survey: spat, small, small box, market and market box. The model included a fixed effect for year and a random effect for bar, as well as a negative binomial distribution and a log link function. The indices were standardized separately for each NOAA code and for each oyster stage. The models were implemented in R using the INLA package (Lindgren and Rue, 2015). Years with no observations or with all zeros for a stage were removed prior to the analysis because they are inestimable (i.e., the solution is undefined as the logarithm of zero). The resulting standardized indices were used to fit the population dynamics model.

Only bars with at least ten years of data were included because those with fewer than five years probably would not be informative for estimating trends over the entire 18 season time series and few bars were sampled for only five to ten years.

2.4.2 Empirical Estimates of Natural Mortality

Calculations of "observed" natural mortality (M) were used in sections 4.1 (Model Fit and Diagnostics) and in section 4.4 (Comparison of Natural Mortality Rates) to explore the reasonableness of the assessment model estimates of natural mortality. Observed values were calculated from the counts of live and dead oysters observed in the annual Maryland fall dredge survey (Tarnowski, 2016). In order to produce estimates of M in a manner consistent with the assessment, only oyster bars with 10 or more years of observations were used (section 2.4.1).

2.4.2.1 *Methods*

A general description of the Maryland fall dredge survey methodology is presented in 2.3.1. Dead oysters (boxes) are a pair of articulated valves with intact hinge ligament. Recent boxes have gaping valves and the interior of the shells have not yet been colonized by fouling organisms. Old boxes contain no oyster meat and the interior of the shells have been colonized. Recent boxes can be assumed to be 1-2 weeks old, based on an unpublished 2002 study in the Choptank River by the Maryland Department of Natural Resources (summarized in Vølstad et al., 2008). Dead oysters are categorized by age and size: recent market box, recent small box, old market box, and old small box.

Two estimates of natural mortality were calculated: total natural mortality, based on the sum of all box counts, and recent natural mortality, based on the sum of recent boxes.

Total annual natural mortality was calculated for each NOAA code and harvest season as the grand mean of all data collected during that harvest season as:

$$M = \frac{100 * (Total\ Market\ Box + Total\ Small\ Box)}{(Market\ Live + Small\ Live) + (Total\ Market\ Box + Total\ Small\ Box)}$$

where: Total Market Box = Old Market Box + Recent Market Box and

Total Small Box = Old Small Box + Recent Small Box.

Recent natural mortality based solely on recent boxes was calculated as:

$$M = \frac{100 * (Recent\ Market\ Box + Recent\ Small\ Box)}{(Market\ Live + Small\ Live) + (Recent\ Market\ Box + Recent\ Small\ Box)}$$

2.4.2.2 *Results and Discussion*

Most NOAA codes were represented by 7 or more bars (Table 6). Five NOAA codes were ultimately represented by only 1 or 2 bars (005, 082, 129, 174 and 268), but all but one of these NOAA codes were small (less than 7,000 acres). In general, larger NOAAs were represented by more bars (Figure 12).

The calculated values for total and recent natural mortality are presented in Tables 7 and 8.

Natural mortality of oysters in the Maryland portion of Chesapeake Bay is neither constant nor random over time, but a reflection of both environmental and disease effects. The relationship between salinity, oyster disease and total mortality is complex, but natural mortality is clearly influenced by disease (Figure 13). There are two oyster diseases that are known to have significant impact on oyster mortality in Chesapeake Bay since the 1950s (Andrews and Wood, 1967; Burreson and Ragone Calvo, 1996). Figure 13 represents data collected on a subset of 43 bars sampled annually for oyster disease by the fall dredge survey. *Haplosporidium nelsoni* (MSX) is intolerant of lower salinities found in Maryland Chesapeake Bay and is generally restricted to waters below the Chesapeake Bay Bridge, but its range expands in years of drought that cause higher salinities (Tarnowski, 2017). Such an expansion of range (percent of positive bars) and associated rise in disease prevalence (proportion of infected oysters) was seen during the 1999-2002 drought, along with a simultaneous rise in natural mortality (Figures 13-15). *Perkinsus marinus* (dermo) is tolerant of all salinities found in Maryland Chesapeake Bay and by the late 1990s was enzootic throughout Chesapeake Bay. Unlike MSX, dermo disease is always operating, causing some minimum mortality due to disease (minimum values of three to five percent).

Both total and recent natural mortality show regional differences and changes in mortality relative to other areas over time (Figures 14-15). In general, higher total natural mortality is seen in the Tangier Sound region and Patuxent/Potomac River complex relative to the Maryland bay-wide average. However, the Choptank region generally had lower total and recent natural mortality than the Maryland-wide average. However, natural mortality in the Choptank region during the 1999-2002 drought was the highest seen in the Maryland portion of Chesapeake Bay.

Both estimates of natural mortality reflect observed data, but may fall short in accurately representing annual natural mortality. Total natural mortality can overestimate annual mortality by including deaths from previous years because boxes can persist longer than 12 months (Christmas et al., 1997). It has been suggested that recent natural mortality is a better measure of annual natural mortality than total mortality (Vølstad et al., 2008). However, recent natural mortality can underestimate annual natural mortality because it does not include natural mortality older than two weeks or natural mortality that occurs soon after sampling. Both MSX and dermo disease cause mortalities during and beyond the October - November sampling events of the fall dredge survey (Albright et al., 2007).

2.4.3 Model Derived Natural Mortality

2.4.3.1 *Background*

As with observed natural mortality calculated from box counts (described above), model-based estimations of natural mortality (M) were also used in sections 4.1 (Model Fit and Diagnostics) and in section 4.4 (Comparison of Natural Mortality Rates) to explore the reasonableness of the assessment model estimates of natural mortality. The annual natural mortality rate (i.e., the fraction of oysters that die each year from non-fishing sources of mortality) can be estimated using the box count method (Ford et al., 2006). For a sample, the box count mortality rate is calculated by dividing the number of boxes in the sample by the sum of the number of boxes (i.e., shells of dead oysters with both valves still articulated by the hinge ligament) and live oysters in the same sample,

$$M_b = \frac{b}{b+l}.$$

Estimates of natural mortality rates for the Maryland portion of Chesapeake Bay are obtained using the box count method with samples from 43 fixed sites, which are then averaged to obtain the “observed” mortality index (Tarnowski, 2017). The box count method can also be applied to samples from the Maryland Department of Natural Resources fall dredge survey in a NOAA code to obtain regional estimates of natural mortality for the NOAA code. While the box count method is a logical choice for these annual survey data because of its minimal data requirements (counts of live oysters and boxes from a single sample in a year is sufficient to calculate an estimate of natural mortality), it relies on strong assumptions to ensure unbiased estimates and is not a statistical estimator.

Violations of the assumptions of the box count method may lead to bias in the estimates of natural mortality obtained using the method. The assumptions of the box count method include that boxes persist in the environment for only one year, and that live oysters and boxes are equally collected and retained by the survey gear. These assumptions may be violated for oysters in the Maryland portion of Chesapeake Bay, as there is evidence that some boxes remain intact for longer than one year (Christmas et al., 1997; Ford et al., 2006) and that the efficiency of dredge survey gear is lower for boxes than it is for live oysters relative to divers (Marenghi et al., 2017; Powell et al., 2007). Efficiency is defined here as the number of live oysters or boxes that remain intact in a dredge sample relative to the number present per the area swept (divers are assumed 100% efficient). Efficiency may be lower for boxes than for live oysters because boxes are more likely to be broken apart by the dredge or because the dredge does not collect boxes as efficiently as live oysters.

Quantifying the uncertainty in the natural mortality rate is an important component of understanding natural mortality and its interannual variability. Because the box count method is not a statistical estimator, it can only provide point estimates of natural mortality. Ratio estimators can be used with the box count method to estimate uncertainty, but they are likely to overestimate the precision because observations of live oysters and boxes are treated as independent.

Despite its potential to result in biased estimates of natural mortality, the implications of using the box count method for a population that does not adequately meet the assumptions have not been investigated, nor have there been attempts to modify the method to correct for potential violations of the assumptions. Therefore, we developed a new statistical method for estimating natural mortality that corrects for boxes persisting for longer than one year and for unequal efficiencies between live oysters and boxes and quantifies uncertainty. The approach was applied to adult oysters in the Maryland portion of Chesapeake Bay to understand spatial and temporal patterns in natural mortality by NOAA code.

2.4.3.2 *Methods*

A Bayesian model was developed and fitted to observations of live oysters and boxes from the Maryland Department of Natural Resources fall dredge survey to estimate natural mortality rates for each year and region (i.e., NOAA code). The model included bar and year effects, allowed for boxes to persist for longer than one year, estimated the rate at which boxes break down, and included a correction to account for the difference in catchability between live oysters and boxes.

Data

The data used in this model were counts of adult (i.e., small and market) live oysters and adult-sized boxes per half Maryland bushel of cultch in individual dredge tows. Numbers were normalized to per half Maryland bushel of cultch because it is the subsample volume for the majority of dredge samples during the fall survey. Spat were not included because spat boxes are rarely observed. Only data from bars that were sampled every year during 1990-2017 were used in this analysis. These years were chosen because the set of fixed sites called disease bars were first sampled annually in 1990, and 2017 was the most recent fall survey data available at the time. The model also allowed for the use of replicate tows on the same bar, which were treated as independent samples of counts for a given bar. The fall survey data in a given calendar year was used to estimate a natural mortality rate from the same calendar year.

Model Structure

The model was developed to use data from individual bars within a NOAA code to estimate natural mortality rates for that NOAA code. This was done for all NOAA codes with sufficient data in the Maryland portion of Chesapeake Bay. Although this model was developed to estimate number of live oysters and boxes per half Maryland bushel of cultch on each bar, the cultch volume used to normalize the counts does not affect the estimate of natural mortality because observations of live oysters and boxes come from the same samples (i.e., effort is the same for observations of live oysters and boxes). Note that numbers were all normalized to be per half Maryland bushel of cultch for all data or parameters that refer to numbers of live oysters or numbers of boxes in the following model description.

Likelihood Functions

The likelihood functions in the model described how well the observed number of live oysters or boxes fit the model estimates. The model allowed multiple observations for a bar in a year. Observation n of the number of live adult oysters $l_{n,i,y}$ on bar i in year y followed a Poisson distribution with a mean parameter $\lambda_{i,y}$ for bar i in year y,

$$l_{n,i,y} \sim Pois(\lambda_{i,y}) .$$

Likewise, observation n of the number of boxes $b_{n,i,y}$ on bar i in year y followed a Poisson distribution with a mean parameter $\beta_{i,y}$ specific for bar i and year y,

$$b_{n,i,y} \sim Pois(\beta_{i,y}) .$$

Box Dynamics Model

We developed a box dynamics model to estimate changes in boxes relative to live oysters over time. The model tracked a pool of boxes on each bar and included additions through natural mortality and losses through disarticulation. To correct for boxes persisting for longer than one year and for unequal efficiencies for live oysters and boxes, the mean number of boxes for a bar i in year y, $\beta_{i,y}$, were treated as a time series in the model. We calculated $\beta_{i,y}$ as the sum of boxes from natural mortality that occurred in previous years that have not yet disarticulated and boxes from natural mortality that occurred in year y corrected for their difference in efficiency,

$$\beta_{i,y} = \beta_{i,y-1} e^{-d} + \frac{\delta_{i,y}}{R_q},$$

where $\beta_{i,y-1}$ is the mean number of boxes from the previous year at the same bar, d is the instantaneous box disarticulation rate (i.e., the rate at which the hinge ligament connecting the two valves of a box fails; years^{-1}), which is the same for all bars and years, $\delta_{i,y}$ is the number of oyster deaths at bar i in year y given the same efficiency as for live oysters, and R_q is the ratio of the efficiency of live oysters to the efficiency of boxes which was constant for all bars and years. Because of the time series structure of the box dynamics model, one additional year of data was required to estimate the number of boxes at the beginning of the time series. R_q converted the efficiency of $\delta_{i,y}$ from the efficiency of live oysters to that of boxes, which was necessary because the other terms in the above equation assume the efficiency of boxes.

We parameterized the box dynamics portion of the model as a function of the natural mortality rate for each NOAA code. In the Maryland portion of Chesapeake Bay, the oyster fishery takes place in the fall and winter, while natural mortality occurs in the summer. Because observations from the survey take place after natural mortality, we needed to parameterize the model to be in terms of the number of oysters alive after natural mortality and the natural mortality rate. The number of oysters that die from natural mortality, $\delta_{i,y}$, was calculated as the difference between the number of live oysters before natural mortality and the number at the time of the survey,

$$\delta_{i,y} = \tau_{i,y} - \lambda_{i,y},$$

where $\tau_{i,y}$ is the number of live oysters at bar i in year y after the fishing season ends and after growth has occurred but before natural mortality occurs, and $\lambda_{i,y}$ is the number of live oysters after natural mortality occurs at bar i in year y.

Because there was no survey at the end of the fishing season before natural mortality occurred, $\tau_{i,y}$ was not directly estimable using the fall dredge survey data. Thus, another relationship with a variable that can be estimated using the fall dredge survey data was needed. If natural mortality was the only source of mortality after the fishing season, $\lambda_{i,y}$ can be modeled as the product of $\tau_{i,y}$ and the survival rate over the period where natural mortality occurs,

$$\lambda_{i,y} = \tau_{i,y}(1 - M_{r,y}),$$

where $M_{r,y}$ is the annual natural mortality rate for oysters in NOAA code r and year y. Note that the natural mortality rate was assumed to be the same for all bars in a NOAA code. The above equation can be solved for $\tau_{i,y}$,

$$\tau_{i,y} = \frac{\lambda_{i,y}}{1 - M_{r,y}},$$

and then substituted into the first equation for $\delta_{i,y}$ to remove $\tau_{i,y}$ as a variable,

$$\delta_{i,y} = \frac{\lambda_{i,y}}{1 - M_{r,y}} - \lambda_{i,y}.$$

The number of oysters that die from natural mortality at bar i in year y, $\delta_{i,y}$, is now specified in terms of variables that are estimable using the fall dredge survey data ($\lambda_{i,y}$) or of interest ($M_{r,y}$).

Priors and Model Parameterization

To provide additional constraints, we included priors on the log$_e$ scale by assuming that estimates of $\lambda_{i,y}$ from different bars in the same NOAA code were distributed normally with a mean parameter $log_e(\Lambda_{r,y})$, specific for each NOAA code r and year y, and standard deviation σ, which is the same across NOAA codes and years,

$$log_e(\lambda_{i,y}) \sim N(log_e(\Lambda_{r,y}), \sigma).$$

Similarly, log$_e$ scale estimates of $\beta_{i,0}$ from different bars in the same NOAA code were assumed to be distributed normally with a mean parameter for year 0, $log_e(B_{r,0})$, and standard deviation σ,

$$log_e(\beta_{i,0}) \sim N(log_e(B_{r,0}), \sigma),$$

where σ is shared in both of the above equations.

The fundamental parameters (i.e., parameters estimated directly in the model) were $log_e(\lambda_{i,y})$, $log_e(\beta_{i,0})$, d, $M_{r,y}$, σ, $log_e(\Lambda_{r,y})$, and $log_e(B_{r,0})$. The efficiency ratio R_q could not be estimated within the model because there was not enough information in the data to determine its value, therefore it was specified as a constant,

$$R_q = 1.68,$$

based on the averaged estimated efficiencies of live oysters and boxes from dredge efficiency studies (Marenghi et al., 2017; Powell et al., 2007). The efficiency ratio was calculated for each life stage (juvenile, submarket, and market) and sampling location from data in the two studies, then all values were averaged to obtain the ratio of the efficiencies.

Priors on $log_e(\lambda_{i,y})$ and $log_e(\beta_{i,0})$ were improper, uniform priors over all possible values.

For the box disarticulation rate, we used a normal prior with mean μ_d and standard deviation ϕ_d,

$$d \sim N(\mu_d, \phi_d),$$

where $\mu_d = 0.51$ and $\phi_d = 0.04$ were based on results from box disarticulation studies (Christmas et al., 1997; Ford et al., 2006). The values for μ_d and ϕ_d were calculated using data on the mean time since death (d) for samples from each year, season, and habitat type in Christmas et al. (1997) and assuming exponential decay to convert mean time since death to an instantaneous disarticulation rate (yr^{-1}). Instantaneous disarticulation rates (d^{-1}) were reported in Ford et al. (2006) and were converted to instantaneous disarticulation rates (yr^{-1}) for samples from each month and site. The mean and standard error of these estimates were used as estimates of μ_d and ϕ_d, respectively.

The annual natural mortality rate for each NOAA code and year, $M_{r,y}$, had a prior that followed a diffuse beta distribution with α and β parameters of 1,

$$M_{r,y} \sim Beta(1,1).$$

A beta distribution was chosen because annual natural mortality rates must be between 0 and 1.

A uniform prior was placed on σ to restrict the parameter to a reasonable range between 0 and 3,

$$\sigma \sim uniform(0,3).$$

Normal priors were assumed for $log_e(\Lambda_{r,y})$ and $log_e(B_{r,0})$,

$$log_e(\Lambda_{r,y}) \sim N(\mu_\Lambda, \psi_\Lambda)$$

$$log_e(B_{r,0}) \sim N(\mu_B, \psi_B),$$

where μ_Λ and μ_B are means and ψ_Λ and ψ_B are standard deviations. The mean hyperparameters were estimated from the mean of all observed values of live oysters (for μ_Λ)and boxes (for μ_B) for all NOAA codes and years. To ensure that these priors were relatively non-informative, ψ_Λ and ψ_B were both set at 5.

Model Implementation

The posterior distributions of the parameters were obtained using Stan through the R package RStan (Stan Development Team, 2018). Stan uses Hamiltonian Monte Carlo with a No-U-Turn sampler (HMC/NUTS) to estimate posterior distributions for all model parameters. Three independent chains were run with 2,000 burn-in iterations and 2,000 post-burn-in iterations per chain. The number of iterations was chosen such that effective sample sizes were close to 1,000 for all model parameters. A model was considered to have converged if all three chains had similar posterior distributions for all parameters, as indicated by a Gelman and Rubin potential scale reduction statistic (Gelman and Rubin, 1992) below 1.1, and if there were no divergent samples in the posterior. Divergent samples are a sampling issue unique to the algorithm used by Stan.

All NOAA codes with at least two complete time series of dredge survey observations (live oysters and boxes) during 1991-2017 (i.e., the bars had at least one fall survey dredge sample at each bar in every year from 1990-2017) were included in the model to estimate natural mortality rates on the NOAA code level.

Comparison of Model Natural Mortality with the Box Count Natural Mortality

To compare the difference in the natural mortality estimated between the box count method and the Bayesian model, natural mortality rates on the NOAA code level were also calculated using the box count method and the same data used in the model. For each sample, an estimate of the natural mortality rate was calculated, then these estimates were averaged by year and NOAA code to obtain an estimate of natural mortality from the box count method for a NOAA code in a year.

Dynamic Factor Analysis

We used dynamic factor analysis (DFA) to describe common trends in natural mortality among NOAA codes. DFA is used to determine common trends among time series that are relatively short and non-stationary such as time series of fisheries indices of abundance (e.g., Peterson et al., 2017; Zuur et al., 2003). Median estimates of natural mortality by year in each NOAA code from the Bayesian model were converted to instantaneous values, and each time series was standardized by subtracting the mean and dividing by the standard deviation of the time series. The mean and standard deviations were also examined for patterns.

We implemented DFA models in a similar manner to Holmes et al. (2018), Peterson et al. (2017), and Zuur et al. (2003). The main choices in the analysis were the choice of the covariance matrix of the error term (hereafter, “covariance matrix”) and the number of trends. A covariance matrix was chosen *a priori*, whereas model comparisons were used to select the number of trends.

A covariance matrix with equal value along the diagonal and zeros in the off-diagonals (i.e., equal variance and no covariance) was selected for parsimony and because the standardized natural mortality estimates should have similar error variances given that they were estimated from the same types of data using the same model.

DFA models with one to four trends were compared using corrected Akaike information criterion (AIC_c). Models with AIC_c that was less than five units different from the lowest AIC_c were considered similar and the fits and observed values were examined (Burnham and Anderson, 2002). The most parsimonious model with the lowest AIC_c, given that the fits to the data were reasonable, was chosen as the “best” model.

DFA models were implemented using the R package MARSS (Holmes et al., 2012), which uses maximum likelihood estimation to estimate parameter values.

2.4.3.3 *Results*

Natural Mortality from Model and Comparison with Box Count Estimator

In the Maryland portion of Chesapeake Bay, 29 NOAA codes had sufficient data to estimate natural mortality using the Bayesian model. The median number of bars in a NOAA code with adequate data to include in the model was five, and the maximum number of bars was 11 (Table 9).

For all parameters, the Gelman and Rubin potential scale reduction statistic was below 1.1 and there were no divergent samples in any of the posteriors. The lowest effective sample size was 951 for the annual natural mortality estimate in NOAA code 337 in 1994. All other effective sample sizes were above 1,000, and most of the parameters had the maximum possible effective sample size of 6,000.

Throughout the results we refer to estimates from the Bayesian model as “model natural mortality” and estimates from the box count method as “box count natural mortality.” These estimates are on the annualized scale (fraction per year) unless otherwise noted.

Across NOAA codes, model natural mortality was generally higher and more variable in the beginning of the time series (1991 to 2002) and lower and less variable at the end (Figures 16-20; Table 10). Despite similar temporal patterns, the year in which natural mortality first began to be lower and less variable varied among the regions of the bay. For example, in most of the Tangier Sound region (Figure 16), natural mortality became lower and less variable later than in most NOAA codes in the Choptank region (Figure 17).

The average (over years) of median instantaneous natural mortality from the model by NOAA code during 1991-2017 varied from 0.10 to 0.40 (annualized: 0.10 to 0.33; Figure 21a). In general, average natural mortality was lower in both the northern part of the bay and farther upstream in the tributaries. Likewise, the standard deviations associated with the median instantaneous natural mortality were typically higher in parts of the bay where the average median instantaneous natural mortality was higher (Figure 21b). However, there were some exceptions. For example, the NOAA codes 053, 137, and 637, did not have the highest average values relative to other NOAA codes, but they had the highest standard deviations of all modeled NOAA codes.

Estimates of uncertainty were relatively low. The estimated standard deviation of the model natural mortality posterior distributions varied from 0.003 to 0.214, with an average of 0.035. Uncertainty was also consistent across years, with the average standard deviation by year varying from 0.021 in 2014 to 0.051 in 2003 with a mean of 0.035. There was no clear relationship between the magnitude of the natural mortality rate and the amount of uncertainty associated with it.

In general, model natural mortality and box count natural mortality followed a similar pattern (Figures 16-20). During periods of low natural mortality over multiple years, the model and box count estimates of natural mortality were similar. However, the model natural mortality usually deviated from the box count mortality the most in two situations. First, the natural mortality from the model was often higher than the box count method estimates in years with a relatively high natural mortality event (e.g., 1995 in the Manokin River; Figure 16C). Secondly, in the two to three years following a relatively high natural mortality event, the model natural mortality was usually lower than the box count natural mortality (e.g., 1996-1997 in the Manokin River; Figure 16C).

In the sections below that refer to model natural mortality by region, mean and standard deviations (SDs) unless otherwise noted were calculated by using point estimates of the median model natural mortality from the years mentioned and all NOAA codes in the region (unless specific NOAA codes are mentioned), converting them to instantaneous values, taking the average or standard deviation, then back-transforming to the annual rate.

Tangier Sound Region

In the NOAA codes of the Tangier Sound region, model natural mortality was higher (mean = 0.33) and more variable (SD = 0.32) pre-2007, and then lower (mean = 0.14) and less variable (SD = 0.08) during 2008-2017 (Figure 16). The patterns in natural mortality were not entirely consistent among all NOAA codes in the region, but all NOAA codes experienced relatively high natural mortality events in 1992 (mean = 0.66) and 1999 (mean = 0.62), and most NOAA codes had high natural mortality events in 1995 (mean = 0.63). Many of the NOAA codes (six of eight) experienced low natural mortality in 1993 (mean = 0.14). Seven of eight NOAA codes had low natural mortality in 2011 (mean = 0.07).

Choptank Region

The patterns of natural mortality as estimated by the model were most consistent among the NOAA codes in the Choptank region (Figure 17). Lower (mean = 0.09) and less variable (0.07) natural mortality started at latest in 2004 (pre-2004 mean = 0.36, SD = 0.43), earlier than in Tangier Sound. The Choptank region had a consistent peak in natural mortality in 2002 (mean = 0.87) among all NOAA codes, followed by lower natural mortality in 2003 (mean = 0.21) in most of the NOAA codes. There was also relatively low natural mortality in 1994 (mean = 0.04) in all NOAA codes except in 337.

Eastern Bay Region

In the Eastern Bay region (which includes NOAA codes from the Chester River), the patterns were not as consistent among NOAA codes as in the Choptank (Figure 18). Natural mortality was lower (mean = 0.12) and less variable (SD = 0.10) after 2007 in most of the Eastern Bay Region NOAA codes, but the contrasts between the beginning and end of the time series were not as conspicuous as in other regions (pre-2007 mean = 0.26; SD = 0.23). Like in the Choptank region, there was high natural mortality in 2002 across all NOAA codes (mean = 0.55). Within the Eastern Bay region, the Eastern Bay and Miles River NOAA codes had similar natural mortality patterns with high mortality in 2002 and 2007, and the Lower Chester River and Mid Chester River (NOAA Codes 131 and 231) had a pattern that was distinct from the Eastern Bay and Miles River pattern.

Chesapeake Bay Mainstem

The NOAA codes of the Chesapeake Bay Mainstem region did not follow the same pattern of natural mortality rates over time (Figure 19). NOAA codes 27, 127, and 229 had a peak in 2002 followed by lower natural mortality rates through the end of the time series (for these NOAA codes, mean in 2002= 0.58; pre-2003 mean = 0.35; post-2002 mean = 0.10). South Mid-Bay and Lower Bay West (NOAA codes 27 and 229) also had high natural mortality events in 1992 (median = 0.61 and 0.86, respectively). Upper Bay (NOAA code 25) was different than the other mainstem NOAA codes, with low natural mortality throughout the time series (time series mean = 0.09), except for two relatively large years of natural mortality in 1996 and 2011 (median = 0.33 and 0.51, respectively).

Patuxent and Potomac Region

Natural mortality for NOAA codes in the Patuxent and Potomac Rivers region had different patterns than NOAA codes in the other regions (Figure 20). All NOAA codes except the St. Mary's River (078) had high natural mortality during 1999-2002 (mean = 0.56), and all NOAA codes experienced a large natural mortality event in 2002 (mean = 0.65). Following 2002, natural mortality was lower (mean = 0.14; pre-2003 mean = 0.38) and less variable (SD 0.13; pre-2003 SD = 0.34). The patterns in the upper and lower Patuxent (NOAA codes 168 and 368) were similar, with high natural mortality in 1991-1992 (mean = 0.68) and 1999-2002 (mean = 0.57), followed by low natural mortality during 1993 – 1998 (mean = 0.15) and 2003-2017 (mean = 0.14). In contrast, the Potomac tributaries (NOAA codes 78, 174, and 274) did not have similarly high natural mortality early in the time series.

Box Disarticulation Rate

One parameter was estimated for the box disarticulation rate in all regions of the model. The instantaneous box disarticulation rate posterior was higher (mean = 1.12 or 67% of boxes disarticulate each year) than the prior that was created from literature values (mean = 0.51 or 40% of boxes disarticulate each year; Figure 22).

Dynamic Factor Analysis

After standardizing the natural mortality time series, some common patterns among NOAA codes were visible (Figure 23). In particular, most NOAA codes had substantial variability with several high peaks during 1991-2002, but few NOAA codes had high values after 2002. DFA was able to describe the time series relatively well with two trends (Figure 24). The two-trend model had a lower AIC_c than the one, three, and four trend models.

The first DFA trend indicated fluctuating natural mortality during 1991-2002 (with peaks in 1992, 1995, 1999, and 2002). After 2002, the trend was relatively low and consistent (Figure 24). The second DFA trend had some variability during 1991-1999 with smaller magnitudes and opposite direction (i.e., if there was a peak in trend 1, it corresponded to a low value in trend 2 and vice versa) than in trend 1 (Figure 24). Trend 2 also displayed a distinct increase in natural mortality from 2000-2002, followed by a decline in 2003-2005, and a relatively stable pattern during 2006-2017.

The loadings on the DFA trends are a measure of how much a NOAA code influences each trend, and magnitudes of 0.2 or greater can be regarded as having a relatively strong influence (Zuur et al., 2003).

All NOAA codes except for 025 had positive loadings on trend 1. All positive loadings had magnitudes of greater than 0.2, and the largest loading magnitudes were in the NOAA codes in the Tangier Sound region and the Patuxent and Potomac Rivers region. For most NOAA codes, the magnitudes of the loadings were higher for trend 1 than for trend 2 (Figure 24).

The loadings were less consistent among regions for trend 2 (Figure 24). All NOAA codes in the Tangier Sound region except 043 and 062 had negative loadings on trend 2 (and the magnitude of the loadings for 043 and 062 were negligible). Negative loadings also occurred for NOAA codes 229 (Lower Bay West) and 168 (Lower Patuxent River). NOAA codes in the Choptank region and Eastern Bay region all had positive loadings on trend 2, as did most NOAA codes in the Mainstem and Patuxent and Potomac Regions.

2.4.3.4 *Discussion*

The model and box count method had similar natural mortality patterns in most years, likely because the two corrections included in the model (for boxes remaining intact for longer than one year and for the difference in dredge efficiency between live oysters and boxes) offset each other on average. The amount of difference in the natural mortality rate estimated by the two methods depends, in part, on the values of the efficiency ratio and the box disarticulation rate. If the efficiency of live oysters is higher than that of boxes (e.g., Marenghi et al., 2017; Powell et al., 2007), the natural mortality rate estimated by the model will be higher than the box count method, whereas when there are boxes persisting for longer than one year, the model will estimate lower natural mortality relative to the box count method. For oysters in the Maryland portion of Chesapeake Bay, these two effects largely offset one another in most years, resulting in model natural mortality rates that are similar to box count natural mortality rates.

However, there are two situations where the net effect of the corrections leads to a substantial difference between natural mortality estimated by the model and by the box count method. In years of high natural mortality, model natural mortality tends to be higher than box count natural mortality, while in the years following the high natural mortality, model natural mortality estimates are lower than estimates from the box count method. These differences arose because the corrections did not balance out in these years. The correction for difference in efficiency acts as a scalar on the natural mortality rate, causing the scale of the correction to always be the same, while the size of the correction for boxes persisting for longer than 1 year depends on the number of boxes observed in previous years. When a large pulse of boxes occurs, as happens during a high natural mortality event, the effect of the correction for boxes remaining intact longer than one year will be relatively large in the years following the pulse of boxes. A fraction of this pulse remains intact through the next year (the fraction depends on the box disarticulation rate), and thus it is likely that a large portion of the boxes seen in the next year will be attributed to natural mortality from the previous year. The effect of boxes from the previous years is often substantial because a high natural mortality event also reduces the number of oysters alive the next year. In contrast, the box count method assumes that all boxes observed came from oysters that died that year. Therefore, in the years following a pulse of boxes, the box count method will treat residual boxes from previous years as contributing to that year's mortality, resulting in a higher estimate of natural mortality compared to the model. These differences in how observations of boxes are interpreted between the model and the box count method can create substantial differences in the estimated natural mortality rates between the two methods.

One consideration that was not addressed in the model or in the box count method is that there are boxes from mortality events during a year that disarticulate before the survey (Ford et al., 2006). Because oysters die from natural mortality throughout the summer and the fall dredge survey does not start until October, some boxes likely disarticulate before the survey. Ford et al. (2006) deployed boxes from recently sacrificed oysters in early July and checked them monthly for disarticulation; after about 100 days (in early October and 3 months after deployment), approximately 20% of the boxes had disarticulated. The value of the efficiency ratio can be modified to account for the boxes that disarticulated before the survey, and when this was done, natural mortality increased by 17.8% on average for all years and NOAA codes. This additional correction can easily be incorporated into the model and changes the estimates of natural mortality. Including boxes that disarticulate before the survey changes the balance between corrections included in the model such that the corrections no longer balance each other out in most years.

The Bayesian model likely provides more accurate estimates than the box count method because it incorporates corrections for two important assumptions from the box count method. However, the model requires information on relative efficiency and box decay rates to correct for these effects. The relative efficiency may differ depending on the survey gear (Chai et al., 1992) and potentially habitat characteristics (Powell et al., 2007).

Results from DFA indicated that the patterns in natural mortality were consistent among most regions of the Maryland portion of Chesapeake Bay. In most NOAA codes, the trends and loadings from the dynamic factor analysis indicated that natural mortality was more variable in the in the beginning of the time series as compared to the end (apparent in trend 1), there was a large increase of natural mortality in 2002 (trend 2), and that this increase was followed by a decrease where natural mortality was consistently below average from 2003-2017 (trends 1 and 2). In contrast, the Tangier Sound region (except 043 and 062) and two other NOAA codes located near the region (NOAA codes 229 and 168) loaded differently on the trends. Although these NOAA codes load similarly on the first trend, the negative loadings on the second trend suggest that Tangier Sound experienced less of an increase in its natural mortality rate in 2002 compared to most other NOAA codes. Finally, Upper Bay (NOAA code 025) had different loadings than the other NOAA codes, with a small negative loading on the first trend and a small positive one on the second.

Relating environmental data such as winter temperature, summer temperature, summer salinity, and disease levels to natural mortality patterns could explain the distinct natural mortality patterns in the Tangier Sound region and the Upper Bay. Tangier Sound is in the southernmost part of the Maryland portion of Chesapeake Bay and therefore is subject to the highest salinities. Because of its high salinity, MSX is typically found consistently in this region and only spreads to other regions of the Maryland portion of Chesapeake Bay during years of low freshwater flow when salinity increases throughout the bay (Tarnowski, 2017). On the other hand, Upper Bay is in the northernmost, freshest part of the Bay and is subject to freshets that can cause oyster mortality (Tarnowski, 2012). Investigating the relationship between natural mortality, disease data, and environmental conditions may allow for a better understanding of why natural mortality patterns differ in the Tangier Sound region (and in some nearby NOAA codes) and in the Upper Bay compared to the other NOAA codes. Future research on changes in natural mortality rates should focus on the effects of environmental factors.

3.0 Stage-Structured Assessment Model Description

3.1 Overview

Statistical, stage-structured models for oysters were constructed for 36 NOAA codes located in the Maryland portion of Chesapeake Bay that had Fall Survey data available during 1999-2017. These are similar to models developed by Wilberg et al. (2011) and Damiano (2017). The models were built in Template Model Builder (Kristensen et al., 2015) to estimate abundance by stage, natural mortality rates, amount of available habitat, oyster density and exploitation rates. The models were fitted to standardized indices of density from the Maryland Department of Natural Resources fall dredge survey (Section 2.4.1), an index of recent natural mortality (Section 2.4.2), and estimated exploitation rates from dealer reported buy tickets from the 1999-2000 through the 2017-2018 oyster seasons (section 6.1) and estimates of small and market oyster density from patent tong surveys (section 2.3.2) using a maximum likelihood approach.

In making decisions about analyses, the stock assessment team sought to achieve the following objectives: Respond to the specific requests in Sustainable Oyster Population And Fisheries Act of 2016 within the timeframe and resource limitations; Use as much of the data as possible while recognizing the limitations of the available data; Conduct a comprehensive review of the data with a focus on their ability to reflect population dynamics and their utility to support a stock assessment; Critically review the limitations of each data source to support the corresponding estimating procedure(s); To the degree possible use estimates from Maryland and the surrounding region; Attempt to represent the spatial differences in oyster dynamics and fishery management to the degree possible; Investigate the spatial scale at which assessment tools can produce effective management guidance; Incorporate as much of the oyster biology as possible; And use multiple techniques to determine the degree of correspondence in the results.

During development of the stage-structured stock assessment model, the assessment team had to make decisions about which data sources to prioritize in model fitting. These decisions were necessary because of conflicting information in the data about model parameters. The priorities selected by the assessment team were:

Priority 1) fit the fall dredge survey data because it is the most extensive (temporally and spatially) data set for monitoring oyster population dynamics in Maryland.

Priority 2) fit the patent tong density data because they serve as ground truth data for abundance estimates.

Priority 3) achieve a close correspondence between stage-structured model estimates and box count mortality rates. Changes in natural mortality rates are important for oyster dynamics and the fall dredge survey data are thought to describe these patterns well.

Priority 4) match the fishery dependent estimates of fishing mortality rates. These data were given the lowest priority in model development because potential issues with the data and spatial patterns of the exploitation made these estimates less reliable than the other data sources (as described in section 8.1.3.6).

3.2 Assessment Model

3.2.1 Population model

The models were stage-based using the five stages described in the fall dredge survey: spat (recently settled oysters), small (≥ one year old and <76mm), market (≥ 76mm), small box, and market box. The model year began October 1 which is the beginning of the oyster season for all gears except power dredge which begins November 1. The model year coincides with the timing of the fall dredge survey. The processes being modeled included recruitment (natural and planted), growth from small to market sizes, natural mortality (including disease-related mortality) of smalls and markets, the effect of fishing on small and market oysters (fishing mortality), changes to habitat over time, and the disarticulation of small and market boxes. Model variables and parameters are described in Table 11. Catch was converted from bushels to number of individual oysters using a conversion factor of 228 individuals per bushel. The model also used a value of 8% for the number of small oysters (less than 3 inches, 76 mm) in a bushel. These values were based on a field study conducted for this assessment (Appendix III).

The initial abundance of spat, smalls, and markets in the first year were estimated parameters. The model estimated the spat abundance each year as the sum of the estimated number of naturally produced spat and the number of planted spat,

$$N_{y+1,\mathrm{sp}} = R_y + N_{a,y} S_a.$$

The number of spat planted was multiplied by a survival rate of 15 percent based on densities of spat one to two months after planting relative to the initial planting density (K. Paynter, UMCES, unpublished data).

The number of smalls each year was estimated by calculating the number of spat that survive natural mortality from the previous year to become smalls and adding those to the smalls already in the population that survived natural mortality and harvest, but did not grow to be markets, and the number of wild seed planted that survived natural mortality,

$$N_{y+1,\mathrm{sm}} = N_{y,\mathrm{sp}} e^{-M_{sp}} + \left((N_{y,\mathrm{sm}} - C_{y,\mathrm{sm}})(1 - G) + W_y\right) e^{-M_y}.$$

Harvest was modeled as a pulse before natural mortality and growth occurred. This is believed to be a reasonable assumption given that the majority of natural mortality and growth of eastern oysters have been observed during spring and summer months (Shumway, 1996; Vølstad et al., 2008). The probability of growth from the small to market stage and the natural mortality rates for smalls and markets each year were estimated parameters. The natural mortality of spat was assumed to be known and constant at an instantaneous rate of 0.7 per year (approximately 50 percent survival) based on estimates of density of age-0 and age-1 oysters in the Great Wicomico River, VA (Southworth et al., 2010). These model equations were also used to track the number of planted oysters alive at each stage (to address TOR 5 and for inclusion in the reference point model).

The number of markets each year was calculated as the sum of the number of smalls that survive harvest and natural mortality to grow into markets, and the number of markets already present from the previous year that survived natural mortality and harvest,

$$N_{y+1,\mathrm{mk}} = (N_{y,\mathrm{sm}} - C_{y,\mathrm{sm}})Ge^{-M_y} + (N_{y,\mathrm{mk}} - C_{y,\mathrm{mk}})e^{-M_y}.$$

The exploitation rate was calculated as the number of markets harvested divided by the estimated abundance of markets at the beginning of the year,

$$u_y = \frac{C_{y,\mathrm{mk}}}{N_{y,\mathrm{mk}}}.$$

The instantaneous fishing mortality rate was calculated from the exploitation rate under the assumption that fishing mortality preceded natural mortality,

$$F_y = -\log(1 - u_y)$$

The model also tracked the number of boxes in the small and market size categories to assist in estimating natural mortality rates. The number of boxes each year was calculated as the sum of the number of boxes from previous years that did not disarticulate and the number of adult oysters (small or market) that survived harvest but experienced natural mortality,

$$B_{y+1,s} = B_{y,s}e^{-b_s} + (N_{y,s} - C_{y,s})(1 - e^{-M_y}).$$

It was assumed that all smalls and markets became boxes after experiencing natural mortality, although the catchability parameter for boxes also includes boxes that disarticulate before the time of the survey. The abundance of small and market boxes in the first year were estimated as parameters.

The initial amount of habitat (in 1999) was estimated as the amount of habitat in 1980 adjusted for degradation until 1999,

$$H_{1999} = H_{1980} e^{-d_n (1999-1980)} \ .$$

The rate of habitat loss was an estimated model parameter. After the first year, the area of oyster habitat was estimated for each year using an exponential decline with additions for shell planting and habitat restoration (adjusted for overlap with previous habitat),

$$H_{y+1} = H_y e^{-d_n} + cH_{a,y}.$$

Oyster habitat in Chesapeake Bay has been modeled as an exponential decline previously (Wilberg et al., 2011), and an exponential decline model is appropriate given the degradation of oyster habitat that has been documented in some regions (Rothschild et al., 1994; Smith et al., 2005). The area of habitat added through shell additions and restoration projects was reduced by 20% to reflect overlap in these activities with habitat already in the system (Maryland Department of Natural Resources, unpublished data).

3.2.2 Observation model

The model predicted indices of density for the fall dredge survey and the index of recent mortality. Predicted indices of density were calculated as the product of catchability and density at the beginning of the season for live oyster stages and boxes per unit of habitat and recent natural mortality,

$$\hat{I}_{N\ y,s} = q_{N,s} \frac{N_{y,s}}{H_y},$$

$$\hat{I}_{B\ y,s} = q_{B,s} \frac{B_{y,s}}{H_y},$$

$$\hat{I}_{M,y} = q_M M_y.$$

Catchability (q_N and q_B) was assumed to be the same for the live small and market categories and for the small and market box categories based on the survey dredge efficiency experiments of Powell et al. (2007) and Marenghi et al. (2017). The model also predicted density of small and market oysters (by stage) for comparison with patent tong survey estimates of density,

$$\hat{D}_{y,s} = N_{y,s} / H_y \ ,$$

which assumed that the patent tongs were 100% efficient in sampling small and market oysters.

3.2.3 Model fitting

Model parameters were estimated by minimizing the negative log likelihood function and penalties for some of the parameters. The objective function was the sum of the negative log likelihood components and penalties,

$$-LL = L_{sp} + L_{sm} + L_{mk} + L_{smb} + L_{mkb} + L_D + L_M + L_F + G_p + b_p + q_{d,p} + q_p + R_p + M_p + N_p + B_p.$$

A lognormal negative log likelihood function (with additive constants ignored) was used for all indices in the model as well as for log-scale fishing mortality,

$$L_X = log_e(\sigma_X) + \sum_y \frac{1}{2}\left(\frac{log_e(X) - log_e(\hat{X})}{\sigma_X}\right)^2.$$

If data were not available for a year, that year was not included in the likelihood function. The log-scale standard deviations (SD) for each of the time series from the fall dredge survey were the average of standard errors (SEs) over time from the index standardization model. For the recent natural mortality rate time series, we assumed a log-scale SD of 0.40 because the SD was difficult to estimate from the data for many NOAA Codes given the relatively low number of recent boxes observed. The log-scale SD for the fishing mortality rate time series was specified at 0.75. When the estimated SEs from the depletion analyses were used as the values for the log scale SD for the fishing mortality rate time series, this time series dominated the others because many of the SEs were quite low. However, given the fishery dependent nature of these estimates, we adopted the common approach of down weighting these estimates in favor of the survey estimates. Through several sensitivity trials, we found that a value of 0.75 provided an acceptable tradeoff between fitting the fall dredge survey data, the patent tong survey data, and matching patterns of natural mortality rates over time from box counts.

Similarly, the negative log likelihood function for the patent tong survey density followed a lognormal distribution with a small constant added because observed density was zero in some locations,

$$L_X = log_e(\sigma_X) + \sum_y \frac{1}{2}\left(\frac{log_e(X+0.001) - log_e(\hat{X}+0.001)}{\sigma_X}\right)^2.$$

The small value added to the densities (1/2 the minimum positive observed density) set a lower limit on the density that was considered informative. The log-scale SDs were calculated from the coefficient of variation of the estimated patent tong densities. If more than one patent tong survey was conducted in a NOAA Code, the values of the log-scale SD were averaged.

Penalties were incorporated on some of the parameters to stabilize the estimates and to include outside information in the parameter estimation (Maunder, 2003). The probability of growth was penalized using a beta distribution penalty with a median of 0.6 based on the fraction of oysters expected to grow from small to market size based on a von Bertalanffy growth model fitted to size-at-age data from known age oysters in Maryland oyster sanctuaries (Paynter et al., 2010) and a stable age distribution for oysters,

$$G_p = -(\alpha - 1)\log \mathrm{G} - (\beta - 1)\log(1 - \mathrm{G}).$$

The parameters of the beta distribution were chosen such that its mean was 0.6 with an SD of 0.08 (α = 22.5, β = 15).

Lognormal penalties were also applied to the disarticulation rate of boxes based on field-based estimates from Maryland and Delaware Bay (Christmas et al., 1997; Ford et al., 2006),

$$b_{p,s} = \frac{1}{2}\left(\frac{log_e(\bar{b}_s) - log_e(b_s)}{\sigma_{b,s}}\right)^2.$$

The log-scale standard deviations (SD) for each penalty were assumed to be known. The means for the disarticulation rate of boxes were assumed to be 0.523 for smalls and 0.453 for markets. The log-scale SD for growth was assumed to be 0.48 for both stages based on the variability observed in Christmas et al. (1997) and Ford et al. (2006).

We included a lognormal penalty for the habitat loss parameter because models for many regions had difficulty in estimating a reasonable value,

$$d_p = \frac{1}{2}\left(\frac{log_e(\bar{d}) - log_e(d)}{\sigma_d}\right)^2.$$

The mean (4.4% yr^{-1}) and log-scale SD (0.25) of the prior was from Rothschild et al. (1994)

A lognormal penalty for the differences in catchability between the small-market size categories and the other two catchability parameters was included to stabilize their estimates,

$$q_{d,p,X} = \frac{1}{2}\left(\frac{log_e(\bar{q}_{d,X}) - \left(log_e(q_{sm,mk}) - log_e(q_X)\right)}{\sigma_{q_{d,X}}}\right)^2.$$

The means (-0.173 for spat and -0.59 for boxes) and log-scale SDs (0.282 for spat and 0.179 for boxes) were based on the mean differences between these categories observed in Powell et al. (2007) and Marenghi et al. (2017) and the SEs of the estimates from those studies.

Some models had inadequate information in the data to estimate realistic abundance and density levels. For these NOAA codes (5, 39, 82, 86, 88, 96, 129, 131, 168, 192, 231, 274 and 337), we included a lognormal penalty on the catchability of small and market oysters for the fall dredge survey,

$$q_p = \frac{1}{2}\left(\frac{log_e(\bar{q}_{sm,mk}) - log_e(q_{sm,mk})}{\sigma_{q_{sm,mk}}}\right)^2.$$

The mean and log-scale SD of the penalty was estimated from the estimates of catchability for the rest of the NOAA codes with reasonable estimates of density based on surveys, fishery performance and other factors.

Penalties on the recruitment deviations (R_p), natural mortality deviations (M_p) and deviations from a stable stage distribution in the first year (N_p and B_p) were included to improve model stability. The assumed log-scale standard deviations were 2.0 for the recruitment deviations, 0.5 for the natural mortality deviations, and 0.25 for the deviations from a stable stage distribution for live oysters and boxes.

3.2.4 Sensitivity Analyses

Sensitivity analyses were conducted on a range of assumed parameters in the model identified by the assessment team during model development. Specifically, sensitivity analyses were conducted using alternative values for the penalty on q_B (assuming a 20% lower mean value), α and β values of the G penalty that made it less informative (standard deviation = 0.2), the number of oysters per bushel (218 per bushel), the fraction of new habitat created when planting shell or artificial substrate (0.5), the fraction of small oysters in a bushel (by number 1% and 12% - the 25th and 75th percentiles of the observed distribution), the assumed reporting rate (100% - all harvest reported, and 80%), a less restrictive standard deviation on the habitat decay penalty, lower (5%) planted spat survival and forcing the model to have a similar catchability for all stages (live and boxes).

4.0 Stage-Structured Assessment Model Results

4.1 Model Fit and Diagnostics

Fits of the individual NOAA code-specific models to all data sources were acceptable overall with the fishery-dependent data generally fitting less well than the fishery-independent data (Figures 25-60). When patent tong survey data were available, the models often achieved better fits to density data, although some models were unable to arrive at densities as low as the observed values (e.g., NOAA codes 25, 60, 127 and 131). However, the assessment team determined that the lack of agreement between the model and the patent tong density data in these four NOAA codes was acceptable given the perceived quality of the sampling locations relative to the NOAA code as a whole. The models fit the fall survey indices for all NOAA codes across all oyster stages relatively well with little patterning among the residuals. Additionally, the models fit the index of recent natural mortality relatively well in all NOAA codes. Fits to the fishing mortality rate time series were generally worse than model fits to the fall survey indices in most years and NOAA codes, with the model often estimating lower values of exploitation than were estimated in the depletion analyses. This lack of fit is partially due to the decision of the assessment team to down weight the fishing mortality time series because of perceived deficiencies in this fishery-dependent data source (Section 6.1). Model parameters were reasonably precisely estimated (Table 12), although several NOAA Codes had relatively higher uncertainty in their estimates (5, 82, 129 and 331).

In about one third of the NOAA codes, the stage-structured model estimates of the natural mortality rates were substantially higher than the box count natural mortality rates (Figures 61-66). The assessment team explored several changes in the assessment model in an effort to reduce the difference between model-based and box count estimates of the time series of natural mortality. In particular, the team attempted combinations of 1) modifying the penalty distribution on the difference between live and box catchability and 2) modifying the penalty distribution for the box decay rate. In all cases, models that had closer estimates (than the base model) to the box count natural mortality rates had larger densities and population sizes. Thus, there appears to be a conflict in the data between the low natural mortality rates reflected by the box count mortality and the population sizes and density estimates reflected by the patent tong survey data. It is clear, however, that these differences are caused by issues beyond the relative catchability of live oysters and boxes, and the box decay rate. This conflict likely arises because the stage-structured assessment model also must match the dynamics of live oysters over time and account for patterns of harvest. For example, one potential cause of this conflict that the team did not fully explore is the timing of the fall dredge survey relative to the fishery. The model treats the fall dredge survey as occurring at the beginning of the year before harvest. However, in some locations and years, the fall dredge survey is conducted one to two months after the start of the fishing season. Harvest before the fall dredge survey would remove market oysters from the population and could cause the model attribute fishing mortality to natural mortality. However, some NOAA codes with extremely low fishing mortality also had substantially higher estimate of natural mortality from the stage-structured model than the box count method.

Because of these issues, the assessment team chose to prioritize matching the density data over matching the box count natural mortality rate estimates.

4.2 Model Outputs

4.2.1 Bay Wide Estimated Market Abundance

Estimated abundance of market oysters varied between approximately 600 million and 200 million individuals over the assessment period (Figure 67). Estimated market abundance was highest in 1999 (note that model years indicate the beginning of the fishing season), the initial year of the time series. It decreased to about 200 million individuals by 2002 and remained close to that level until 2009. After 2009 estimated market abundance increased through 2013 and decreased thereafter. In the beginning of the time series, estimated market abundance was highest in the Choptank River and Eastern Bay regions. After 2006, the Choptank River and Tangier Sound were the regions with the highest abundance. Maryland-wide, estimated market abundance was higher in 2017 than it was during 2002-2007, but it is lower it was in 1999. This pattern of some recovery differed among regions, with some regions showing little to no recovery and others showing substantial increases in market oyster abundance.

4.2.2 Tangier Region

In the Tangier Sound region, estimated abundance of market oysters fluctuated between 25 and 125 million individuals during the assessment period. Estimated abundance declined in Tangier Sound between 1999 and 2006, increased between 2006-2012 and then declined through 2017 (Figure 68). Estimated market oyster abundance was highest in the Nanticoke River (NOAA code 62), lower Tangier Sound (NOAA code 192) and the upper Tangier Sound (NOAA code 292). Trends in abundance over time differed among NOAA codes, but estimated market abundance for the region was lower in 2017 than it was in 1999, but above levels estimated between 2005 and 2007.

The Big Annemessex River (NOAA code 5) has consistently had the lowest abundance of market oysters among NOAA codes in the Tangier Sound Region (Figure 69), which is consistent with its small area. The estimated abundance of spat, small, and market oysters fluctuated over time, but did not show substantial trends (Figure 69). The estimated exploitation rate was low throughout the time series except for a large increase to about 0.75 in the 2015-2016 season. Estimated natural mortality was relatively constant over time and averaged about 0.55. Habitat was estimated to have declined from around 60% to 40% of the amount of habitat present in 1980. Similar to estimated abundance, density remained relatively constant over time with the densities of small oysters usually less than 2 oysters m^{-2}, and the densities of markets usually below 1 oyster m^{-2}. Estimates from this NOAA code appear to have a higher uncertainty than

Estimated abundance of market oysters in Fishing Bay (NOAA code 43) was low compared to other NOAA codes in the Tangier Region except between 2010 and 2015 when estimated abundance approached 20 million individuals (Figure 70). The estimated abundance of spat, small, and market oysters remained low until the 2010-2011 season when a large recruitment event occurred resulting in an increase in small and market abundance in the subsequent years. There has been a decline in the most recent years (Figure 70). The estimated exploitation rate was low (less than 5%) until the 2007-2008 season, after which it increased until it reached approximately 80 % in the 2013-2014 season. The exploitation rate has remained above 50% yr^{-1} since that time. Estimated natural mortality rates were above 50% yr^{-1} during the early 2000s and declined to less than 25% in the 2007-2008 season; it has remained relatively low since then. Over the time series, estimated habitat declined from around 50% to 30% of the amount present in 1980. The estimated density of small and market oysters had a pattern similar to small and market abundance over time, with densities peaking at around 15 and 4 oysters m^{-2} for small and market oysters, respectively (Figure 70).

Estimated abundance of market oysters in the Honga River (NOAA code 47) was consistent over time compared to other NOAA codes in the Tangier region (Figure 71). The estimated abundance of spat, small, and market oysters was relatively low between 1999 and 2006, increased between 2006 and 2015, and then declined in the most recent years (Figure 71). The estimated exploitation rate remained relatively low until 2008 when it increased to approximately 40% and reached a peak of approximately 75% in 2016, but decreased to less than 25% in the most recent year. There were no substantial trends in estimated natural mortality, but it was relatively high (> 50%) in about half the years for the assessment period. Over the time series, estimated habitat declined from around 45% to 25% of the amount present in 1980. Similar to abundance of small and market oysters, estimated density was relatively low until it started to increase in 2007, reached a peak of approximately 7 and 2 oysters m^{-2} between 2010 and 2015 and has declined in the most recent year (Figure 71).

The Manokin River (NOAA code 57) had the second lowest estimated abundance of market oysters among all NOAA codes in the Tangier region (Figure 72). The estimated abundance of spat, small, and market oysters was low during the first half of the time series except for a peak during the early-mid 2000s (Figure 72). There was a substantial recruitment event in 2010 that resulted in relatively high abundance of small and market oysters during the latter half of the time series. Estimated exploitation rates were relatively high (approximately 10-20% yr^{-1}) during the beginning and end of the time series but relatively low (< 10% yr^{-1}) otherwise. Estimated natural mortality rates were relatively high throughout the time series (average of approximately 40% yr^{-1}) and peaked in 2005 at approximately 80% yr^{-1}. Over the time series, estimated habitat declined from around 40% to 20% of the amount present in 1980. The estimated density of small and market oysters followed a similar trend to abundance and density reached a peak of approximately 12 and 4 individuals m^{-2} for small and market, respectively, between 2010 and 2015 (Figure 72).

The Nanticoke River (NOAA code 62) had a relatively high estimated abundance of market oysters compared to NOAA codes Maryland wide, and had the highest estimated abundance in the Tangier Sound region in the most recent year (Figure 73). Estimated abundance of spat, small, and market oysters was relatively high at the beginning of the time series, declined to a minimum in the early to mid-2000s, and has since increased to levels equal to or above the beginning of the time series (Figure 73). The estimated exploitation rate was approximately 10% yr^{-1} in 1999, declined to levels at or below 5% until 2012 when it increased to approximately 13%. Since 2012, exploitation rate has remained between 10-15%. Estimated natural mortality rates were high in the early 2000s reaching a peak of approximately 80% in 2002. After 2002, estimated natural mortality rates declined and have remained at less than 20% in almost all years since 2008. Between 1999 and 2011, estimated habitat declined from around 70% to 60% of the amount present in 1980. In 2011 there was a large amount of shell planted that increased habitat to approximately 75% of the habitat present in 1980 followed by a relatively small decline in the most recent years. Estimated densities of small and market oysters were highest at the beginning and end of the time series reaching a peak of approximately 5 and 6 individuals m^{-2} for small and market oysters, respectively (Figure 73).

Compared with other NOAA codes in the Tangier Sound region, the estimated abundance of market oysters in Pocomoke Sound (NOAA code 72) was relatively consistent during the assessment period (Figure 74). The estimated abundance of spat, small, and market oysters remained low until the 2010-2011 season when a large recruitment event occurred resulting in an increase in small and market abundance in subsequent years, although there was a decline in the most recent year (Figure 74). The estimated exploitation rate was low (< 10%) before 2011. It increased to approximately 60% in 2013 and has remained relatively high since then. Estimated natural mortality was relatively high throughout the assessment period (averaging approximately 40% yr^{-1}) and peaked at approximately 80% in 2005. Over the time series, estimated habitat declined from around 50% to 30% of the amount present in 1980. Estimated density of small oysters was relatively low prior to 2011 when it increased to approximately 17 individuals m^{-2}. There was a subsequent decline to less 10 individuals m^{-2} in the most recent years. Estimated density of market oysters was almost always between two and three individuals m^{-2} throughout the time series (Figure 74).

The Wicomico River (NOAA code 96) had one of the lowest market abundance estimates relative to other NOAA codes in the Tangier Sound region (Figure 75). The estimated abundance of spat, small and market oysters was relatively low until 2010 after which it increased, peaked between 2010 and 2015, but decreased in the most recent years (Figure 75). The estimated exploitation rate was low (<5%) until 2008 after which began to increase and reached a peak of approximately 60% in 2015; it decreased thereafter to approximately 20% yr^{-1} in the most recent year. Estimated natural mortality was highest in the early 2000s with a peak of approximately 80% in 2001 and has been relatively low (average of approximately 20% yr^{-1}) in recent years. Over the time series, estimated habitat declined from around 70% to 55% of the amount present in 1980. Similar to abundance, the estimated density of small and market oysters was relatively low except between 2010 and 2015 when the estimated density peaked at approximately 10 individuals m^{-2} for both small and market oysters. There has been a decrease in estimated density of small and market oysters in the most recent year to approximately three individuals m^{-2} (Figure 75).

Tangier Sound South (NOAA code 192) has had consistently high estimates of market abundance across the time series compared to other NOAA codes in the Tangier Sound region (Figure 76). The estimated abundance of spat, small and market oysters has fluctuated over the time series with no substantial trends except for a decrease in the most recent years (Figure

76). Estimated exploitation rates increased over most of the time series starting at less than 5% yr^{-1} in 1999 and reaching approximately 60% in 2015 with a decrease to approximately 30% in the most recent year. Estimated natural mortality decreased over the time series from a maximum of approximately 80% in 2001 to approximately 20% in the most recent year. Over the time series, estimated habitat declined from around 50% to 30% of the amount present in 1980. Estimated density of small oysters fluctuated between one and four individuals m^{-2} with no substantial trends except for a decrease to less than one individual m^{-2} in the most recent year. Estimated density of market oysters fluctuated over time but remained below one individual m^{-2} and also decreased in the most recent year (Figure 76).

Tangier Sound North (NOAA code 292) had consistently high estimates of market abundance compared to other NOAA codes in the Tangier Sound region (Figure 77). Estimated abundance of spat, small and market oysters increased after 2010 after which abundance remained generally higher than during the first half of the time series (Figure 77). Estimated exploitation rates increased from approximately 1% in 1999 to approximately 80% in 2016, but decreased to approximately 50% in the most recent year. Estimated natural mortality was relatively high in the early to mid-2000s with peaks of approximately 70% yr^{-1} but has been less than 40% yr^{-1} since 2006. Over the time series, estimated habitat declined from around 50% to 35% of the amount present in 1980. Estimated small oyster density remained below 10 individuals m^{-2} except for during 1999 and 2011, and estimated market oyster density remained below three individuals m^{-2} except during 2013 (Figure 77).

4.2.3 Choptank Region

Maryland-wide, the Choptank region had the highest estimated abundance of market oysters during most years (Figure 78). The number of market oysters in the Choptank region began increasing in the 2002-2003 season, and this increase accelerated beginning in 2012 resulting in an approximate four-fold increase by 2014. However, estimated market abundance has declined in recent years and in 2017 is estimated to be below the 1999 level. The NOAA codes with the highest estimated abundance in the region were the Little Choptank River (NOAA code 53) and Broad Creek (NOAA code 537; Figure 78).

The Little Choptank River (NOAA code 53) had consistently high estimated abundance of market oysters relative to all NOAA codes in the Choptank region (Figure 79). The estimated abundance of spat, small, and market oysters was relatively high in the 1999-2000 season, declined to a minimum in the early 2000s, and has since returned to levels similar to the 1999-2000 season (Figure 79). The estimated exploitation rate was highest in 1999-2000 season at about 15 and has declined in recent years to less than 3% yr^{-1}. Estimated natural mortality rates reached a peak of around 90% in the early 2000s and have remained relatively low (averaging about 25% yr^{-1}) since that time. Between 1999 and 2012, estimated habitat declined from around 60% to 45% of the 1980 habitat and has since remained unchanged. Similar to the trend in estimated abundance, the estimated density of small and market oysters was relatively high in 1999, declined to less than 1 oyster m^{-2} in the early 2000s, and increased in recent years to between 5 and 10 individuals m^{-2} for small and market oysters (Figure 79).

The lower Choptank River (NOAA code 137) had the lowest estimated abundance of market oysters relative to all NOAA codes in the Choptank region (Figure 80). The estimated abundance of spat, small, and market oysters declined to a minimum in the early 2000s, increased between 2010 and 2015 to levels similar to the 1999-2000 season, and decreased in the most recent years (Figure 80). The estimated exploitation rate was low until the 2006-2007 season when it increased to 30% and averaged about 30% yr^{-1} until 2013 after which it increased to about 60%. The estimated natural mortality rate reached a peak of approximately 90% in the early 2000s after which it declined and has remained relatively low (average about 15% yr^{-1}). Estimated habitat has declined from approximately 50% to 30% of the amount of habitat present in 1980. The estimated density of small and market oysters was highest at the beginning and end of the time series (approximately 1 individual m^{-2}) and was lowest during the 2000s (approximately 0.1 individual m^{-2}; Figure 80).

The estimated abundance of market oysters in the middle Choptank (NOAA code 237) declined in the beginning of the time series, returned to 1999 levels by 2014 and has declined thereafter (Figure 81). Estimated abundance of small oysters was highest at the beginning and end of the time series with a minimum the early to mid-2000s (Figure 81). Estimated spat density had no consistent pattern and fluctuated between less than 1 million to approximately 20 million during the assessment period. Estimated exploitation rates were highest at the beginning and end of the time series and reached a peak of approximately 12% in the most recent year. Estimated natural mortality was highest in the early 2000s with a peak of approximately 75% in 2002 and has been relatively low (< 25%) since 2004. Estimated habitat declined from around 70% to 55% of the amount of habitat present in 1980. Estimated small oyster density was highest in 2000 (2 individuals m^{-2}) and has been ≤ 1 individual m^{-2} since that time. Estimated market oyster density was approximately two individuals m^{-2} between 1999 and 2002, decreased to a minimum of < 0.5 individuals m^{-2} in the mid-2000s and increased to approximately two individuals m^{-2} in the most recent three years (Figure 81).

Compared to other NOAA codes in the Choptank region, the estimated abundance of market oysters in the upper Choptank River (NOAA code 337) was relatively consistent during the assessment period (Figure 82). The estimated abundance of spat, small and market oysters was highest at the beginning of the time series, then showed an increasing trend, followed by a decline in the recent years (Figure 82). Estimated exploitation was highest in 1999 (approximately 5%) and has remained low (< 1%) almost every year since then. Estimated natural mortality was highest in the early 2000s reaching a peak of approximately 60% in 2002 and has been relatively low since 2005 (< 25%). Estimated habitat declined from around 80% to 70% of the amount of habitat present in 1980. Similar to abundance, estimated density of small and market oysters was highest at the beginning of the time series (approximately 6-7 individuals m^{-2}). Estimated small oyster density remained below 3 individuals m^{-2} since 2003. Estimated market density decreased in the mid-2000s to approximately 2 individuals m^{-2} and then increased in the most recent years to approximately four individuals m^{-2} (Figure 82).

The estimated abundance of market oysters in Harris Creek (NOAA code 437) was relatively low compared to other NOAA codes in the Choptank region until 2012, after which market abundance is estimated be among the highest in the Choptank region (Figure 83). The estimated abundance of spat, small and market oysters was highest at the beginning and end of the time series with a low period during the mid-2000s (Figure 83). Estimated exploitation rate was highest in 2000 (approximately 20%) and has generally decreased since then to less than 5% yr^{-1}. Estimated natural mortality did not have a consistent trend over time, but reached a peak of approximately 90% in 2002 and has since fluctuated between approximately 10 and 60% yr^{-1}. Between 2000 and 2012, the estimated habitat declined from around 40% to 30% of the amount of habitat present in 1980. After 2012 the estimated habitat increased due to major restoration efforts, but declined in the most recent year. The estimated density of small and market oysters was high at the beginning of the assessment period, reached peaks of approximately 20 to 30 individuals m^{-2} between 2010 and 2015 and then decreased in the most recent years (Figure 83).

Broad Creek (NOAA code 537) had high estimated abundance of market oysters compared to the other NOAA Codes in the Choptank region (Figure 84). The estimated abundance of spat, small, and market oysters was generally highest at the beginning and end of the time series, although there was a substantial peak in recruitment in the 2012-2013 season (Figure 84). The estimated exploitation rate has varied widely through the time series with periodic peaks in excess of 40%. The estimated exploitation rate has declined in recent years. Estimated natural mortality was highest in the early 2000s with a peak of approximately 80% in 2002 and has been relatively low (less than 40% yr^{-1}) in most years since 2002. Estimated habitat declined from around 50% to 40% of the amount of habitat present in 1980 during the years of 1999-2011 and slightly increased in the most recent years. Similar to abundance, estimated density of small and market oysters was highest at the beginning and end of the time series with a peak of approximately 60 and 15 individuals m^{-2} during 2010-2015 for small and market oysters, respectively, but has decreased in the most recent year (Figure 84).

The Tred Avon River (NOAA code 637) had lower variability in the estimated abundance of market oysters than other NOAA codes in the Choptank region (Figure 85). The estimated abundance of spat, small, and market oysters was highest at the beginning and end of the time series with a low period during the mid-2000s (Figure 85). Estimated exploitation rates were at their highest in 2000 (approximately 17%) but were relatively low (less than 7%) since 2001. Estimated natural mortality was highest in the early 2000s with a peak of approximately 80% in 2002 and has been relatively low (less than 25% yr^{-1}) since 2002. Estimated habitat declined from around 75% to 65% of the amount of habitat present in 1980 during 1999-2013 and has remained relatively stable since then. Estimated small oyster density was highest in 1999 (approximately 9 individuals m^{-2}) and has been less than three individuals m^{-2} since then. The estimated density of market oysters was highest at the beginning and end of the assessment period during which time it averaged approximately 4 to 5 individuals m^{-2} (Figure 85).

4.2.4 Eastern Bay

Maryland wide, the Eastern Bay region had the highest estimated abundance of market oysters among regions in 1999, but estimated abundance declined substantially with an approximate 85% decrease over the assessment period (Figure 86). Most NOAA codes in this region had a similar pattern of decline in estimated abundance of market oysters during the assessment period. Eastern Bay (NOAA code 39) and the middle Chester River (NOAA code 231) had the highest estimated market abundance among NOAA codes in the Eastern Bay region at the beginning of the assessment period.

Eastern Bay (NOAA code 39) had the highest estimated abundance of market oysters among NOAA codes in the Eastern Bay region (approximately 50% of the regional total in recent years; Figure 87). The estimated abundance of spat, small, and market oysters was highest during the early 2000s and declined to approximately 25% of levels estimated in the early 2000s (Figure 87). Estimated exploitation was highest in 2000 (approximately 40%) and declined to an average of approximately 10% yr^{-1} in the most recent years. Estimated natural mortality was highest between 2000 and 2010 when it reached a maximum of approximately 60%, but has been relatively low (less than 25%) in recent years. Estimated habitat declined from around 80% to 70% of the amount of habitat present in 1980. The estimated density of small and market oysters was highest at the beginning of the assessment period (approximately 2 individuals m^{-2}) and has remained ≤ 2 individuals m^{-2} (Figure 87).

The estimated abundance of market oysters in the Miles River (NOAA code 60) was less variable than some of the other NOAA codes in the Eastern Bay Region (Figure 88). The estimated abundance of spat, small, and market oysters was highest during the early 2000s and generally declined to approximately 25% of levels estimated in the early 2000s (Figure 88). Estimated exploitation was highest in 1999 (approximately 40% yr^{-1}) but remained relatively low (≤5%) in most years. Estimated natural mortality was highest between 2000 and 2010 when it reached a maximum of approximately 60% but has been relatively low (less than 25%) in recent years.

Estimated habitat has declined from around 65% to 45% of the amount of habitat present in 1980. The estimated density of small and market oysters was highest at the beginning of the assessment period (approximately 2 to 4 individuals m^{-2}) and remained at ≤ 2 individuals m^{-2} since 2008 (Figure 88).

The Wye River (NOAA code 99) had one of the lowest market abundance estimates for the entire time series relative to other NOAA codes in the Eastern Bay region (Figure 89). The estimated abundance of spat, small and market oysters was highest during the early 2000s and declined by approximately 75% since the early 2000s (Figure 89). Estimated exploitation rates were relatively low (≤5%) in most years but were highest the beginning of the time series (peak at approximately 45% yr^{-1}). Estimated natural mortality was highest in the early 2000s, reaching a peak of approximately 60% yr^{-1}, and remained relatively low (< 40% yr^{-1}) since 2003. Estimated habitat declined from around 55% to 35% of the amount of habitat present in 1980. Estimated density of small and market oysters was highest at the beginning of the assessment period (approximately 2 to 4 individuals m^{-2}) and remained ≤ 2 individuals m^{-2} since 2003 (Figure 89).

The estimated abundance of market oysters in the lower Chester River (NOAA code 131) was relatively stable over time compared to other NOAA codes in the Eastern Bay region (Figure 90). The estimated abundance of spat, small and market oysters declined by approximately 75% of levels estimated in the early 2000s (Figure 90). Estimated exploitation rates were highest in 1999 (approximately 25%), but remained relatively low (≤10% yr^{-1}) in most years since 1999. Estimated natural mortality was highest in the early 2000s reaching a peak of approximately 60% yr^{-1} and has remained relatively low (≤ 40%) since 2003. Estimated habitat was relatively constant through 2005 at approximately at 60% of habitat present in 1980 and then declined to around 50% of the amount of habitat present in 1980. The estimated density of small and market oysters was highest at the beginning of the assessment period (approximately 2 to 6 individuals m^{-2}) and remained at ≤ 2 individuals m^{-2} to the present (Figure 90).

The estimated abundance of market oysters in the middle Chester River (NOAA code 231) comprised approximately half of the market abundance in the Eastern Bay region in 1999, but it declined by about 90% by the final year of the assessment period (Figure 91). The estimated abundance of spat, small, and market oysters was highest during the early 2000s and declined substantially since the early 2000s (Figure 91). Estimated exploitation declined from approximately 10% in 1999 to 1% in 2016, but it increased to approximately 12% in the most recent year. Estimated natural mortality was highest between 2000 and 2010 when it reached a maximum of approximately 70%, but it has been relatively low (less than 25% yr^{-1}) in the most recent years. Estimated habitat has declined from around 65% to 45% of the amount of habitat present in 1980. The estimated density of small and market oysters was highest at the beginning of the assessment period (approximately 5 to 7 individuals m^{-2}) and remained ≤ 2 individuals m^{-2} since 2006 (Figure 91).

The upper Chester River (NOAA code 331) had the lowest estimated abundance of market oysters among all NOAA codes in the Eastern Bay Region (Figure 92). Estimated abundance of spat, small, and market oysters was highest during the early 2000s and it declined by more than 75% of levels estimated in the early 2000s (Figure 92). Estimated exploitation rates were low during all years except during 2010 when it was estimated at approximately 60%. Estimated natural mortality remained relatively constant at approximately 25% yr^{-1} except for an increase to approximately 75% in 2010. Estimated habitat declined from around 50% to 30% of the amount of habitat present in 1980. Estimated density of small and market oysters remained relatively constant at ≤ 2individuals m^{-2} with a decreasing trend over time. The assessment team concluded that estimates from this region have a higher uncertainty than most of the other regions.

4.2.5 Chesapeake Bay Mainstem

The Chesapeake Bay Mainstem region had a relatively consistent proportion of estimated market abundance among all regions over the assessment period (Figure 93). Estimated market abundance decreased over the assessment period to approximately 30% of the 1999 estimate (Figure 93). NOAA codes with the highest estimated market abundance in this region were the Upper Bay north of the Chesapeake Bay Bridge (NOAA code 25) and the Mid-Bay directly south the Chesapeake Bay Bridge (NOAA code 127).

The proportion of estimated market abundance in the Upper Bay (NOAA code 25) decreased more than the other NOAA codes in the Mainstem region (Figure 94). The estimated abundance of small and market oysters was highest during 1999-2010 and was relatively low during 2010-2017 (Figure 94). Estimated exploitation averaged approximately 3% yr^{-1} before 2015 and then increased to approximately 10% yr^{-1} in recent years. Estimated natural mortality was relatively high during 1999-2017, fluctuating between 20% to 80%. Estimated habitat declined from around 60% to 40% of the amount of habitat present in 1980. Estimated density of small and market oysters was relatively low with less than 1 individual m^{-2} (Figure 94).

Estimated market abundance in the South Mid-Bay NOAA code (NOAA code 27) was among the lowest in the Mainstem region (Figure 95). The abundance of spat, small and market oysters was relatively high in 1999, then decreased until 2012 when a large recruitment event caused an increase in small and market abundance; however, estimated abundance returned to low levels after 2014 (Figure 95). Estimated exploitation fluctuated substantially with several of the highest values in the most recent six years. Estimated natural mortality was highest in the early and mid-2000s with peaks of approximately 60% yr^{-1} and was relatively low (≤ 30% yr^{-1}) in most other years. Estimated habitat declined from around 70% to 50% of the amount of habitat present in 1980. Estimated density of small and market oysters was low (< 0.2 to 0.6 individuals m^{-2}) during 1999-2017 (Figure 95).

Estimated abundance of market oysters in the North Mid-Bay (NOAA code 127) was among the highest in the Mainstem region (Figure 96). Estimated abundance of spat, small and market oysters generally declined by approximately ≥ 75% during 1999-2017 (Figure 96). Estimated exploitation rates were low during all years (usually less than 1%) with the highest value in the most recent two years (approximately 5%). Estimated natural mortality averaged about 40% yr^{-1} during 2000-2010 but has been relatively low (< 20% yr^{-1}) in recent years. Estimated habitat declined from around 65% to 45% of the amount of habitat present in 1980. Similar to abundance, estimated density of small and market oysters was highest at the beginning of the assessment period (approximately 4 to 7 individuals m^{-2}) and remained ≤ 2 individuals m^{-2} since 2010 (Figure 96).

Estimated abundance of market oysters in the Lower Bay East (NOAA code 129) was among the lowest in the Mainstem region (Figure 97). Estimated abundance of spat, small, and market oysters was highest during the mid-2000s (Figure 97). Estimated exploitation rates fluctuated substantially with spikes in 2008, 2014, and 2017 (50%, 80%, and 25%). Estimated natural mortality was relatively high except during 2004 and 2010-2012 when it dropped to approximately 25%. Estimated habitat has declined from around 30% to 10% of the amount of habitat present in 1980. There were no strong trends in estimated small and market density over time and it fluctuated between less than one to approximately 10 and 5 individuals m^{-2} for small and market oysters, respectively. The assessment team concluded that estimates from this region have a higher uncertainty than most of the other regions.

Estimated abundance of market oysters in the Lower Bay West (NOAA code 229) was among the lowest for NOAA codes in the Mainstem region (Figure 98). Estimated abundance of spat, small, and market oysters was highest during the mid-2000s and in the most recent years (Figure 98). Estimated exploitation was low (less than 3% yr^{-1}) until it started to increase in 2008 reaching a peak of approximately 20% in the most recent year. Estimated natural mortality did not have substantial trends over time and fluctuated between approximately 10% to 50% yr^{-1}. Estimated habitat declined from around 50% to 30% of the amount of habitat present in 1980. Estimated density of small and market oysters showed no substantial trends over time and average approximately 0.75 to 1 individual m^{-2} during the assessment period (Figure 98).

4.2.6 Patuxent and Potomac Region

The Patuxent and Potomac Rivers region had a relatively consistent proportion of estimated market abundance among regions over the assessment period (Figure 99). Estimated market abundance fluctuated between approximately 15 and 50 million oysters. The estimated market abundance was lower in the last year (approximately 25 million) than in 1999 (approximately 35 million). NOAA codes in the Patuxent River (168 and 268) generally had the highest abundance among NOAA codes in this region, although the relative proportion of estimated market oysters has increased in the St. Mary's River (NOAA Code 78) since 2011.

The St. Mary's River (NOAA code 78) was routinely in among the top four NOAA codes for estimated market abundance in the Patuxent and Potomac Region (Figure 100). Estimated abundance of spat and small oysters did not have substantial trends over time but estimated market abundance had a spike in 2014 and returned to pre-2014 levels in the most recent years (Figure 100). Estimated exploitation rates were relatively high at the beginning and end of the assessment period (≥ 25%) and reached a maximum of approximately 75% in the most recent year. Estimated natural mortality was relatively high in most years (greater than 50%) except for 2003 and 2012-2014. Estimated habitat declined from around 55% to 35% of the amount of habitat present in 1980. Estimated small oyster density had no substantial trends over time and fluctuated between < 5 to approximately 40 individuals m^{-2}. Estimated market density remained < 5 individuals m^{-2} until it increased to approximately 12 individuals m^{-2} in 2015 and returned to < 5 individuals m^{-2} in the most recent year (Figure 100).

Smith Creek (NOAA code 86) consistently had the second lowest estimated abundance of market oysters among NOAA codes in the Patuxent and Potomac Region (Figure 101). Estimated abundance of spat, small and market oysters had no strong trends over time except for an increase in market abundance during 2010-2015 followed by a decrease in the most recent year (Figure 101). Estimated exploitation rates were near zero except for in 1999 (approximately 30%) and 2012-2017, when it reached a peak of approximately 40%. Estimated natural mortality decreased over time from about 75% to about 40%. Estimated habitat declined from around 65% to 45% of the amount of habitat present in 1980. Estimated density of small oysters fluctuated between approximately 2-10 individuals m^{-2}. Estimated density of market oysters increased from approximately 2.5 individuals m^{-2} in 1999 to 5 individuals m^{-2} in 2015 followed by a decrease to approximately 2 individuals m^{-2} in the most recent year (Figure 101).

Estimated abundance of market oysters in the lower Patuxent River (NOAA code 168) was consistently among the highest in the Patuxent and Potomac Region (Figure 102). The estimated abundance of spat, small and market oysters was highest during 2010-2015 and generally higher in the latter half of the assessment period compared to the first half (Figure 102). Estimated exploitation was low (approximately 0-1% yr^{-1}) until 2009. It increased to about 50% in 2015 and declined to approximately 25% in 2017. Estimated natural mortality was highest during the early to mid-2000s reaching a peak of approximately 70% in 2001 and has been relatively low (< 40%) since 2008. Estimated habitat declined from around 70% to 55% of the amount of habitat present in 1980. Estimated density of small and market oysters was generally low during the first part of the assessment period, reached a peak of 17 and 6 individuals m^{-2} for small and market oysters, respectively, during 2010-2015, and decreased to less than 5 and 2 individuals m^{-2} in 2017 (Figure 102).

Estimated abundance of market oysters in Breton and St. Clements Bay (NOAA code 174) has consistently been the lowest in the Patuxent and Potomac Region (Figure 103). Estimated abundance of spat, small, and market oysters was at its highest levels in the beginning and end of the assessment period (Figure 103). Estimated exploitation was 0% yr^{-1} during most years but ranged from approximately 5% to 40% during a few years. Estimated natural mortality was highest in the early 2000s when it reached a peak of approximately 75% in 2003; it has averaged approximately 25% yr^{-1} since 2006. Estimated habitat declined from around 50% to 30% of the amount of habitat present in 1980. Similar to abundance, estimated density of small and market oysters was highest at the beginning and end of the assessment period but always stayed below 0.15 individuals m^{-2} (Figure 103).

The middle Patuxent River (NOAA code 268) had one of the lowest estimates of market abundance among NOAA codes in the Patuxent and Potomac region (Figure 104). The estimated abundance of spat, small, and market oysters was generally highest in the early 2000s. Market abundance increased during 2010-2015 and declined in the most recent years (Figure 104). Estimated exploitation rates were low until 2005, reached a peak of approximately 30% in 2015, and decreased to approximately 20% in the most recent year. Estimated natural mortality was highest in the early 2000s reaching a peak of approximately 90%, but has remained relatively low (average of approximately 40% yr^{-1}) since 2003. Estimated habitat declined from around 60% to 35% of the amount of habitat present in 1980. Estimated density of small and market oysters was highest in the early 2000s and during 2010-2015 reaching peaks of approximately 2 individuals m^{-2}, but it declined in the most recent year to ≤ 1 individual m^{-2} (Figure 104).

The Wicomico River (NOAA code 274) was routinely among the top four NOAA codes for estimated market abundance in the Patuxent and Potomac Region (Figure 105). Estimated abundance of spat, small, and market oysters was generally highest in the early to mid-2000s (Figure 105). Estimated market abundance has remained at approximately 5 million since 2007. Estimated exploitation rates were low until 2012, reached a peak of approximately 30% in 2013, and decreased to < 5% in the most recent year. Estimated natural mortality was highest during the early to mid-2000s reaching peaks of approximately 75% yr^{-1} and has been relatively low (<40%) in the most recent years. Estimated habitat declined from around 60% to 40% of the amount of habitat present in 1980. Similar to abundance, estimated density of small and market oysters was highest in the early to mid-2000s and was usually less than 2 individuals m^{-2} since that time (Figure 105).

The upper Patuxent River (NOAA code 368) had a relatively consistent proportion of estimated market abundance among NOAA codes in the Patuxent and Potomac Region (Figure 106). Estimated abundance of spat, small, and market oysters was highest in 1999 or 2000 and decreased to less than 50% of those levels over the rest of the assessment period (Figure 106). Estimated exploitation was relatively low (less than 5%) during most of the assessment period until 2013, after which it reached a peak of approximately 20%in 2016. Estimated natural mortality was highest in the early 2000s reaching a peak of approximately 80% in 2001 and has been relatively low (average of approximately 25% yr^{-1}) since 2001. Estimated habitat declined from around 60% to 35% of the amount of habitat present in 1980. Estimated density of small and market oysters was usually less than 1 individual m^{-2} (Figure 106).

4.2.7 Western Shore Region

The Western Shore Region consistently had the lowest estimated abundance of market oysters among all regions (Figure 107), which was not surprising because it is the smallest region. Estimated market abundance was highest in 2000 and decreased from approximately 30 to 5 million oysters. Only two NOAA codes are included in this region and both had a relatively similar proportion of the estimated abundance of market oysters except during the early 2000s when the Severn River (NOAA code 82) had approximately 6 times the estimated abundance of market oysters compared to the South River (NOAA code 88).

The Severn River (NOAA code 82) had the highest estimated abundance of market oysters in the Western Shore region during the early 2000s, but abundance decreased substantially by the end of the assessment period (Figure 108). Estimated abundance of spat, small, and market oysters was highest during the early 2000s and decreased to less than 25% of those levels for the remainder of the assessment period (Figure 108). The estimated exploitation rate was less than 4% yr^{-1} for all years. The estimated natural mortality rate was similar in most years and averaged approximately 30% yr^{-1} except for 2011 when it peaked at approximately 75%. This peak in natural mortality was likely an artifact of the model trying to fit the patent tong density data the next year. Estimated habitat declined from around 65% to 50% of the amount of habitat present in 1980. The estimated density of small and market oysters was at approximately ≤ 3 individuals m^{-2} for most of the assessment period. The assessment team concluded that estimates from this region have a higher uncertainty than most of the other regions.

The South River (NOAA code 88) had approximately 50% of the estimated market abundance among NOAA codes in the Western Shore region except during the early 2000s (Figure 88). Estimated abundance of spat, small, and market oysters was highest in 2000 and was generally reduced to less than 25% of those levels for the remainder of the assessment period (Figure 109). Estimated exploitation was relatively low (≤ 10% yr^{-1}) until 2012 when it started to increase, reached a peak of approximately 50%, and declined to approximately 20% in the most recent year. Estimated natural mortality was relatively high during 2000-2010 with a peak of approximately 80% in 2001, but it was relatively low during 2010-2017. Estimated habitat declined from around 70% to 55% of the amount of habitat present in 1980. Estimated density of small and market oysters remained at ≤ 5 individuals m^{-2} for most of the assessment period (Figure 109).

4.3 Sensitivity Analyses

We tested the sensitivity of the model to changes in the values of 11 of the penalty distributions and assumed parameters. Generally, the model was insensitive to changes in these assumptions (Figures 110 - 112). Modifying the parameters for led to a less than 10% change in the parameter estimates, on average, for all sensitivity scenarios (Figure 110 - 112), except for changing the penalty standard deviation (SD) for habitat loss and forcing the fall dredge survey catchability parameters to be the same (Figure 112). When the SD of the penalty for the habitat loss rate was loosened, the rate changed by over 30% on average, but the other performance measures were relatively unchanged. When the model was forced to estimate a single catchability for all stages of the fall dredge survey, the transition probability, average natural mortality rate and average abundance changed by about 20-30%.

4.4 Comparison of Natural Mortality Estimates - Three Methods

A unique feature of oysters is that natural mortality can be estimated from field observations of live oysters and boxes (Section 2.4.2). Additionally, the assessment team developed a statistical model that corrects for assumptions of the empirical method (e.g., unequal efficiencies between live oysters and boxes) and allowed for estimation of uncertainty (Section 2.4.3). The assessment team considered this additional information on natural mortality rates to be a valuable tool for examining the 'reasonableness' of assessment model-based estimates.

The estimated natural mortality from the assessment model was typically higher than the box count and natural mortality model estimates (Figures 61 – 66). The box count and natural mortality model almost always followed a similar pattern over time, and in some NOAA codes, assessment model natural mortality also followed the same pattern (e.g., most NOAA codes in the Choptank region; Figure 62). However, in other NOAA codes, natural mortality from the assessment model had peaks that were not present in the patterns from the box count and natural mortality model (e.g., 2010 in NOAA code 47: Honga River, Figure 61C; 2005, 2008, and 2010 in NOAA code 231: Mid Chester River, Figure 63E). Estimates of uncertainty were usually higher in the assessment model than in the natural mortality model, although this was not consistent for all NOAA codes (e.g., in NOAA code 43: Fishing Bay, uncertainty was higher in the natural mortality model than in the assessment model in most years from 2000-2005; Figure 61B).

While some differences in estimates among the methods may be caused by using different subsets of fall dredge survey data (or in the case of the assessment model, by standardizing the fall dredge survey data before using them), most are likely due to structural differences between the methods. For example, the box count method relies only on the fall survey data in a year to estimate a natural mortality rate for the same year. The natural mortality model is more complex and includes differences in dredge efficiency between live oysters and boxes and box disarticulation dynamics that link observations of boxes over multiple years. The assessment model includes more structure and more data, as it tracks live oyster abundance (by stage) over time and is fitted to other data sources to estimate additional parameters. Differences in the pattern of natural mortality between the assessment model and the other methods may be because there is disagreement among the data sources in the assessment model and estimating a higher natural mortality rate is likely necessary to get the best fit to all the data sources assuming the model structure (other versions of the assessment model seemed to indicate that this was the case). The box count method and natural mortality models do not rely upon additional data sources and do not need to estimate parameters that are not pertinent to natural mortality estimation. Therefore, these methods have more flexibility to closely match the fall dredge survey box data.

One potential important difference between the assessment model and the other two methods is that the box mortality and natural mortality models assume that all oysters that die become boxes that are still available during that year's survey. In the assessment model, the catchability of boxes includes the fraction of boxes that disarticulate prior to the survey. The prior on relative catchability of boxes in the assessment model includes an assumption that 20 percent of boxes disarticulate before the fall dredge survey, which is not included in the box count method or in the efficiency ratio of the natural mortality model. A sensitivity analysis for the natural mortality model that included this process increased median natural mortality by about 17.8 percent on average across all years and NOAA codes. Accounting for boxes decaying before the survey in the assessment model and not in the box count method or natural mortality model could partially account for consistently higher natural mortality in the assessment model compared to the other methods, although other differences between the assessment model and the box count method and natural mortality also may contribute.

5.0 Biological Reference Points

5.1 Background

Maryland law requires that fishery management plans contain the best available estimates of sustainable harvest rates (biological reference points) determined through a stock assessment (Natural Resources Article §4-215). Specifically, statute requires target and threshold (upper limit) reference points for fishing levels (i.e., fishing mortality or exploitation rate) and a threshold (lower limit) reference point for abundance. Additionally, there must be objective and measurable means to determine if the oyster fishery is operating within the reference points. These reference points have not been estimated for oysters in Maryland for use in management of the fishery prior to this assessment.

There are several reasons why reference points have not been previously developed for oysters. Unlike most fished species, oysters create their own habitat in the form of the shells of both live and dead individuals (Powell and Klinck, 2007). Therefore, harvesting oysters removes a portion of the habitat. In addition, the planting of hatchery-reared or wild oysters as well as the placement of oyster shell have been widely used management measures for decades. Most methods for estimating reference points rely on implicit assumptions about constant ecosystem and habitat conditions and assume that all production is coming from wild sources, which are not appropriate assumptions for oysters. Therefore, the assessment team developed exploitation reference points using a model that explicitly links the population and habitat dynamics (e.g., Wilberg et al., 2013) and includes effects of planted oysters.

Oyster abundance in Maryland is far below the levels during the 1800s (Newell, 1989; Rothschild et al., 1994; Wilberg et al., 2011). However, the Chesapeake Bay has experienced substantial changes in habitat since that time. For example, in the 1600s-1700s, oyster reefs were described as navigation hazards (Kennedy and Breisch, 1983), and reef morphology has changed substantially during the past 200 years (DeAlteris, 1988). Because of these changes the amount of potential for recovery of oyster abundance is highly uncertain. Furthermore, the potential amount of recovery likely varies spatially within Maryland. Therefore, the assessment team did not develop target reference points for abundance because the potential for oyster recovery is difficult to determine.

5.2 Abundance Reference Points

The threshold (or lower limit) abundance reference point identifies an overfished or depleted status and represents an abundance of oysters below which there are likely to be biological, social, ecological and/or economic consequences. It is important to note that an overfished status can be triggered for reasons other than fishing (e.g., an extended period of low recruitment or an extreme natural mortality event).

The threshold abundance reference point proposed by the stock assessment team is the minimum estimated number of market oysters during the period 1999-2017 for each NOAA code. The choice of the time-series minimum as an abundance threshold is based on the idea that oysters in most NOAA codes have been able to increase in abundance from their lowest observed levels, but it is unknown whether populations would be able to persist below those levels. Additionally, abundance during 1999-2017 is likely the lowest it has been during the last several hundred years. Market-size oysters were chosen because they are the targeted size group of the fishery and they also produce more eggs per individual than small oysters because market oysters have both higher fecundity and a higher proportion of female animals in the market size classes. This reference point is proposed as an operational definition for “overfished” or "depleted" status, similar to the previous abundance reference points for blue crabs in Chesapeake Bay.

Given the current low abundance of oysters relative to historic periods and significant changes in the ecosystem (e.g., habitat loss, disease), the stock assessment committee was unable to generate a suitable method for calculating an abundance target. Therefore, the stock assessment team has included the development of a target abundance reference point in the research recommendations associated with this report (Section 10).

5.3 Fishing Mortality Rate Reference Points

Maryland law states that fishery management plans "Shall prevent overfishing while attempting to achieve the best and most efficient utilization of the State's fishery resources" (Natural Resources Article §4-215). As such, fishery management plans should contain an upper threshold (limit) reference point for fishing mortality (also expressed as exploitation rates) to identify overfishing. Furthermore, target reference points should be identified to achieve the best utilization of the resource. The stock assessment team recommends estimating the target exploitation rate (U) as that which provides maximum sustainable yield (MSY). If U_{MSY} is achieved annually, it is expected to result in a maximum harvest over time, while resulting in a stable or increasing oyster population (given current abundances of oysters in Maryland). As a limit reference point, the stock assessment team recommends estimating U_{crash} which represents the absolute maximum on sustainable harvest. If U_{crash} is exceeded over time it will result in eventual disappearance the population. As noted above, the limiting rate for oyster population growth is likely their ability to produce shell (Powell and Klinck, 2007; Mann et al., 2009; Wilberg et al., 2013). Therefore, shell production is an important process to include in sustainable harvest reference point calculations for oysters.

5.3.1 Methods

The target (U_{MSY}) and limit (U_{crash}) reference points were estimated using a fishing mortality reference point model that was modified from the model presented in Wilberg et al. (2013). This model describes population growth as a logistic function of abundance with carrying capacity determined by the amount of habitat. The amount of habitat depends on habitat production from living oysters, habitat loss and a maximum amount of potential oyster habitat in the system.

The assessment team modified the Wilberg et al. (2013) model to better match the assumptions and data sources of the assessment model (Section 3). Specifically, terms were added for planted oysters and shell or other substrate and terms were removed for the effect of fishing on habitat loss. The model was also reconfigured to be a discrete time version with the fishery modeled as a pulse at the beginning of the year (as was done in the stage-structured assessment model). Several of the original parameters in the Wilberg et al. (2013) model were not estimable, so they were fixed at values from the literature as described below. Lastly, the model required a parameter to convert from habitat in units of oysters to habitat in units of area. A discrete time version of the model was fitted with linked habitat dynamics to estimates of market-sized oyster abundance and area of habitat from the assessment models for each NOAA code.

The model includes a pulse fishery at the beginning of the year, so harvest (C_y) occurs before reproduction, natural mortality, and shell production. The abundance after harvest, but before reproduction and habitat growth (N_y^*), was calculated as the abundance at the beginning of the fishing season (N_y) less the harvest (C_y),

$$N_y^* = \hat{N}_y - C_y \ .$$

The abundance of market-sized oysters in the next year was calculated as the sum of oysters that survived harvest, net production from the population, and the number of market-sized oysters from planted sources (n_y),

$$\hat{N}_{y+1} = \left(N_y^* + rN_y^* \left(1 - N_y^* / \hat{H}_t \right) + n_y \right) e^{\varepsilon} \ ,$$

where *r* was the intrinsic rate of increase and $\hat{H}_y$ was the carrying capacity based on the available habitat (in units of oysters). A process error was included for each year, ε.

The amount of habitat in the next year was calculated as the sum of habitat in the current year, habitat production from live oysters and habitat added through planting (*h*) less the habitat that decayed,

$$\hat{H}_{y+1} = \left(\hat{H}_y + qN_y^* \left(1 - \hat{H}_y / T \right) - d\hat{H}_y + f \times h_y / q_h \right) e^{\delta} \ ,$$

where *q* was the intrinsic rate of habitat production, *T* was the maximum potential amount of habitat, *d* was the rate of habitat loss, *f* was the fraction of overlap of habitat plantings with previous habitat, *h* was the area of planted habitat (shell and artificial substrate), q_h was a factor to convert between habitat in units of area and units of oysters and δ was a process error. The *d* parameter was always fell to the lower bound when we tried to estimate it within the model. Therefore, we specified the value of d = 0.16 yr^{-1} based on the rate of shell degradation estimated for Maryland (Wilberg et al., 2013). This value is similar to that observed in Delaware Bay, 0.18 yr^{-1} (Powell and Klinck, 2007). Because the amount of habitat added was in units of area, it had to be converted to units of oysters by dividing by q_h and adjusted by the amount of overlap.

The maximum potential amount of habitat was not estimable given the available data, so we specified the maximum potential habitat using date from the Yates surveys during the early 1900s (Yates, 1912),

$$T = Y / q_h \ .$$

Because the Yates survey estimates were in units of area, they needed to be converted to units of oysters by dividing by q_h. The q_h parameter was specified at a value of 1/20, assuming that 20 market oysters per m^2 was the average maximum density. This is approximately the maximum density of market oysters that was estimated for Harris Creek after large-scale habitat restoration and planting efforts and was near the maximum observed density of market oysters in patent tong surveys in Maryland.

The parameters were estimated by fitting the model to estimates of market oyster abundance and area of habitat from the stock assessment models for each NOAA code. The overall negative log likelihood function (NLL_t) was the sum of the individual likelihood functions for abundance (NLL_N), habitat (NLL_H), the random process errors (NLL_P) and a penalty to constrain the process error standard deviation (NLL_σ),

$$NLL_t = NLL_N + NLL_H + NLL_P + NLL_\sigma .$$

We assumed lognormal process errors for market-sized abundance, where the "observed" abundance (N_y) and its observation error variance ($\sigma^2_{N,y}$) were the estimates from the stage-structured assessment model,

$$NLL_N = 0.5\sum\left(\log_e N_y - \log_e \hat{N}_y\right)^2 / \sigma^2_{N,y} .$$

Similarly, we assumed a lognormal error distribution for habitat with observed habitat (Hy) and its variance ($\sigma^2_{H,y}$) from the stage-structured assessment model,

$$NLL_H = 0.5\sum\left(\log_e H_y - \log_e (q_h \hat{H}_y)\right)^2 / \sigma^2_{H,y} .$$

The log-scale standard deviation for the estimates of habitat were increased by 0.2 in all years over those estimated in the stage-structured assessment models to reflect that the habitat was not explicitly linked to the population dynamics in that model.

The process errors were assumed to be normal on the log scale with a common variance term for both errors,

$$NLL_P = -Y \log\left(\frac{1}{\sqrt{2\pi\sigma^2_P}}\right) + 0.5\left(\sum \varepsilon_y + \sum \delta_y\right) / \sigma^2_P ,$$

where σ_P^2 was the estimated variance of the process errors and Y was the number of years. Lastly, we assumed a normal prior for the log of σ_P, NLL_σ, with a median of 0.2 and a log-scale SD of 0.2.

We adopted state-space version of the reference point model because variability in recruitment and natural mortality have been important aspects of oyster population dynamics in Maryland and observation error versions of the model failed to converge for many NOAA codes.

The exploitation rate that is expected to produce maximum sustainable yield (u_{MSY}) can be estimated from the parameters of the model as,

$$u_{MSY} = \frac{r}{2}\left(1 - \frac{d}{q}\right).$$

Similarly, the maximum limit on a sustainable exploitation rate (u_{crash}) can be estimated as,

$$u_{crash} = r\left(1 - \frac{d}{q}\right).$$

The stock assessment committee recommends using $u_{targ} = u_{MSY}$ and $u_{lim} = u_{crash}$.

For comparing estimates of market abundance and exploitation rates to the reference points, we used the point estimates.

Accounting for plantings

The estimated reference points described above assume that all production of new oysters and habitat is derived from the wild population. However, planting of oysters, shell and artificial substrate have been conducted to supplement the fishery and to attempt to restore oyster populations. We calculated an exploitation rate that accounts for the number of planted oysters that remain in the population assuming that planted oysters are harvested before wild oysters,

$$u_{comp} = \frac{C_y - n_y^*}{N_y - n_y^*},$$

where n_y^* was the number of planted market oysters that remain in the population at the beginning of the year assuming that planted oysters are harvested before wild oysters and have the same natural mortality rates as wild oysters,

$$n_y^* = n_y + (n_{y-1}^* - H_{y-1})e^{-M_{y-1}}$$

The number of planted oysters remaining in the population after harvest was set to zero if $H_{y-1} > n^{*}_{y-1}$. This formulation of the reference point assumes that oysters are planted with the goal of growing them out for harvest (i.e.,it includes a "credit" for planting oysters). In cases where plantings are for restoration efforts instead of to supplement the fishery, the exploitation rate calculated from the total N should be used.

We did not calculate exploitation rate reference points modified for shell plantings without spat. However, if shell plantings equal or exceed the amount of harvest, then the reference points should revert to the traditional estimates from a production model of r/2 for u_{MSY} and r for u_{crash}. Estimates could be modified for shell plantings short of full replacement using a linear interpolation, but in most NOAA codes and years the amount of shell planting is small relative to the harvest.

We tested the sensitivity of the reference point model to different values of the d parameter. This parameter was not able to be estimated within the model, so it was set to 0.16 in the base model. For the sensitivity analyses we fixed the value of d to half (0.08) and twice (0.32) of the value used in the base model.

5.3.2 Results

5.3.2.1 *Abundance Reference Points*

The year with the minimum estimated abundance of market-size oysters varied by NOAA code (Figure 113). The minimum value was reached during 2000-2007 for 22 NOAA codes. Four NOAA codes had their minimum estimated market abundance in the last year (2017) and two had their minimum estimated market abundance in the second to the last year. The majority of NOAA codes had market abundance well above the limit abundance reference point in 2017 (Figures 114-119). However, NOAA Codes in the Chester River (131, 231 and 331) and 127 had their minimum value in the last year. In addition, NOAA Codes 129 and 192 had their lowest values in the second to the last year.

5.3.2.2 *Model Fits*

The reference point models fitted the assessment estimates of abundance and habitat relatively well for almost all NOAA codes (Figure 120). The most notable issue in the residuals was that initial habitat was estimated to be very low for some NOAA codes that had very high levels of estimated abundance in the first year (e.g., 99 and 231). The q parameter was estimated at the upper allowable bound for 11 of 36 NOAA Codes (Table 13). The upper bound for q was set at 4, which implies that every live market oyster “produces” 4 units of market oyster habitat per year. While this value may seem high, it should be noted that the reference point model only includes market oysters, but small oysters also contribute to habitat. Furthermore, the amount of habitat produced by each oyster depends on a wide variety of factors including whether the oyster is alive or dead, the orientation of the shell in relation to the bottom and other oysters and the growth rate of oysters. While it is possible that the upper bound of q is set at too low a value, some sensitivity analyses (not shown) indicate that the estimates of reference points were insensitive to this value. This insensitivity makes sense because as q increases, u_{MSY} approaches r/2.

5.3.2.3 *Exploitation Rate Reference Points*

For this assessment, fishing mortality rate reference points are expressed in terms of exploitation rate (U). Estimates of the proposed limit reference point, U_{crash}, ranged from zero to 0.45 and estimates of the proposed target, U_{MSY}, ranged from zero to 0.22 among NOAA codes (Figures 121 and 122). Estimates of the target and limit reference point were highest, on average, in the southernmost NOAA Codes, Tangier Sound and the Potomac Tributaries, and decreased for the more northerly regions. Throughout the remainder of this section, the target u_{MSY} is referred to as u_{targ} and the limit u_{crash} is referred to as u_{lim}.

We did two comparisons of exploitation rates relative to reference points: one with an exploitation rate that was calculated for total harvest, and one with an exploitation rate that was calculated with a “credit” for planted oysters. There was substantial variability among NOAA codes and regions in their status relative to the exploitation rate reference points (Figures 123-134).

In Tangier Sound, one NOAA code (5, Big Annemessex River) was estimated to be below u_{targ} in 2017, one (47, Honga River) was estimated near u_{targ}, and the remaining seven were estimated to be above u_{lim} using the reference point estimation that does not account for planting (43, 57, 62, 72, 96, 192 and 292; Figure 11). When accounting for planting, the exploitation rates relative to the reference point in the last year were similar, with only Tangier Sound South (192) moving below u_{lim} (Figure 124).

In the Choptank River region, the estimated exploitation rate in 2017 was above u_{lim} in NOAA codes 137, 237, 437 and 637, and below u_{lim} in 53 and 337 (Figure 125). After accounting for planting in the exploitation rate estimates, only two NOAA codes (137 and 537) were above u_{lim} (Figure 126).

In the Eastern Bay region, the estimated exploitation rate in 2017 was above u_{lim} in all NOAA codes (39, 60, 99, 131, 231 and 331; Figure 127). After accounting for planted oysters, the estimated exploitation rate was below u_{lim} in two NOAA codes (131 and 231) and higher than u_{lim} in four (39,60, 99 and 331; Figure 128). The u_{lim} estimate was low across NOAA codes in this region.

In the Chesapeake Bay Mainstem region, the estimated exploitation rate in 2017 was above u_{lim} for all NOAA codes (Figure 129). Accounting for planted oysters, the estimated exploitation rate was below u_{lim} in four NOAA codes (25, 27, 127, and 229) and still above u_{lim} in 129 (Figure 130).

The estimated exploitation rate in 2017 was higher than u_{lim} in all NOAA codes in the Patuxent and Potomac Rivers region (168, 268, 368, 78, 86, 174 and 274; Figure 131). In 174, the estimated exploitation rate was near the target. After accounting for planting, the exploitation rates in all the NOAA codes except 274 were still above u_{lim} (Figure 132).

In the Western Shore region, the estimated exploitation rate in 2017 was zero for NOAA code 82, but above u_{lim} for NOAA code 88 (Figure 133). After adjusting the exploitation rate for planted oysters, both NOAA codes were well below u_{lim} (Figure 134).

Most of the NOAA codes had estimated exploitation rates above u_{lim} in 2017 (32 of 36). using the exploitation rate adjusted for planted oysters, 17 of 36 NOAA codes were above u_{lim} in 2017.

Relative to the base model, the uMSY and ulim estimates for almost all NOAA Codes changed very little (Figures 135 - 136). The only exception to this was for NOAA Code 437 where UMSY increased from approximately 0.01 to 0.12 when d was set to 0.32 (Figures 139 - 140). There was little difference in the base model estimates of UMSY in NOAA Code 437 when d was set to 0.08.

5.3.2.4 *Considerations*

The correct exploitation rate to use for comparison depends on the intent when the oysters were planted. If oysters were planted with the intent of supplementing the fishery, then the exploitation rate that accounts for planted oysters should be the most appropriate for comparison with the reference points. If, however, the oysters were planted as part of restoration efforts to increase population size, then the exploitation rate that does not include planted oysters should be used.

6.0 Contribution of Sanctuaries

This section addresses Term of Reference (TOR) 4*:*

Include sanctuaries and restoration efforts in sanctuaries in the development of stock assessment approaches.

6.1 Sanctuaries in the Assessment Model

The stock assessment team addressed this TOR by: 1) including substrate and spat plantings (i.e.,restoration efforts) explicitly in the stage-structured assessment model and 2) conducting the assessment at the NOAA code level. Substrate additions (shell and alternative) increase habitat in the stage-structured model. Plantings of spat and wild seed also increase abundance of spat and small oysters, respectively. For the limit abundance reference point, oysters in sanctuaries count towards the limit within a NOAA code.

There are large spatial differences in harvest pressure in Maryland. Sanctuaries represent one end of this continuum by mandating locations from which harvest is not permitted. A few NOAA codes are complete or nearly complete sanctuaries (e.g., Severn, upper Chester and upper Choptank, and Nanticoke Rivers). For these NOAA codes, modeling them separately explicitly accounts for the timing of sanctuary status on harvest and how that should affect the population dynamics. However, for most other NOAA codes, sanctuaries and public harvest areas are both present. We were not able to reduce the spatial resolution of our modeling efforts because reported harvest at the bar level is not thought to be accurate enough to support a finer spatial scale.

Several research recommendations could improve how sanctuaries are included in future assessments. These include improving accuracy of harvest reporting, increased surveying in sanctuaries, improvements in oyster habitat mapping and improvements in understanding larval transport.

6.2 Contribution of Oysters in Sanctuaries to Reference Points

As stated above, oysters in sanctuaries count towards the abundance threshold reference point within a NOAA code. The issue has also been raised about whether target and limit exploitation rates could be increased in areas outside of sanctuaries, or if sanctuaries should provide some amount of 'credit' in surrounding public fishery areas. The biological basis for this is that sanctuaries are expected to (eventually) support large adult oyster populations that will provide a source of larvae to neighboring areas. The assessment team was not able to address this question for the exploitation rate reference points for several reasons outlined below.

1) The potential for increased productivity in areas outside of sanctuaries relies on larvae being the limiting factor in oyster abundance in a region. If the limiting factor is available habitat, then an increase in larval supply will not result in increased numbers of spat. In most areas, the amount of available habitat is highly uncertain and has not been surveyed since the late 1970s-early 1980s.

2) The connectivity among areas within and outside NOAA codes would have to be known to ensure sustainable harvest. While progress is being made in understanding larval dispersal (North et al., 2010), the contributions of oysters in one part of Chesapeake Bay to another has yet to be estimated Maryland-wide. Furthermore, the amount of interannual variability in larval dispersal is not well understood. This variability is caused in part by variability in larval survival, settlement and post-settlement survival. Lastly, larval transport models have yet to be

validated for oysters in Maryland. Therefore, trying to fine tune reference points for these effects seems premature.

3) If abundance of adult oysters does not increase in a sanctuary, there is not an additional production to increase harvest rates in another area. For example, oyster abundance in NOAA code 331 (upper Chester River) has not increased despite being a sanctuary. Therefore, there is no increased production in this sanctuary to allocate to nearby areas.

4) If oyster abundance increases because of greater spat settlement, then amounts of sustainable harvest will increase even if the u_{targ} reference point remains unchanged. For example, if u_{targ} = 0.1 and there are 10 million market oysters in a NOAA code, then the target level of harvest would be 1 million oysters. If the number of oysters increased to 15 million because of increased spat sets caused by larval supply from a sanctuary, then the target level of harvest would increase to 1.5 million oysters (10% of the standing stock).

Overall, substantial improvements in information are needed to quantify the effect of sanctuaries on oysters in areas outside of sanctuaries. If oysters increase outside of sanctuaries because of larval supply from sanctuaries, then the currently proposed reference points would allow for increases in harvest.

7.0 Contribution of Plantings, Including Aquaculture

This section addresses Term of Reference (TOR) 5:

Examine how hatchery plantings (aquaculture and public fishery) impact spawning potential in the fishery.

This is a challenging TOR to address because once oysters are planted on public bottom or in sanctuaries they cannot always be readily distinguished from wild oysters. Also, aquaculture uses diploid and triploid oysters, the latter of which are specifically bred not to spawn. Cultured oysters may also be harvested year-round and sometimes at a smaller size than wild-harvested oysters, which complicates determination of whether they are harvested before or after they spawn.

Methods

Our approach to address this term of reference was to make a broad comparison among 1) the estimated abundance of market-sized oysters from the stage-structured assessment model, 2) the estimated number of market-size oysters generated by hatchery plantings using two assumptions about planted spat survival during their first two months (15% - base model, 5% sensitivity analysis), and 3) the number of market-size oysters harvested from leased grounds. While this simple comparison provides a perspective on the relative importance of planted oysters to wild oysters there are several important caveats to the analysis: 1) the harvest of oysters from lease grounds is used as a proxy value for the number of market-size oysters that may be on lease grounds, 2) a mortality rate is applied to hatchery spat to project the number of market-sized oysters present in the population and this rate may vary spatially and temporally, 3) the reproductive output per individual is similar among wild and planted oysters, and 4) aquaculture data are not currently available on a NOAA code scale so this comparison must be done on aggregate for the entire Maryland portion of Chesapeake Bay. This aggregation will mask important spatial variation in the contribution of planted and aquaculture oysters because areas with plantings often receive higher fishing pressure than neighboring areas.

Plantings in leased areas

Data on aquaculture planting numbers and harvest were summarized from leaseholder reports. The data included the bushels planted on leases, the number of individuals planted on leases by ploidy (diploid or triploid) and the bushels of oysters harvested. When harvest was reported by individual count, those values were converted to bushels assuming 300 oysters per bushel.

These data have a number of caveats:

1) At the time of this assessment, the numbers were still preliminary estimates.
2) Purchase and plantings of shellfish were verified by receipts when possible.
3) The number of active leases and number of acres under lease varies by year.
4) Diploid individuals largely represent spat-on-shell plantings from remote setting tanks.
5) Triploid individuals largely represent cultchless seed plantings, though some small percentage is remote set triploid spat-on-shell.
6) In 2012 and 2013, higher diploid bushel totals are likely due to remote setting planting events reported by the bushel with no corresponding spat per bushel density figure given to allow for conversion to # of individuals.
7) In all years, there is diploid planting reported by the bushel that is attributable to market oysters that were either wild harvested by the leaseholder and planted during the commercial oyster season or market product purchased from other dealers (less common).
8) Some market oysters on leases may not be harvested in a given year, such that the harvest numbers represent minimum estimates of market oysters on leases.

Plantings in non-lease areas

We used the stage-structured assessment models to estimate the number of market-size oysters from plantings each year. To estimate the number of market oysters from plantings, the number of spat planted and wild seed were tracked through the population model using the mortality and growth rates estimated from the models from Section 3 and assumptions about survival during the first two months after planting (15% - base model and 5% - sensitivity analysis). The number of market oysters from plantings were then subtracted from overall market abundance to estimate the number of market oysters from wild production. This approach potentially double counts wild seed that originated from another location in Maryland, but in recent years most wild seed originated from Virginia. These calculations assume that planted oysters experience the same mortality rates as wild oysters after October 1 of the year in which they were planted. In locations where oysters are planted in a sanctuary, their mortality rates are likely to be lower than those of oysters outside the sanctuary because of a difference in fishing mortality. In public harvest areas, planted oysters may be subject to higher fishing mortality rates than wild oysters.

Results

The number of oysters planted on leases in the Maryland portion of Chesapeake Bay increased by 30% from 231.7 million in 2012 to 301.3 million in 2016 (Table 14). Additionally, the proportion planted oysters that are triploid more than doubled to 34% in 2016 from 15% in 2012 as the number of triploid oysters planted increased while diploid oysters planted remained relatively constant (Table 14).

The number of oysters harvested from commercial shellfish leases in the Maryland portion of Chesapeake Bay increased from approximately 1.0 million in 2012 to 22.2 million in 2017 (Table 15). The number of market-size oysters estimated from the stage-structured model as 'wild origin' was, on average, 18 times greater than the number harvested on leases during 2012-2017. The estimated number of market-sized oysters generated from hatchery and wild plantings in non-lease areas was substantially greater than the number of oysters reported harvested from leases.

The number of oysters harvested from leases is not equivalent to the total number of market-size oysters present, but the magnitude of lease harvest is small relative to the estimated abundance of oysters of wild origin indicating that the spawning potential of these oysters is likely small relative to the population outside of leases at the Maryland-wide scale. In addition, any potential shift in the proportion of triploid oysters planted on leases would further erode the contribution of these animals to the total spawning potential.

Market-sized oysters from non-lease plantings, which are nearly all diploid, can potentially contribute a substantial larval subsidy to the wild oyster population in some NOAA codes and some years. However, using the available data, it is not possible to differentiate wild produced spat from those from planted oysters. Developing a mechanism to mark hatchery oysters prior to planting so that they can be differentiated from wild oysters would be extremely helpful in analyses to address this question.

8.0 Index-Based Approaches

8.1 Using Depletion Analyses to Estimate Exploitation Rates and Abundance

8.1.1 Objectives

This analysis was conducted to estimate the initial abundance and the fraction of oysters harvested each fishing season (exploitation rates) using reported harvest and effort data. The analysis was conducted for the 1999-2000 to 2016-2017 harvest seasons, using 36 NOAA codes from Maryland Chesapeake Bay (Table 16). Estimates were generated by NOAA code and Maryland bay-wide. This analysis was also conducted to explore the potential of using depletion analyses as a simple management tool. The assumptions of this analysis and a description of how the data meet those assumptions is provided in section 2.2.2.

8.1.2 Methods

8.1.2.1 *Selection of data*

Depletion analyses were used to estimate initial abundance for a given season based on observations of how the catch per unit of effort (CPUE) changes as a function of the cumulative harvest during a season (Leslie and Davis, 1939; Seber, 2002). Gear-specific buy ticket harvest data were used to calculate CPUE and represent the decrease in oyster density over the harvest season. If there were fewer than 50 harvest reports for any gear within a harvest season, that gear was excluded from the analysis since this small reported harvest indicated insufficient fishing pressure by that gear to cause a measurable response in the population. A preliminary analysis showed that sample sizes < 50 generally produced nonsensical estimates.

Six NOAA codes were excluded from the analysis. Three Potomac River NOAA codes (177, 277 and 377) were excluded, because they are in the management jurisdiction of the Potomac River Fisheries Commission and corresponding landings are not reported to the Maryland Department of Natural Resources. Additionally, NOAA codes 055, 094 and 098 were excluded because they had insufficient reported harvest. Additionally, these three NOAA codes do not contain any Maryland fall dredge survey sampling sites. (Section 2.3.1).

8.1.2.2 *Precision of the estimates*

Precision of the initial abundance and exploitation rate estimates was estimated using a Monte Carlo randomization approach. For initial abundance estimates, a random number was drawn from a normal distribution with mean and standard deviation equal to the y-intercept and its standard error estimate, respectively, from the depletion analyses. This random number was then divided by a random number drawn from a normal distribution with mean and standard deviation equal to the slope and its standard error estimate, respectively, from the depletion analyses. This process was repeated 100,000 times (for each season and NOAA Code) to produce a distribution of initial abundance estimates. A distribution of exploitation rate estimates was developed by dividing the total harvest from all gears for each harvest season and NOAA code by each of the 100,000 initial abundance estimates. Presentation of the results includes 95 percent confidence intervals determined by using the 0.0250 and 0.975 percentiles of the obtained distribution as upper and lower boundaries.

The distributions of initial abundance and exploitation fraction are known to be skewed (DeLury, 1951; Ricker, 1975) so the variance properties of normal distributions cannot be used to describe the variability of these estimates. Therefore, the widths of the confidence intervals were used to characterize precision (uncertainty) of initial abundance (N_0) estimates.

8.1.2.3 *Distribution of estimates by NOAA code, harvest season and dominant gear*

We examined the efficacy of the buy ticket data and depletion analysis to produce estimates of exploitation rate and initial abundance through examination of the distribution of the number of years of estimates in the time series for each NOAA code, and the percent of estimates produced for each harvest season. Because there are no estimates possible for areas without reported harvest, we calculated a "relative percent of estimates" for each harvest season as:

$$100 * \frac{Number\ of\ estimates}{Number\ of\ NOAA\ codes\ with\ reported\ harvest}$$

Another concern was the interchangeability of estimates produced from different gear-based CPUEs. Estimates produced from CPUEs of a "dominant" gear are not gear-specific estimates, but overall estimates using that gear as a survey method to measure reduction in oyster density over the harvest season in that NOAA code. These area-specific exploitation rates reflect contributions of all harvest gears but do not provide information about the relative contribution of the gears used in an area or whether some gears produce higher exploitation rates than others. We examined the distribution of dominant gears used to produce estimates and the distribution of estimates produced from dominant gear CPUEs.

8.1.2.4 *Examination of gear effects*

We calculated gear-specific exploitation rates and conducted ANOVA to determine if there were significant differences between gear-specific exploitation rates by NOAA code and harvest season. Gear-specific exploitation rates were calculated as:

$$U_{gear} = U_{overall} * 100 * \frac{Harvest_{gear}}{Harvest_{all\ gears}}$$

8.1.2.5 *Relationships*

Relationships between reported harvest, exploitation rate and estimates of initial abundance were examined through regression analysis.

8.1.3 Results and Discussion

8.1.3.1 *Data selection, regression analysis and choice of dominant gear*

As described in the methods, the analysis was conducted with the purpose of estimating a single value of exploitation and initial abundance for each NOAA code and harvest season. With 18 harvest seasons and 39 NOAA codes, there were a total of 702 NOAA code/harvest season combinations. Of these 113 had no reported harvest, resulting in 589 NOAA/harvest seasons for which estimates of initial abundance and exploitation rate were possible. Additionally, estimates were not developed for NOAA code/harvest seasons with less than 50 harvest reports, and in some cases estimates of regression and initial abundance could not be calculated because the regression produced a positive slope or failed to converge on an estimate of the slope and y-intercept. Ultimately, 270 estimates of initial abundance and exploitation rate were developed, which represented 46 percent of the 589 NOAA codes/harvest season combinations with harvest (Table 17).

Analysis of the 12 NOAA codes that produced 75 percent of the total time series harvest showed that the depletion estimates were based on an average of 74 percent of each NOAA code's total time-series harvest (Table 18), which indicates that the dominant gear reflects most of the harvest in most NOAA codes. This result provides justification for the selection of a dominant gear to produce a time series of estimates.

8.1.3.2 *Distribution and precision of the estimates*

The distribution of initial abundance estimates was highly skewed, with a median value of 13,581 bushels (Figure 135). Ninety percent of values were less than 100,000 but values ranged as high as 990,175. The high values were due to the extremely low regression slope values. (The negative slope estimates were very low, ranging from- 0.01 to -0.00001, with an average of -0.001 and a median of -0.003.) These results indicate that the high initial abundance estimates should be carefully considered before inclusion in stock dynamic models or used in management.

In contrast, exploitation rates followed a fairly symmetrical distribution, ranging from 0.003 to 0.85 with mean and median values of 0.37 (Figure 136). There was a wide distribution of values (0.00 to 0.85), with no apparent trends over the time series (Figure 137). However, this result reflects only 18 to 72 percent of NOAA codes with harvest per year (Table 19), so missing estimates could change the overall lack of trend.

The distribution of the width of the 95 percent confidence intervals of initial abundance estimates was strongly right skewed with many upper outliers - the highest value was a width of over 19,000,000 bushels. Excluding this value from consideration, the median width was 13,021 bushels (Figure 138).

The distribution of the width of the 95 percent confidence intervals of the exploitation estimates was also strongly right skewed with many upper outliers; however, the median width was only 0.26 (Figure 139).

8.1.3.3 *Estimates by NOAA code, region, harvest season and dominant gear*

Seventeen of the 39 NOAA codes had estimates of exploitation and initial abundance for at least half of the time series (Table 17). The number of years of for which estimates were possible was highly correlated with the cumulative time-series reported harvest (r = 0.75).

The Tangier Sound (37 percent of total harvest), Choptank River (25 percent) and Eastern Bay (19 percent) regions accounted for 81 percent of the cumulative time-series harvest (Table 17). Similarly, harvest was not distributed evenly within the regions. Two or three NOAA codes account for approximately 70 percent of the regional harvest. This indicates that an incomplete set of depletion-based estimates may provide adequate guidance for the stock assessment model if there are sufficient estimates for the highest producing NOAA codes to characterize the time series.

All regional time-series-mean exploitation rate estimates were between 31 and 39 percent (Table 20) and showed no strong correlation to regional harvest (r = 0.30).

The percent of estimates generated for NOAA codes with harvest increased over the time series (Figure 140), ranging from 18 percent in 1999-2000 to 72 percent in 2016-2017 (Table 19). Of particular concern are 1999-2000, 2003-2004 and 2004-2005, when less than 10 estimates were available Bay-wide, representing less than 20 percent of NOAA codes with reported harvest.

Most estimates were derived from power dredge CPUEs, followed by hand tong and patent tong data (Figure 141, Table 21). CPUEs from power dredging were used to develop estimates of initial abundance and exploitation rate for 13 NOAA codes, for a total of 123 estimates (45 percent of estimates). These NOAA codes had between one and 18 years of estimates, with a median of ten years of estimates. The average exploitation rate in these NOAA codes was 0.43 with an average initial abundance of 24,651. The second most common gear was hand tong, representing ten NOAA codes, for a total of 70 estimates (25 percent of estimates). These NOAA codes had between two and 18 years of estimates, with a median of seven years. The average exploitation rate in these NOAA codes was 0.33 with an average initial abundance of 49,042 bushels. Five NOAA codes were represented by patent tong harvest, for a total of 55 estimates (20 percent of estimates). These NOAA codes had between eight and 14 years of estimates, with a median of 11 years. The average exploitation rate in these NOAA codes was 0.32 with an average initial abundance of 69,166 bushels. Five NOAA codes were represented by diver harvest (39, 99, 131, 268 and 368), for a total of 27 estimates (ten percent of estimates). These NOAA codes typically had four or fewer years of estimates with an average exploitation rate of 0.36 and an average initial abundance of 24,651 bushels. No estimates were derived from Sail Dredge data.

8.1.3.4 *Examination of gear effects*

The comparison of gear-specific exploitation rates showed that there was a difference in the exploitation rates produced by different gears (Table 22). ANOVA and Duncan's Multiple Range Test found that power dredges produced a significantly higher ($p < 0.001$) exploitation rate than all other gears (0.28) followed by patent tongs (0.17), hand tongs (0.16) and divers, with a significantly lower rate than all other gears (0.12).

An additional pair-wise comparison analysis was conducted to determine if CPUEs based on different gears produced significantly different estimates of overall exploitation rate in the same NOAA code and harvest season. Sufficient sample sizes were available to test comparisons between power dredge-, patent tong- and hand tong–based estimates, and between hand tong- and diver-based estimates (Table 23). Power dredge-based exploitation rates were significantly higher than both patent tong and hand tong rates ($p < 0.001$), patent tong exploitation rates were significantly higher than hand tong rates ($p = 0.003$), but hand tong exploitation rates were not significantly different from diver rates ($p = 0.065$).

8.1.3.5 *Relationships*

At the NOAA code level, there was no relationship between exploitation rate and harvest in the same season (Figure 142, $n = 268$, $P = 0.57$), nor between exploitation rate and harvest in the next season (Figure 143, $P = 0.43$), so these data do not suggest an ability to use this method as a tool to predict harvest or effort.

There was a strong relationship between harvest and that season's initial abundance (Figure 144, $P < 0.001$). Closer examination of the NOAA codes with most harvest showed that the relationship is generally linear (Figure 145).

8.1.3.6 *Conclusions*

This analysis indicated that estimates of abundance and exploitation rates can be produced from commercial CPUE data via a Leslie depletion method modified for daily catch limits. The validity of the estimates is based on the assumptions of the Leslie depletion method being met. Estimates were produced for approximately half of the season/area combinations. These estimates were based on a "dominant" gear for each NOAA code. The use of a dominant gear was justified because the time series should be based on a single gear due to gear-specific catchability, and the dominant gear produced the maximum number of annual estimates for each NOAA code.

With respect to the spatial coverage, the data represented only NOAA codes with reported wild-caught harvest. Areas with no reported harvest have no associated estimates of abundance and exploitation rate. However, it is reasonable to assume that low oyster densities are the primary reason for lack of harvest.

Because the actual harvest is thought to be under-reported, initial abundances by region/NOAA code are likely to be underestimated. Furthermore, the uncertainty in initial abundance estimates appears to be relatively high and there are extreme upper outliers among the estimates, suggesting caution in using the absolute abundance estimates.

Exploitation rates varied considerably among NOAA codes, but variability was less in NOAA codes with moderate to high harvest. In these high harvest NOAA codes exploitation rates appeared to be estimated with better precision and little skewness and can therefore be seen as more reliable estimates of the status of the fishery and the stock than estimates of abundance. This is particularly relevant due to the fact that oyster harvest in Maryland is concentrated in just a few areas (Tangier Sound, Choptank River and Eastern Bay). Harvest rates for these areas appear to be sufficiently large to generate a decline in CPUE through the season that can be well estimated by a regression model with reasonable precision. These results also suggest that any use of depletion analysis for management may be constrained to the high harvest NOAA codes.

9.0 A Comparison of Index and Model-based Approaches

This section addresses Term of Reference 3:

Compare estimates of stock status generated by index and model-based approaches. Justify selected approach.

The assessment team considered whether index approaches can be used in lieu of the full stage-structure model. The exploitation rate estimates from the depletion analyses were considered as an alternative to exploitation rates from the stage structured model, and indices of density from the fall dredge survey were considered relative to estimated market abundance from the stage-structured model.

9.1 Exploitation Rate Reference Points

Exploitation rates are estimated by the depletion analyses (using only the commercial harvest and effort data) and also by the stage-structured stock assessment model. The depletion analyses are presented and fully discussed in section 8.1. The estimates from both methods (calculated as log F) are compared in the model fit plots in Section 4.1 (Figures 25-60). The stage-structured model estimated lower exploitation rates than the depletion method in most NOAA Codes and years. The stock assessment committee thought this lack of agreement was acceptable because of perceived issues with the estimates from the depletion analyses. The main issues include:

1) Depletion analysis can only be used in areas with enough harvest to produce a measurable decline in catch per unit effort (CPUE). A decline in fishery CPUE may not be observed because the harvest is not sufficient to reduce CPUE. In particular, because daily harvest is constrained by the allowable number bushels per vessel per day, catch per license per day may not be a sufficiently responsive metric to changes in oyster abundance. This is especially true since two licensed individuals on the same vessel may each catch their full daily bushel limit, so that a vessel with two licenses on board has, effectively, twice the limit of a vessel with one license. Potential issues with using the depletion method include changes in fishing locations during the course of the season, inaccuracies in reported harvest or effort or insensitivity of the metric of CPUE we used to changes in abundance. In addition, in areas with large sanctuaries, the depletion method likely overestimates the exploitation rate because it only reflects the change in abundance in the fished areas.

2) From a practical perspective, in many years it was not possible to obtain estimates of exploitation rates using only the depletion method. This was caused either by a lack of harvest in a NOAA code or by infeasible estimates from the depletion model (a positive relationship between cumulative catch and CPUE). Therefore, relying on this method to monitor the exploitation rates relative to their limit and target would rely on sufficient fishing pressure in all NOAA Codes, which is likely infeasible.

In the end the depletion method did not work as well as we had originally hoped, and it does not appear to be practical to use it alone for monitoring the status of the stock relative to the exploitation rate and abundance reference points, with the possible exception of limiting the analysis to only the NOAA codes with consistently high harvest (Section 8.1).

9.2 Abundance Reference Points

Two methods were compared for monitoring abundance relative to the threshold reference point. The first method was the estimated market abundance from the stage-structured model relative to the minimum abundance reference point (minimum estimated market abundance during 1999-2017) described in Section 4. The second approach used only the fall dredge survey standardized indices (index approach, Section 2.4.1). We used the standardized time series of market oyster density from the fall dredge survey (average number per half bushel).

We chose the minimum non-zero value from the time series during 1999-2017 as the limit reference point (Figures 146-151).

We compared estimated market-size oyster abundance relative to the threshold abundance reference point from the stage-structured assessment model to that from the market oyster index. In particular, we compared the year of the time-series minimum and the status in the most recent year relative to the limit and the status relative to the limit reference point in recent years.

9.3 Results

The index-based approach for abundance produced very similar results to the stage-structured assessment model for some NOAA codes, but was substantially different for others. There was a close correspondence in the year of minimum abundance or density in the Tangier Sound and Choptank River regions with no NOAA codes having more than a one-year difference in the year of the minimum (Table 24). Similarly, there was a close correspondence in the trends over time relative to the reference points in these two regions (Figures 147-148 and Figures 114-115).

The other regions had larger differences in both the year of the minimum and the pattern over time between the stage-structured model and the standardized fall survey estimates (Table 24, Figures 149-152 and Figures 116-119). In the Eastern Bay Region, the NOAA codes in the Chester River (131, 231 and 331) had similar patterns of estimated market abundance an indices of market density, but the patterns were different for the other NOAA Codes in the region (39, 60 and 99). In these latter NOAA codes, the index of density was farther above the minimum value in the most recent years than it was for estimated abundance. This similar pattern of higher levels relative to the minimum in the most recent years for the indices of market density were also present in all NOAA Codes in the Chesapeake Bay Mainstem Region, most of the NOAA Codes in the Patuxent and Potomac Rivers Region (268, 368, 174 and 274) and both NOAA Codes in the Western Shore Region (82 and 88). Many of the NOAA codes had large difference in the year of the minimum value (Table 24), with ten of 20 NOAA Codes having differences of at least three years.

These differences arise because the stage-structured model estimates abundance, but the indices from the fall dredge survey reflect density (number per area). The stage-structured model includes changes in oyster habitat over time, whereas the standardization of fall dredge survey time series does not include any adjustments for changes in habitat. Therefore, it is possible that abundance could decrease, but densities could remain relatively high if habitat has declined substantially. Under conditions of declining habitat, an index of density could lead to a different conclusion about stock status relative to an abundance reference point. Substantial declines in oyster habitat have been documented in Maryland (Rothschild et al., 1994; Smith et al. 2005). The Maryland fall dredge survey index in units of number per bushel of cultch likely is an index of density because it is a ratio of numbers to amount of shell material collected in the dredge (Wilberg et al., 2011).

9.4 Conclusions

We recommend using the stage-structured for evaluation of the status of abundance relative to a limit reference point model because it can easily be compared to both the exploitation rate and abundance reference points. Furthermore, we recommend using the stage-structured model for monitoring the status of the exploitation rate relative to its target and limit reference points. The stage-structured assessment model integrates more available data than the other methods, including a trend in habitat over time. If the goal is to maintain abundance above the minimum estimated level during 1999-2017, then including changes in habitat is an important consideration. Because the stage-structured models integrate more data on density of oysters and changes over time than the depletion analyses, the estimates of exploitation rates should be more accurate and reliable. There is potential to use the depletion analysis in limited NOAA codes that have consistently high harvest, particularly if more accurate harvest data become available.

It may be possible to use alternative analyses of the fall dredge survey data to monitor stock status relative to reference points that does not rely on running the full stage-structured assessment model. In particular, an index of abundance may be able to be created from the fall dredge survey data (rather than an index of density), by dividing the numbers caught by the area swept as is done for oysters in other regions (e.g., Delaware Bay) and other species like finfish, clams and scallops. However, this approach would require further development. In this assessment, we did not use a number per area swept index of abundance because 1) the length of the dredge tow began being recorded in 2005, which would shorten the time series by about six years, and 2) approximately 20% of tows result in a full dredge. These full dredges complicate calculation of a number per area metric because the dredge stops collecting new individuals at an unknown point along the dredge path. Given the time constraints for this assessment, we were not able to develop a satisfactory approach to correct for full dredges.

10.0 Research Recommendations

The following research recommendations were developed by the stock assessment team (Maryland Department of Natural Resources and University of Maryland Center for Environmental Science) in the process of completing this stock assessment. They are arranged by category rather than in order of priority.

Data

- Develop mechanisms to improve accuracy and resolution of reported harvest data including bar level data, the number of licensed individuals on a vessel, and the hours spent harvesting.

- Conduct fishery dependent sampling of oyster size distribution to better quantify the number of oysters per bushel and the number of under-sized oysters per bushel.
- Conduct research to better quantify growth rates that can be incorporated into stock assessment models.
- Conduct research to better quantify natural mortality of wild and hatchery -planted spat.
- Develop a means to mark hatchery-reared planted spat so that the proportion of planted versus wild oysters can be determined in subsequent surveys.

Natural Mortality

- Studies to improve estimates of box decay rate. Because box abundance is a critical element in the estimation of annual mortality, understanding how long boxes persist under varying conditions will improve estimates of natural mortality.
- Explore the effects of timing of the harvest relative to when fall survey is occurring to see if explains some of the difference between model-based and box count estimates of natural mortality.
- Research to better define longevity and identify primary sources of natural mortality of oysters.
- Examine resiliency of oyster populations to high natural mortality events.

Exploitation Rates

- A survey conducted just prior to and directly following the fishery would provide a direct means to estimate exploitation within a given year and could provide a snap shot of conditions relative to selected reference points.

Habitat

- Conduct more ground-truthing surveys on unverified current SONAR data so that existing sonar data can be accurately utilized in determining oyster habitat.
- Develop comprehensive maps of current oyster habitat within the Maryland portion of Chesapeake Bay.
- Studies designed to quantify the rate of habitat decay would better inform the assessment and reference point models; and would contribute to development of a shell budget.
- Develop a mechanism to better understand how shell plantings contribute to habitat and how habitat is quantified.
- Conduct research examining how harvest gears impact oyster habitat.

Sanctuaries and Spatial Scale

- The contribution of sanctuaries to oyster population and fishery dynamics within a NOAA code is an important question for management and will require finer scale spatial survey data within and outside of sanctuaries as well as more accurate bar-level harvest data than is currently available.
- Conduct research to help elucidate how individual NOAA codes (as well as sanctuaries and fished areas) contribute to one another's oyster populations. This would allow for a more complete stock assessment model that incorporates feedback among areas rather than the current assessment which treats each NOAA code as though it is an isolated population.

Assessment Model

- Incorporate a shell budget into stage structured assessment in order to allow internal estimation of biological reference points.
- Continue to improve the stock assessment model based on lessons learned from this assessment and as new information becomes available.
- Examine alternative spatial structure for stock assessment.

Biological Reference Points

- Fishing reference points for oysters should account for the accretion and loss of shell since oysters produce their own habitat that is required for population growth. Developing a spawner per-recruit type analysis that instead of egg production represents shell per recruit. Research is needed to determine the ratio of shell per recruit that is suitable for target and threshold reference points.

- Research on target levels of abundance including biological limits of abundance (e.g. necessary conditions for successful fertilization).

Aquaculture

- Developing an aquaculture data base that tracks plantings, standing stock and harvest of diploid and triploid oysters at the NOAA code spatial scale would be improve the model's ability to quantify the contribution of aquaculture plantings to the population dynamics within the NOAA code.

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12.0 TABLES

Table 1. Oyster harvest from the Maryland portion of Chesapeake Bay beginning with the 1889-1890 season through the 2017-2018 season.

Season	Bushels Harvested	Season	Bushels Harvested	Season	Bushels Harvested
1889-90	10,450,087	1945-46	2,322,185	1983-84	1,076,884
1890-91	9,945,058	1946-47	2,157,838	1984-85	1,142,493
1891-92	11,632,730	1947-48	2,027,381	1985-86	1,557,091
1892-93	10,142,500	1948-49	2,702,814	1986-87	976,162
1897-98	7,254,934	1949-50	2,495,787	1987-88	363,259
1900-01	5,685,561	1950-51	2,170,556	1988-89	397,180
1904-05	4,500,000	1951-52	2,339,976	1989-90	413,113
1906-07	6,232,000	1952-53	2,642,147	1990-91	416,720
1910-11	3,500,000	1953-54	2,129,115	1991-92	318,128
1916-17	4,120,819	1954-55	2,878,755	1992-93	123,618
1917-18	2,461,603	1955-56	2,799,788	1993-94	78,817
1918-19	3,743,638	1956-57	2,259,882	1994-95	164,673
1919-20	4,592,001	1957-58	2,190,074	1995-96	193,629
1920-21	4,959,962	1958-59	1,968,894	1996-97	171,630
1921-22	4,435,186	1959-60	2,114,899	1997-98	278,292
1922-23	3,687,489	1960-61	1,635,123	1998-99	413,010
1923-24	3,440,810	1961-62	1,495,235	1999-00	345,850
1924-25	2,787,047	1962-63	1,243,498	2000-01	316,630
1925-26	2,367,122	1963-64	1,383,617	2001-02	109,175
1926-27	2,571,540	1964-65	1,340,177	2002-03	47,141
1927-28	2,260,898	1965-66	1,645,144	2003-04	19.028
1928-29	1,993,591	1966-67	3,014,670	2004-05	57,558
1929-30	1,839,772	1967-68	3,000,272	2005-06	130,323
1930-31	1,775,738	1968-69	2,509,701	2006-07	154,236
1931-32	2,041,043	1969-70	2,533,275	2007-08	66,807
1932-33	1,626,214	1970-71	2,395,528	2008-09	87,358
1933-34	1,835,364	1971-72	2,900,547	2009-10	114,236
1934-35	2,100,233	1972-73	2,925,236	2010-11	103,608
1935-36	2,407,693	1973-74	2,845,924	2011-12	101,398
1936-37	3,081,063	1974-75	2,559,112	2012-13	330,064
1937-38	3,245,816	1975-76	2,449,440	2013-14	417,784
1938-39	3,403,549	1976-77	1,891,614	2014-15	375,244
1939-40	3,129,403	1977-78	2,311,434	2015-16	380,163
1940-41	3,430,269	1978-79	2,197,457	2016-17	213,397
1941-42	2,792,069	1979-80	2,111,080	2017-18*	179,779
1942-43	2,328,541	1980-81	2,532,321		
1943-44	2,413,349	1981-82	2,308,619	*preliminary	

Table 2. Surface area (acres) and historic oyster bar area (acres) for each NOAA Code in the Maryland Chesapeake Bay. Historic oyster bar area is defined as oyster bottom area charted in the Yates Oyster Survey from 1906 to 1912 plus its amendments. Summary of oyster seed and shell planting data for each NOAA Code in the Maryland Chesapeake Bay during 1999-2017. Habitat is the amount (acres) of material, primarily fresh or dredged oyster shell, planted on the bottom. Hatchery and Wild refer to the number (millions of individuals) of hatchery reared or transplanted wild seed placed on the bottom.

Region	NOAA code	NOAA code name	Surface Acres	Historic Bar Acres	Habitat Acres Planted	Hatchery Seed Planted	Wild Seed Planted
Tangier	5	Big Annemessex River	7,343	4,273	0	0	0
	43	Fishing Bay	31,138	11,933	77.3	20	5.88
	47	Honga River	31,445	20,050	191.2	55.13	8.76
	57	Manokin River	16,320	12,802	12.6	10.24	5.03
	62	Nanticoke River	19,661	1,258	274.9	63.01	69.04
	72	Pocomoke Sound	17,434	4,178	6.1	0	7.25
	96	Wicomico River East	6,621	712	13.1	75.64	4.85
	192	Tangier Sound South	90,266	38,682	1104.4	49.86	73.06
	292	Tangier Sound North	36,250	18,721	303.7	91.03	39.25
Choptank	53	Little Choptank River	19,423	4,183	227.5	1154.97	33.29
	137	Choptank River Lower	35,040	20,220	165.6	142.01	9.14
	237	Choptank River Middle	11,934	7,371	68.4	334.06	75.91
	337	Choptank River Upper	14,142	1,542	46.2	673.29	45.66
	437	Harris Creek	7,310	3,469	462.9	2437.71	34.93
	537	Broad Creek	7,959	2,746	347.3	19.4	82.07
	637	Tred Avon River	6,869	2,402	55.6	544.32	28.92
Eastern Bay	39	Eastern Bay	33,334	15,385	597	141.59	63.86
	60	Miles River	12,778	3,477	48.8	20.14	10.48
	99	Wye River	6,493	1,099	10.9	0.02	0
	131	Chester River Lower	18,183	3,901	194.9	529.68	19.69
	231	Chester River Middle	15,437	5,300	44.2	396.38	312.92
	331	Chester River Upper	7,204	550	0	52.62	0

Table 2 Continued.

Region	NOAA code	NOAA code name	Surface Acres	Historic Bar Acres	Habitat Acres Planted	Hatchery Seed Planted	Wild Seed Planted
Mainstem	25	Bay Mainstem Upper	164,314	25,934	7.4	619.74	624.22
	27	Bay Mainstem Lower Middle	186,830	34,162	106.5	10.32	35.2
	127	Bay Mainstem Upper Middle	56,902	17,373	15.3	42.5	341.69
	129	Bay Mainstem Lower Eastern Shore	130,954	7,741	37.3	0.72	0
	229	Bay Mainstem Lower Western Shore	105,377	23,590	220.6	0	17.96
Patuxent and Potomac Rivers	78	St. Mary's River	6,124	1,182	19.3	23.05	5.16
	86	Smith Creek	890	243	0	0	5.03
	168	Patuxent River Lower	8,880	2,564	96.2	61.43	75.25
	174	St. Clements And Breton Bay	7,045	2,502	0	0	0
	268	Patuxent River Middle	4,573	1,204	2.9	12.07	4.8
	274	Wicomico River West	11,953	4,399	0	186.12	168.27
	368	Patuxent River Upper	18,905	3,999	19.2	137.19	22.01
Western Shore	82	Severn River	7,711	1,291	15.2	229.9	2.15
	88	South River	6,099	1,455	0.2	88.3	37.29

Table 3. Distribution of oyster harvest over NOAA code reporting units in the Maryland portion of Chesapeake Bay.

Harvest Season	Total Reported Harvest	Number of NOAAs with harvest	NOAAs with non-zero harvest (% of total)	NOAAs with no reported harvest																								
1999-2000	345,850	38	97													98												
2000-2001	316,630	30	77						268	229	174					98		94		86						47	43	5
2001-2002	109,175	27	69		368		331		268		174			129		98		94		86	82				55	47	43	
2002-2003	47,141	26	67		368				268	229	174	168				98		94		86	82	78	72		55			5
2003-2004	19,028	20	51	637	368	337	331	274	268		174	168	137		99	98	96	94	88	86	82	78			55			5
2004-2005	57,558	32	82								174					98	96	94		86	82				55			
2005-2006	130,323	34	87				331										96	94			82				55			
2006-2007	154,236	34	87								174				99	98		94									43	
2007-2008	66,807	32	82				331				174				99	98		94			82				55			
2008-2009	87,358	35	90															94			82				55			5
2009-2010	114,236	35	90	637														94							55			5
2010-2011	103,608	33	85								174				99			94			82				55			5
2011-2012	101,398	35	90												99			94			82				55			
2012-2013	330,064	35	90				331											94						60	55			
2013-2014	417,784	35	90				331				174				99			94										
2014-2015	375,244	37	95															94							55			
2015-2016	380,163	35	90				331				174							94							55			
2016-2017	213,397	36	92				331											94			82							
2017-2018	179,779	39	100																									

Table 4. Bushels harvest by gear type from the Maryland portion of Chesapeake Bay beginning with the 1889-1890 season through the 2017-2018 season.

	GEAR						
SEASON	Hand Tong	Power Dredge	Patent Tong	Diver	Sail Dredge	Unknown	Annual Total
1999-2000	228,738	7,978	41,384	57,566	-	10,184	**345,850**
2000-2001	187,412	5,851	39,130	73,489	-	10,748	**316,630**
2001-2002	46,981	9,328	20,715	26,066	-	6,085	**109,175**
2002-2003	10,589	9,180	16,589	8,978	-	1,805	**47,141**
2003-2004	1,490	7,588	3,261	5,366	-	1,323	**19,028**
2004-2005	4,859	28,894	5,143	14,049	-	4,613	**57,558**
2005-2006	27,377	12,863	46,219	38,001	-	5,863	**130,323**
2006-2007	56,012	29,000	29,705	36,282	-	3,237	**154,236**
2007-2008	22,827	20,683	10,841	11,160	-	1,296	**66,807**
2008-2009	10,869	43,988	19,635	9,480	-	3,386	**87,358**
2009-2010	5,506	68,790	33,118	3,029	161	3,632	**114,236**
2010-2011	10,418	52,335	20,911	5,018	9,769	5,158	**103,608**
2011-2012	8,610	64,653	14,323	2,257	6,630	4,925	**101,398**
2012-2013	52,513	196,327	43,712	5,715	18,119	13,678	**330,064**
2013-2014	67,060	227,716	71,455	23,983	17,494	10,077	**417,784**
2014-2015	66,480	167,963	83,578	23,904	23,366	9,954	**375,244**
2015-2016	77,866	118,052	96,348	37,171	37,000	13,727	**380,163**
2016-2017	44,400	71,793	49,390	21,600	17,174	9,041	**213,397**
2017-2018	36,937	76,562	30,814	22,610	11,092	1,764	**179,779**
Gear Total	**966,944**	**1,219,544**	**676,269**	**425,722**	**140,804**	**120,495**	**3,549,778**

Table 5. The gear type used to harvest from the most productive areas within Maryland's portion of Chesapeake Bay varies by area.

Area	NOAA Code	Number of Years with Harvest	Primary Gear	NOAA Total Harvest	%of Total Harvest	Cumulative Percent	Cumulative Harvest (Bu)
Broad Creek	537	18	Hand Tong	**479,232**	14%	14%	479,232
Eastern Bay	39	18	Diver	**394,418**	12%	26%	873,650
Upper Tangier Sound	292	18	Patent Tong	**335,331**	10%	36%	1,208,981
LowerTangier Sound	192	18	Power Dredge	**295,027**	9%	45%	1,504,008
Fishing Bay	43	15	Power Dredge	**228,355**	7%	51%	1,732,363
Lower Patuxent River	168	16	Hand Tong	**149,240**	4%	56%	1,881,603
Honga River	47	16	Power Dredge	**147,627**	4%	60%	2,029,231
Upper Bay Mainstem	25	18	Patent Tong	**118,713**	4%	64%	2,147,944
Pocomoke Sound	72	17	Power Dredge	**112,755**	3%	67%	2,260,698
Lower Choptank River	137	17	Power Dredge	**107,989**	3%	70%	2,368,687
Middle Chester River	231	18	Hand Tong	**94,174**	3%	73%	2,462,861
Little Choptank River	53	18	Hand Tong	**87,563**	3%	76%	2,550,424

Table 6. Maryland Chesapeake Bay NOAA codes, areas, and number of bars sampled by the Maryland Department of Natural Resources fall dredge survey.

Region	NOAA	Acres	Number of Bars	Number of Bars with 10+ Years of Samples
Tangier Sound	192	85,201	20	17
	292	35,090	5	4
	047	29,331	11	7
	043	19,184	8	7
	057	18,317	5	5
	062	16,731	9	9
	072	14,160	7	5
	005	6,615	2	1
	096	5,402	3	3
Choptank River	137	34,076	8	6
	053	18,319	15	11
	237	11,278	9	8
	337	10,659	9	9
	537	7,487	7	6
	437	6,999	10	7
	637	5,850	11	9
Eastern Bay	039	32,576	19	16
	131	17,480	7	4
	231	14,345	13	10
	060	12,002	10	10
	331	6,087	3	3
	099	5,846	5	5
Chesapeake Bay Mainstem	027	236,874	8	8
	025	161,961	12	12
	129	127,304	2	2
	229	109,394	9	6
	127	55,959	8	8
Patuxent River & Potomac River	368	16,828	8	6
	274	11,390	11	10
	168	8,273	11	9
	174	6,278	2	2
	078	5,606	8	7
	268	3,611	1	1
	086	868	3	2
Western Shore	082	6,820	1	1
	088	5,286	9	6

Table 7. Total natural mortality (as a percentage) of eastern oyster for Maryland Chesapeake Bay regions and NOAA codes, as calculated from Maryland DNR fall dredge survey box count data.

Region / NOAA code		1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Bay-wide		27	30	36	51	23	17	15	16	13	13	14	15	9	8	8	9	13	17
Tangier Sound	Region	51	29	36	38	21	30	40	22	7	12	14	19	8	10	11	14	16	14
	292	64	45	30	49	22	35	58	35	11	10	14	19	11	11	12	19	20	14
	192	49	21	37	36	24	35	36	21	7	12	16	26	12	11	11	18	19	16
	043	58	65	54	58	43	48	67	25	2	5	4	3	6	6	9	15	21	21
	047	54	27	30	31	11	24	49	17	3	5	12	15	9	12	19	14	20	17
	072	39	23	35	36	12	15	32	11	3	17	15	11	2	10	9	13	14	9
	062	46	33	26	57	36	16	10	18	7	11	5	5	5	9	4	7	4	9
	096	66	55	48	57	30	34	13	0	26	9	4	7	4	4	6	11	23	34
	057	49	32	26	23	9	23	67	37	7	15	13	17	5	13	13	13	12	12
	005	40	13		0	4	25		67	16	50	0	0	33		0	33	100	0
Choptank River	Region	25	27	36	76	49	13	3	5	9	10	10	8	3	5	7	7	11	17
	537	36	15	28	73	40	4	1	3	11	11	7	4	2	3	5	6	11	11
	137	28	37	49	92	66	16	2	3	4	6	4	3	3	4	5	6	12	18
	053	27	28	45	95	52	6	2	8	13	15	19	18	5	11	12	11	15	29
	437	20	16	24	86	61	8	2	3	9	10	7	6	2	1	4	4	7	15
	237	13	36	32	65	42	29	9	14	7	6	3	6	5	6	7	10	8	20
	637	31	37	36	74	51	18	4	4	10	10	11	6	3	6	7	6	15	16
	337	7	18	25	44	46	15	9	5	3	3	3	5	4	4	8	3	5	9
Eastern Bay	Region	16	26	41	47	34	12	8	24	32	21	22	12	7	5	5	6	10	14
	039	21	32	44	49	28	11	8	34	48	31	26	11	6	3	5	6	11	14
	060	16	30	39	49	42	10	7	27	42	37	31	13	6	9	3	7	13	21
	099	12	35	49	52	53	17	8	10	25	30	26	21	9	4	1	4	7	18
	131	10	23	33	48	26	11	1	8	7	6	15	8	10	8	9	7	13	9
	231	7	16	40	49	36	17	16	11	13	8	7	10	9	4	5	8	4	5
	331	3	9	16	20	22	6	6	5	7	5	32	29	11	21	6	4	6	15
Chesapeake Bay Mainstem	Region	15	25	25	33	11	6	5	10	14	11	15	19	31	12	8	6	11	10
	025	6	10	11	14	7	6	2	4	5	6	3	12	46	11	11	2	5	2
	027	30	42	33	59	14	6	7	14	11	14	18	10	8	7	5	6	14	16
	129	0	45	64	0	4	9	14	21	29	24	34	25	81	36	27	19	18	21
	127	13	18	28	51	26	7	4	11	8	10	11	10	3	4	4	2	2	3
	229	44	60	34	18	6	5	13	15	24	11	18	28	12	10	6	8	12	16
Patuxent River & Potomac River	Region	38	45	40	64	12	17	22	21	14	14	17	19	13	11	9	10	17	23
	168	62	52	55	49	9	8	17	39	22	12	15	19	8	12	13	7	22	29
	268		0	49	94	36	0	14	22	32	1	11	25	8	9	16	12	12	18
	368	35	49	52	60	14	8	7	11	17	15	10	11	5	17	10	4	9	15
	078	31	56	33	88	9	33	53	17	6	16	26	21	19	10	7	16	22	27
	086	82	71	54	62	12	10	39	11	11	16	38	33	2	5	9	15	18	35
	174	40	66	69	76	47	44	42	10	0	4	4	0	23	17	3	25	9	8
	274	23	26	28	50	22	12	6	15	25	10	7	16	9	5	9	2	3	10
Western Shore	Region	12	16	40	42	29	16	11	11	27	6	9	8	6	4	4	3	5	11
	082	4	4	30	58	52	28	18	17	6	2	1	5	0	5	11	11	5	11
	088	16	18	46	34	16	11	9	11	28	7	11	9	7	4	4	2	5	11

Table 8. Recent natural mortality (as a percentage) of eastern oyster for Maryland Chesapeake Bay regions and NOAA codes, as calculated from Maryland DNR fall dredge survey box count data.

Region / NOAA code		1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Bay-wide		6	4	6	9	2	2	1	1	2	1	2	2	0	1	2	1	2	3
Tangier Sound	Region	17	3	6	13	4	6	5	2	2	1	3	3	0	1	2	1	3	3
	292	30	6	2	13	4	11	15	3	1	3	2	2	1	1	3	2	3	1
	192	13	3	8	14	5	5	2	2	2	2	4	6	1	1	2	2	3	2
	043	15	6	8	18	11	4	0	14	0	0	1	0	1	1	2	1	3	3
	047	12	4	3	6	1	5	13	1	1	1	2	1	0	1	3	1	4	4
	072	4	4	8	6	3	3	0	2	1	0	2	1	0	1	1	2	5	1
	062	22	3	3	25	2	2	3	5	1	0	0	0	0	1	0	0	1	3
	096	30	0	0	6	0	2	8	0	0	2	0	0	0	1	1	1	3	2
	057	16	5	1	7	1	8	19	2	2	0	1	3	0	2	3	1	3	4
	005	0	0		0	0	0		0	6	0	0	0	0		0	0	0	0
Choptank River	Region	6	6	6	13	2	0	0	0	2	1	1	1	0	0	1	1	2	3
	537	8	4	5	10	1	0	0	1	2	0	1	0	0	0	1	1	2	2
	137	9	9	10	35	4	1	0	0	1	0	0	0	0	1	0	1	1	5
	053	7	5	9	13	1	0	0	1	2	1	3	3	1	1	1	1	3	6
	437	4	2	3	8	0	0	0	0	2	1	2	0	0	0	1	0	2	3
	237	3	9	4	19	3	1	2	1	2	0	0	0	0	1	1	1	1	4
	637	7	8	2	16	2	0	0	0	1	0	2	1	0	1	1	0	1	1
	337	2	5	1	8	1	0	0	0	0	0	0	0	0	1	1	0	0	2
Eastern Bay	Region	3	4	7	7	1	0	1	2	2	1	3	0	0	0	1	0	0	1
	039	5	6	9	9	1	0	1	3	4	2	4	1	0	0	0	0	0	1
	060	4	6	10	8	1	0	1	3	4	2	6	1	0	0	1	0	0	0
	099	2	4	9	6	2	0	2	1	2	0	0	0	0	2	0	0	1	5
	131	2	3	2	6	1	0	0	1	0	0	0	0	1	1	2	0	0	1
	231	1	2	4	3	0	1	2	0	1	0	0	0	0	0	0	0	0	0
	331	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Chesapeake Bay Mainstem	Region	2	3	4	3	1	0	0	1	4	2	2	2	1	0	2	1	2	3
	025	1	1	1	2	0	0	0	0	1	0	0	1	2	0	2	0	0	0
	027	7	7	7	3	0	1	0	0	1	2	2	0	1	0	2	2	1	1
	129	0	17	20	0	0	0	0	3	13	11	2	1	2	1	11	5	5	7
	127	2	2	5	8	1	0	0	1	1	0	1	0	0	0	0	0	0	0
	229	3	6	8	3	2	0	1	2	6	1	4	7	1	0	1	1	4	6
Patuxent River & Potomac River	Region	7	4	5	8	1	3	2	3	2	1	1	3	1	2	2	1	3	4
	168	21	5	9	10	2	1	5	6	4	2	3	4	0	3	3	2	5	7
	268		0	7	50	0	0	3	5	7	0	0	2	0	1	1	4	0	6
	368	6	7	11	1	1	1	1	2	2	1	0	1	0	3	2	0	0	3
	078	6	5	2	17	2	7	2	3	1	1	2	4	3	1	2	1	3	5
	086	24	7	20	9	0	1	2	0	0	3	3	3	0	0	1	2	4	0
	174	4	6	3	11	0	0	0	0	0	0	0	0	0	0	0	0	0	5
	274	2	1	2	6	0	0	0	1	2	0	0	1	0	0	0	0	0	1
Western Shore	Region	2	2	7	2	1	0	0	3	3	0	2	1	0	0	1	0	0	0
	082	1	0	0	5	0	1	1	1	2	0	0	0	0	0	0	0	0	0
	088	2	3	12	1	1	0	0	3	3	0	2	2	0	0	1	0	0	0

Table 9. The number of oyster bars in the Maryland portion of Chesapeake Bay with a complete fall dredge survey time series for estimating natural mortality with the Bayesian model by region and NOAA code.

Region	NOAA code	Number of Oyster Bars
Tangier Sound	005	NA
	043	5
	047	5
	057	5
	062	6
	072	5
	096	3
	098	NA
	192	9
	292	3
Choptank River	053	6
	137	4
	237	6
	337	6
	437	2
	537	2
	637	4
Eastern Bay	039	6
	060	4
	099	3
	131	2
	231	6
	331	NA
Chesapeake Mainstem	025	11
	027	6
	127	5
	129	NA
	229	3
Patuxent River and Potomac River	168	6
	268	NA
	368	5
	078	5
	086	NA
	174	2
	274	5
Western Shore	055	NA
	082	NA
	088	NA
	094	NA

Table 10. Median natural mortality rates (proportions) from the Bayesian model by region and NOAA code, 1991-1998.

		Years							
Region	**NOAA Code**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**
Tangier Sound	**005**	NA	NA	NA	NA	NA	NA	NA	NA
	043	0.33	0.63	0.30	0.05	0.54	0.65	0.43	0.07
	047	0.53	0.74	0.03	0.09	0.52	0.15	0.19	0.48
	057	0.47	0.63	0.04	0.23	0.79	0.23	0.13	0.18
	062	0.10	0.50	0.07	0.19	0.13	0.12	0.14	0.05
	072	0.53	0.52	0.05	0.24	0.83	0.19	0.37	0.26
	096	0.03	0.69	0.31	0.20	0.31	0.19	0.28	0.14
	098	NA	NA	NA	NA	NA	NA	NA	NA
	192	0.46	0.72	0.15	0.22	0.72	0.27	0.15	0.31
	292	0.35	0.76	0.08	0.12	0.76	0.53	0.15	0.19
Choptank River	**053**	0.53	0.51	0.23	0.01	0.21	0.05	0.10	0.16
	137	0.38	0.52	0.23	0.02	0.27	0.09	0.06	0.11
	237	0.38	0.63	0.50	0.04	0.22	0.24	0.05	0.03
	337	0.08	0.27	0.27	0.13	0.10	0.13	0.02	0.11
	437	0.45	0.24	0.34	0.04	0.26	0.10	0.09	0.07
	537	0.63	0.43	0.12	0.01	0.33	0.10	0.08	0.15
	637	0.76	0.48	0.32	0.05	0.30	0.11	0.07	0.12
Eastern Bay	**039**	0.19	0.36	0.29	0.18	0.32	0.17	0.11	0.11
	060	0.49	0.50	0.25	0.17	0.36	0.21	0.02	0.15
	099	0.60	0.49	0.08	0.21	0.33	0.06	0.09	0.11
	131	0.14	0.35	0.05	0.16	0.07	0.39	0.04	0.08
	231	0.04	0.07	0.04	0.15	0.08	0.22	0.06	0.06
	331	NA	NA	NA	NA	NA	NA	NA	NA
Chesapeake Bay Mainstem	**025**	0.05	0.07	0.05	0.19	0.01	0.33	0.01	0.08
	027	0.10	0.61	0.34	0.26	0.49	0.23	0.19	0.30
	127	0.10	0.02	0.11	0.14	0.10	0.18	0.09	0.10
	129	NA	NA	NA	NA	NA	NA	NA	NA
	229	0.67	0.86	0.03	0.02	0.24	0.33	0.16	0.28
Patuxent River and Potomac River	**168**	0.61	0.84	0.19	0.18	0.25	0.35	0.10	0.32
	268	NA	NA	NA	NA	NA	NA	NA	NA
	368	0.50	0.65	0.04	0.05	0.12	0.04	0.06	0.06
	078	0.20	0.31	0.14	0.13	0.17	0.17	0.14	0.13
	086	NA	NA	NA	NA	NA	NA	NA	NA
	174	0.63	0.21	0.04	0.19	0.45	0.09	0.22	0.23
	274	0.22	0.16	0.03	0.04	0.25	0.21	0.03	0.05
Western Shore	**055**	NA	NA	NA	NA	NA	NA	NA	NA
	082	NA	NA	NA	NA	NA	NA	NA	NA
	088	NA	NA	NA	NA	NA	NA	NA	NA
	094	NA	NA	NA	NA	NA	NA	NA	NA

Table 10. continued

		Years									
Region	**NOAA Code**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**
Tangier Sound	**005**	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	043	0.65	0.71	0.41	0.66	0.30	0.37	0.32	0.22	0.02	0.06
	047	0.60	0.20	0.39	0.28	0.07	0.30	0.46	0.08	0.03	0.08
	057	0.61	0.23	0.23	0.28	0.08	0.28	0.71	0.04	0.04	0.17
	062	0.61	0.08	0.28	0.59	0.26	0.18	0.08	0.22	0.07	0.10
	072	0.48	0.22	0.40	0.38	0.08	0.16	0.25	0.08	0.02	0.25
	096	0.76	0.51	0.32	0.48	0.16	0.27	0.05	0.13	0.34	0.12
	098	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	192	0.54	0.24	0.34	0.42	0.27	0.32	0.28	0.16	0.09	0.17
	292	0.67	0.26	0.22	0.46	0.22	0.42	0.47	0.21	0.15	0.03
Choptank River	**053**	0.35	0.34	0.58	0.95	0.02	0.01	0.01	0.10	0.18	0.15
	137	0.36	0.38	0.53	0.93	0.07	0.02	0.01	0.01	0.08	0.10
	237	0.19	0.45	0.32	0.82	0.19	0.09	0.04	0.12	0.08	0.04
	337	0.08	0.21	0.24	0.50	0.47	0.13	0.04	0.06	0.04	0.06
	437	0.29	0.09	0.24	0.87	0.09	0.02	0.01	0.03	0.15	0.09
	537	0.50	0.06	0.38	0.81	0.08	0.01	0.00	0.02	0.06	0.12
	637	0.45	0.44	0.26	0.88	0.43	0.17	0.04	0.04	0.10	0.05
Eastern Bay	**039**	0.27	0.30	0.44	0.53	0.11	0.01	0.05	0.47	0.56	0.19
	060	0.18	0.31	0.45	0.60	0.35	0.03	0.09	0.38	0.57	0.35
	099	0.18	0.40	0.44	0.57	0.49	0.03	0.03	0.07	0.27	0.27
	131	0.14	0.31	0.37	0.52	0.21	0.03	0.01	0.36	0.23	0.28
	231	0.08	0.25	0.46	0.54	0.29	0.03	0.23	0.05	0.11	0.06
	331	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Chesapeake Bay Mainstem	**025**	0.06	0.15	0.06	0.18	0.05	0.06	0.01	0.06	0.05	0.07
	027	0.38	0.52	0.34	0.77	0.01	0.01	0.02	0.19	0.02	0.22
	127	0.16	0.27	0.29	0.58	0.12	0.02	0.01	0.14	0.03	0.14
	129	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	229	0.48	0.63	0.13	0.24	0.09	0.01	0.14	0.18	0.37	0.06
Patuxent River and Potomac River	**168**	0.70	0.54	0.58	0.59	0.01	0.05	0.24	0.40	0.23	0.08
	268	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	368	0.46	0.55	0.53	0.58	0.02	0.07	0.12	0.17	0.03	0.18
	078	0.41	0.63	0.35	0.78	0.04	0.43	0.51	0.01	0.02	0.14
	086	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	174	0.47	0.72	0.63	0.70	0.16	0.27	0.31	0.10	0.09	0.06
	274	0.32	0.32	0.40	0.54	0.11	0.10	0.05	0.19	0.35	0.19
Western Shore	**055**	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	082	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	088	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	094	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Table 10. continued

Region	NOAA	Years 2009	2010	2011	2012	2013	2014	2015	2016	2017	Mean
Tangier Sound	**005**	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	043	0.06	0.07	0.04	0.11	0.13	0.18	0.15	0.19	0.01	0.28
	047	0.16	0.13	0.12	0.16	0.18	0.13	0.19	0.13	0.19	0.25
	057	0.13	0.21	0.03	0.18	0.14	0.14	0.13	0.13	0.12	0.24
	062	0.06	0.06	0.08	0.14	0.04	0.09	0.06	0.14	0.07	0.17
	072	0.14	0.11	0.03	0.12	0.12	0.16	0.15	0.08	0.15	0.24
	096	0.04	0.11	0.05	0.06	0.12	0.15	0.30	0.41	0.17	0.25
	098	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	192	0.22	0.26	0.07	0.13	0.13	0.31	0.21	0.05	0.09	0.27
	292	0.22	0.24	0.13	0.13	0.15	0.18	0.22	0.18	0.02	0.28
Choptank River	**053**	0.23	0.24	0.02	0.15	0.15	0.13	0.16	0.36	0.16	0.22
	137	0.05	0.06	0.04	0.04	0.07	0.07	0.16	0.27	0.21	0.19
	237	0.03	0.09	0.07	0.06	0.11	0.14	0.05	0.27	0.08	0.20
	337	0.07	0.06	0.06	0.04	0.12	0.02	0.06	0.12	0.15	0.13
	437	0.05	0.06	0.03	0.00	0.08	0.01	0.07	0.19	0.05	0.15
	537	0.04	0.05	0.03	0.02	0.06	0.06	0.15	0.09	0.03	0.16
	637	0.16	0.08	0.02	0.13	0.10	0.09	0.15	0.21	0.15	0.23
Eastern Bay	**039**	0.20	0.09	0.04	0.02	0.06	0.09	0.05	0.17	0.21	0.21
	060	0.26	0.07	0.05	0.07	0.02	0.11	0.03	0.17	0.10	0.23
	099	0.22	0.30	0.02	0.03	0.02	0.06	0.09	0.19	0.28	0.22
	131	0.24	0.07	0.11	0.07	0.09	0.06	0.03	0.08	0.05	0.17
	231	0.07	0.12	0.07	0.06	0.04	0.14	0.03	0.14	0.03	0.13
	331	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Chesapeake Bay Mainstem	**025**	0.03	0.14	0.51	0.01	0.09	0.01	0.08	0.01	0.01	0.09
	027	0.17	0.13	0.04	0.02	0.04	0.07	0.20	0.23	0.26	0.23
	127	0.09	0.05	0.02	0.05	0.04	0.03	0.03	0.05	0.10	0.11
	129	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	229	0.18	0.09	0.11	0.01	0.10	0.05	0.17	0.26	0.06	0.22
Patuxent River and Potomac River	**168**	0.19	0.21	0.03	0.16	0.14	0.08	0.23	0.29	0.06	0.28
	268	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	368	0.12	0.17	0.02	0.09	0.09	0.06	0.11	0.18	0.04	0.19
	078	0.24	0.17	0.04	0.10	0.04	0.14	0.18	0.37	0.09	0.23
	086	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	174	0.05	0.07	0.34	0.26	0.04	0.15	0.12	0.08	0.07	0.25
	274	0.05	0.19	0.07	0.09	0.13	0.03	0.05	0.08	0.01	0.16
Western Shore	**055**	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	082	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	088	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	094	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Table 11. Definitions of stage-structured stock assessment model parameters and variables.

Parameter	Definition
	Indicator variables and subscripts
y	Year (1999-2017)
s	Stage (sp - spat, sm - small, mk - market, smb - sm box, mkb - mk box)
p	Indicator of penalty function for parameter estimation
	Estimated parameters
R_y	Recruitment in each year
M_y	Natural mortality of small and market oysters in each year
b	Rate of disarticulation (separately for small boxes and market boxes)
G	Probability of transitioning from small to market
d_n	Rate of habitat decay
N_0	Initial abundance of small and market oysters
B_0	Initial abundance of small boxes and market boxes
q_N	Catchability of small and market oysters
q_B	Catchability of small boxes and market boxes
q_{sp}	Catchability for spat
q_M	Catchability for index of recent mortality
	Calculated quantities
N_y	Abundance of spat, small, and market oysters (by category)
B_y	Abundance of small boxes and market boxes (by category)
H_y	Habitat
u_y	Rate of exploitation
$\hat{F}_y$	Estimated instantaneous fishing mortality rate
$\hat{I}_{N,y,s}$	Estimated index of relative density of spat, small, and market oysters
$\hat{I}_{B,y,s}$	Estimated index of relative density of small boxes and market boxes
$\hat{I}_M$	Estimated index of recent natural mortality
$D_{y,s}$	Density of oysters (small and market)
L	Negative log-likelihood component
-LL	Total negative log-likelihood objective function
	Data
C	Harvest of oysters by stage (small and market) oysters, some small oysters
S	Rate of survival for planted spat (0.15)
I_N	Index of relative density for spat, small, and market oysters
I_B	Index of relative density for small boxes and market boxes
I_M	Index of recent natural mortality

Table 11 Continued

F_y	Fishing mortality rate from depletion analysis
M_{sp}	Natural mortality of spat
N_a, y	Added spat on shell
S_a	Survival of added spat on shell (0.15 in base model)
W_y	Wild seed (small oysters transplanted from one area to another)
$H_{a,y}$	Added habitat
	Penalty Function Inputs
$\bar{b}$	Mean of the penalty for box disarticulation rates
α, β	Parameters of the beta distribution penalty for growth
$\bar{d}$	Mean of penalty for habitat decay parameter
$\bar{q}_d$	Mean of penalty for difference in catchability
$\bar{q}_{sm,mk}$	Mean of penalty for small-market dredge survey catchability
$Y_{0,p}$	Penalty for deviations from a stable age distribution in 1999
σ_X	Log-scale standard deviation for spat, small, market, small box, market box likelihood
σ_b	Log-scale standard deviation of rate of box disarticulation
σ_d	Log-scale standard deviation of habitat decay
σ_{q_d}	Log-scale standard deviation of difference in dredge catchability
$\sigma_{q_{sm,mk}}$	Log-scale standard deviation of the log catchability

Table 12. Estimates of the probability of transition from the small to market stage (G), rate of disarticulation for small (b_{sm}) and market (b_{mk}) boxes, spat catchability (q_{sp}), live small and market catchability ($q_{sm,mk}$), small and market box catchability (q_B), and rate of habitat decay (d_n).

NOAA Code	G	b_{sm}	b_{mk}	q_{sp}	$q_{sm,mk}$	q_B	d
5	0.67 (0.31)	0.75 (0.59)	0.43 (0.76)	20.03 (0.51)	7.19 (0.46)	3.14 (0.53)	0.03 (0.45)
25	0.69 (0.32)	2.58 (0.52)	1.57 (0.44)	22.7 (0.57)	32.5 (0.46)	4.2 (0.46)	0.03 (0.46)
27	0.64 (0.31)	1.54 (0.5)	0.83 (0.42)	31.8 (0.55)	87.38 (0.42)	34.87 (0.46)	0.02 (0.44)
39	0.61 (0.26)	2.1 (0.46)	0.95 (0.33)	2.3 (0.4)	8.14 (0.29)	5.63 (0.36)	0.01 (0.41)
43	0.49 (0.3)	1.16 (0.45)	1 (0.38)	3.59 (0.57)	5.14 (0.57)	2.67 (0.61)	0.04 (0.5)
47	0.38 (0.35)	1.32 (0.43)	0.89 (0.4)	6.42 (0.63)	8.52 (0.62)	3.05 (0.66)	0.04 (0.52)
53	0.4 (0.26)	2.42 (0.29)	1.4 (0.25)	1.36 (0.36)	5.64 (0.3)	4.01 (0.34)	0.03 (0.42)
57	0.33 (0.33)	1.56 (0.43)	1.13 (0.4)	9.53 (0.36)	10.02 (0.3)	3.9 (0.39)	0.05 (0.38)
60	0.61 (0.28)	1.35 (0.43)	0.99 (0.37)	3.06 (0.5)	11.67 (0.45)	7.84 (0.51)	0.02 (0.45)
62	0.54 (0.25)	1.83 (0.48)	0.66 (0.36)	1.64 (0.41)	3.26 (0.32)	1.27 (0.39)	0.02 (0.41)
72	0.39 (0.33)	2.03 (0.46)	2.09 (0.47)	4.13 (0.6)	6.1 (0.59)	2.45 (0.63)	0.04 (0.5)
78	0.37 (0.32)	1.5 (0.43)	0.85 (0.49)	1.81 (0.43)	3.5 (0.34)	1.27 (0.42)	0.03 (0.39)
82	0.67 (0.31)	0.95 (0.5)	1.65 (0.53)	6.42 (0.6)	7.86 (0.41)	3.3 (0.46)	0.02 (0.43)
86	0.65 (0.31)	1.21 (0.48)	0.79 (0.49)	1.83 (0.49)	4.99 (0.43)	2.65 (0.49)	0.02 (0.44)
88	0.62 (0.32)	1.99 (0.51)	0.97 (0.42)	4.34 (0.56)	5.97 (0.38)	1.44 (0.41)	0.02 (0.43)
96	0.74 (0.28)	1.27 (0.5)	0.82 (0.42)	1.93 (0.54)	3.77 (0.39)	1.95 (0.46)	0.02 (0.43)
99	0.75 (0.23)	1.27 (0.49)	0.83 (0.41)	3.92 (0.49)	12.51 (0.38)	6.14 (0.45)	0.03 (0.47)
127	0.57 (0.3)	2.12 (0.48)	1.52 (0.49)	2.32 (0.56)	8.13 (0.46)	2.29 (0.46)	0.02 (0.45)
129	0.45 (0.45)	0.49 (0.44)	0.54 (0.54)	11.26 (0.55)	15.12 (0.48)	6.54 (0.55)	0.06 (0.39)

131	0.7 (0.3)	1.73 (0.47)	0.95 (0.49)	8.45 (0.57)	10.49 (0.39)	3.3 (0.44)	0.02 (0.44)
137	0.48 (0.29)	1.92 (0.39)	1.11 (0.33)	11.27 (0.54)	33.83 (0.54)	17.7 (0.6)	0.03 (0.49)
168	0.42 (0.28)	0.98 (0.39)	0.89 (0.34)	1.69 (0.43)	4.82 (0.36)	2.5 (0.41)	0.02 (0.43)
174	0.69 (0.31)	0.74 (0.5)	1.02 (0.48)	43.03 (0.84)	79.13 (0.81)	48.97 (0.83)	0.04 (0.5)
192	0.39 (0.3)	1.48 (0.39)	0.85 (0.38)	19.97 (0.45)	15.7 (0.42)	6.15 (0.47)	0.04 (0.42)
229	0.52 (0.31)	0.99 (0.47)	0.83 (0.43)	7.57 (0.59)	24.11 (0.57)	9.62 (0.59)	0.04 (0.48)
231	0.78 (0.25)	1.85 (0.45)	0.99 (0.38)	6.63 (0.56)	8.55 (0.37)	2.18 (0.43)	0.02 (0.44)
237	0.75 (0.25)	1.51 (0.47)	0.69 (0.36)	4.28 (0.45)	12.54 (0.37)	5.04 (0.41)	0.02 (0.42)
268	0.59 (0.34)	1.21 (0.52)	1 (0.53)	6.18 (0.54)	26.72 (0.51)	15.88 (0.57)	0.03 (0.45)
274	0.57 (0.33)	1.92 (0.54)	1.31 (0.47)	2.74 (0.56)	8.57 (0.41)	2.79 (0.46)	0.03 (0.43)
292	0.49 (0.32)	1.28 (0.46)	0.84 (0.38)	2.17 (0.59)	4.03 (0.56)	1.99 (0.6)	0.04 (0.52)
331	0.63 (0.35)	0.52 (0.78)	1.26 (0.59)	8.06 (0.83)	9.29 (0.77)	3.94 (0.78)	0.04 (0.51)
337	0.52 (0.35)	2.41 (0.51)	1.15 (0.43)	1.07 (0.46)	4.35 (0.3)	1.22 (0.38)	0.01 (0.41)
368	0.55 (0.31)	1.44 (0.47)	0.86 (0.42)	8.76 (0.56)	24.22 (0.45)	10.76 (0.49)	0.03 (0.44)
437	0.56 (0.29)	1.87 (0.39)	0.99 (0.36)	0.88 (0.44)	2.87 (0.38)	0.58 (0.42)	0.05 (0.36)
537	0.28 (0.3)	1.87 (0.41)	1.2 (0.35)	1.31 (0.52)	2.48 (0.49)	0.82 (0.53)	0.04 (0.48)
637	0.67 (0.27)	2 (0.46)	0.87 (0.34)	0.97 (0.39)	7.2 (0.34)	3.94 (0.4)	0.02 (0.42)

Table 13. Estimated parameters of the reference point model (H_0 – initial habitat, N_0 – initial abundance, q – per capita rate of habitat production, r – intrinsic rate of increase), σ – process error standard deviation, reference points (limit – U_{LIM}, target – U_{TAR}) and their uncertainty (coefficients of variation in parentheses).

NOAA Code	H_0	N_0	q	r	σ	u_{LIM}	u_{TAR}

Tangier Sound							
5	37,153 (0.32)	410 (0.36)	3.97 (0.43)	0.13 (0.53)	0.20 (0.18)	0.12 (0.50)	0.06 (0.50)
43	86,050 (0.71)	3,675 (0.64)	0.86 (1.39)	0.55 (0.40)	0.51 (0.10)	0.45 (0.45)	0.22 (0.45)
47	161,450 (0.50)	2,850 (0.42)	1.81 (0.76)	0.35 (0.35)	0.33 (0.13)	0.32 (0.35)	0.16 (0.35)
57	43,377 (0.40)	1,154 (0.34)	1.13 (0.69)	0.16 (0.55)	0.26 (0.16)	0.14 (0.53)	0.07 (0.53)
62	48,655 (0.61)	12,161 (0.26)	1.41 (0.48)	0.00	0.26 (0.13)	0.00 (71.58)	0.00 (71.58)
72	80,841 (0.51)	5,076 (0.41)	1.22 (0.71)	0.22 (0.51)	0.32 (0.12)	0.19 (0.49)	0.09 (0.49)
96	11,787 (0.43)	1,529 (0.36)	0.71 (0.70)	0.02	0.28 (0.13)	0.02 (4.07)	0.01 (4.07)
192	479,841 (0.38)	6,791 (0.28)	3.31 (0.52)	0.28 (0.31)	0.24 (0.16)	0.26 (0.30)	0.13 (0.30)
292	121,279 (0.52)	8,144 (0.41)	0.78 (0.75)	0.35 (0.39)	0.34 (0.13)	0.28 (0.41)	0.14 (0.41)
Choptank River							
53	164,338 (0.93)	43,836 (0.45)	0.98 (1.03)	0.04 (726.83)	0.49 (0.10)	0.03 (3.63)	0.02 (3.63)
137	283,610 (0.67)	9,371 (0.42)	3.97 (1.19)	0.15 (0.96)	0.40 (0.11)	0.14 (0.81)	0.07 (0.81)
237	193,299 (0.46)	16,530 (0.29)	2.32 (0.48)	0.00	0.25 (0.14)	0.00 (36.75)	0.00 (36.75)
337	102,460	28,191 (0.26)	3.97 (0.50)	0.00	0.23 (0.13)	0.00 (24.12)	0.00 (24.12)
437	50,326 (0.74)	32,099 (0.41)	0.25 (1.38)	0.05 (123.08)	0.40 (0.11)	0.02 (3.50)	0.01 (3.50)
537	48,925 (0.58)	26,640 (0.34)	0.31 (0.59)	0.33 (0.47)	0.28 (0.13)	0.16 (0.73)	0.08 (0.73)
637	64,012 (0.46)	11,068 (0.23)	1.51 (0.40)	0.00	0.21 (0.14)	0.00 (92.62)	0.00 (92.62)
Eastern Bay							
39	138,741 (1.38)	73,151 (0.21)	1.94 (0.43)	0.02	0.24 (0.13)	0.02 (3.95)	0.01 (3.95)
60	46,401 (1.61)	21,221 (0.15)	2.54 (0.38)	0.00	0.20 (0.16)	0.00 (52.41)	0.00 (52.41)
99	2	7,234 (0.68)	2.98 (0.47)	0.00	0.23 (0.15)	0.00 (101.37)	0.00 (101.37)
131	65,946 (0.91)	22,483 (0.22)	1.87 (0.44)	0.00	0.25 (0.13)	0.00 (23.43)	0.00 (23.43)
231	38	72,701 (0.75)	2.77 (0.56)	0.00	0.30 (0.12)	0.00 (24.67)	0.00 (24.67)
331	51,190 (0.80)	4,217 (0.34)	3.97 (1.12)	0.00	0.23 (0.15)	0.00 (25.35)	0.00 (25.35)

Table 13 Continued.

NOAA Code	H_0	N_0	q	r	σ	u_{LIM}	u_{TAR}
Chesapeake Bay Mainstem							
25	1,268,685 (0.47)	21,797 (0.39)	3.97	0.00	0.34 (0.11)	0.00 (25.30)	0.00 (25.30)
27	777,193 (0.36)	4,960 (0.20)	3.97	0.10 (0.87)	0.26 (0.14)	0.10 (0.75)	0.05 (0.75)

127	210,951 (0.71)	54,600 (0.35)	1.42 (0.52)	0.00	0.29 (0.12)	0.00 (27.60)	0.00 (27.60)
129	89,906 (0.44)	2,720 (0.31)	1.09 (0.71)	0.27 (0.40)	0.28 (0.16)	0.23 (0.40)	0.12 (0.40)
229	253,439 (0.41)	3,027 (0.33)	3.89 (0.53)	0.06 (1.74)	0.25 (0.14)	0.06 (1.18)	0.03 (1.18)
Patuxent River and Potomac River							
168	67,487 (0.39)	2,907 (0.35)	0.92 (0.54)	0.10 (1.27)	0.28 (0.12)	0.08 (0.99)	0.04 (0.99)
268	53,043 (0.49)	2,515 (0.40)	3.37 (0.61)	0.03 (42.07)	0.27 (0.16)	0.03 (2.74)	0.01 (2.74)
368	192,661 (0.41)	5,008 (0.29)	3.97 (1.11)	0.00	0.23 (0.15)	0.00 (25.56)	0.00 (25.56)
78	30,647 (0.48)	3,114 (0.30)	0.67 (0.82)	0.35 (0.39)	0.33 (0.15)	0.26 (0.43)	0.13 (0.43)
86	4,549 (0.33)	381 (0.19)	0.82 (0.43)	0.16 (0.46)	0.20 (0.17)	0.13 (0.45)	0.07 (0.45)
174	59,809 (0.38)	203 (0.41)	3.97	0.01	0.25 (0.16)	0.01 (8.42)	0.00 (8.42)
274	107,760 (0.67)	15,138 (0.31)	2.27 (0.53)	0.00	0.30 (0.12)	0.00 (32.10)	0.00 (32.10)
Western Shore							
82	21,950 (3.58)	22,511 (0.36)	1.16 (0.63)	0.00	0.29 (0.13)	0.00 (25.83)	0.00 (25.83)
88	9,802 (0.65)	4,801 (0.34)	0.73 (0.49)	0.00	0.29 (0.13)	0.00 (31.35)	0.00 (31.35)

Table 14. Oysters by ploidy (and total) planted on leases in bushels and number of individuals during 2012 – 2016. Percent (%) Triploid is the percentage of oysters planted that were triploid.

Year	Ploidy	Bushels	Number (millions)	Total diploid and triploid (millions)	% Triploid

2012	Diploid	6,356	196.0	-	-
2012	Triploid	360	35.7	231.7	15.41
2013	Diploid	17,622	171.5	-	-
2013	Triploid	365	24.4	196.0	12.47
2014	Diploid	800	206.6	-	-
2014	Triploid	-	47.1	253.8	18.57
2015	Diploid	1,157	205.9	-	-
2015	Triploid	-	51.9	257.8	20.15
2016	Diploid	118	198.7	-	-
2016	Triploid	-	102.5	301.3	34.04

Table 15. Number of market-sized oysters (millions) estimated as wild-produced (Wild Production) and from public plantings (Public Plantings) from the stock assessment model (leases not included), compared with the number of oysters (millions) harvested from leases (Harvest from Leases). Market abundance from

wild production and public plantings was estimated under two scenarios of survival of hatchery-reared spat during their first two months after planting: 15% (base model) and 5% (sensitivity analysis).

Year	Wild Production 15%	Public Plantings 15%	Wild Production 5%	Public Plantings 5%	Harvest from Leases
2012	293.2	121.8	279.9	79.7	1.0
2013	288.2	111.2	269.8	65.7	6.7
2014	348.3	117.7	324.7	64.3	10.3
2015	301.3	111.3	285.4	59.7	15.2
2016	196.0	82.1	187.3	42.8	19.4
2017	189.0	81.4	182.6	39.4	22.2

Table 16. NOAA code harvest reporting areas within the Maryland portion of Chesapeake Bay with regional descriptions.

Region	Code	NOAA Name
Tangier Sound	005	Big Annemessex River
	043	Fishing Bay
	047	Honga River
	057	Manokin River
	062	Nanticoke River
	072	Pocomoke Sound
	096	Wicominco River East
	098	Monie Bay
	192	Tangier Sound south of Wenona
	292	Tangier Sound north of Wenona
Choptank River	053	Little Choptank River
	137	Choptank River below Castlehaven
	237	Choptank River shouth of Rt 50 bridge to Castlehaven
	337	Choptank River north of Rt 50 Bridge
	437	Harris Creek
	537	Broad Creek
	637	Tred Avon River
Eastern Bay	039	Eastern Bay
	060	Miles River
	099	Wye River
	131	Chester River below Queenstown Creek
	231	Chester River south of Spaniard Pt to Queenstown Creek
	331	Chester River north of Spaniard Pt
Chesapeake Bay Mainstem	025	Upper Bay - north of bridge and south of Worton Pt.
	027	Lower Bay East - north of Cove Pt. to Area 127
	127	Mid-Bay East/West - south of bridge and north of a line between Fairhaven and Kent Pt.
	129	Lower Bay East - south of Cove Pt. and east of Ship Channel
	229	Lower Bay West - south of Cove Pt. and west of Ship Channel
Patuxent River & Potomac River	168	Patuxent River south of St. Leonard Creek
	268	Patuxent River south of Broomes Island and north of Area 168
	368	Patuxent River north of Broomes Island
	078	St. Mary's River
	086	Smith Creek
	174	Breton and St. Clements Bays
	274	Wicomico River West
Western Shore	055	Magothy River
	082	Severn River
	088	South River
	094	West and Rhode rivers

Table 17. Maryland Chesapeake Bay harvest regions and NOAA codes, NOAA Code harvest rank, gear used for depletion analysis, years of estimates and time-series mean exploitation rate during the 1999-2000 to 2016-2017 seasons.

Region	Region Harvest Rank	Region Total Time-Series Harvest (bushels)	Region % of Cumulative Time Series Harvest	Region Mean Exploitation Rate*	NOAA Codes	NOAA Total Time-Series Harvest (bushels)	Gear Used for Depletion Analysis	Years of Estimates	Mean Exploitation Rate
Tangier Sound	1	1,237,456	37%	0.35	292	335,331	Patent Tong	13	0.23
					192	295,027	Power Dredge	17	0.36
					043	228,355	Power Dredge	9	0.46
					047	147,627	Power Dredge	11	0.40
					072	112,755	Power Dredge	8	0.45
					062	62,157	Power Dredge	9	0.37
					096	23,806	Power Dredge	5	0.50
					057	19,228	Power Dredge	9	0.25
					005	6,586	Power Dredge	1	-
					098	6,584	-		-
Choptank River	2	845,525	25%	0.39	537	479,232	Hand Tong	17	0.34
					137	107,989	Power Dredge	11	0.63
					053	87,563	Hand Tong	5	0.26
					437	84,640	Power Dredge	11	0.66
					237	44,489	Hand Tong	8	0.18
					637	26,281	Hand Tong	4	0.32
					337	15,333	Hand Tong	2	0.35
Eastern Bay	3	643,549	19%	0.33	039	394,418	Diver	15	0.3
					231	94,174	Hand Tong	9	0.35
					060	73,177	Hand Tong	5	0.4
					131	53,574	Diver	4	0.46
					099	22,621	Diver	3	0.22
					331	5,586	Hand Tong	2	0.42
Chesapeake Bay Mainstem	4	320,398	9%	0.37	025	118,713	Patent Tong	9	0.38
					027	81,733	Patent Tong	14	0.31
					129	50,389	Power Dredge	11	0.43
					127	46,665	Patent Tong	6	0.42
					229	22,899	Power Dredge	8	0.28
Patuxent River	5	306,846	9%	0.31	078	67,053	Power Dredge	10	0.42
					168	149,240	Patent Tong	11	0.24
					274	39,306	Hand Tong	10	0.32
					268	27,740	Diver	2	0.46
					368	17,731	Diver	3	0.36
					086	5,062	-	0	-
					174	716	-	0	-
Western Shore	6	16,226	1%	N/A	088	14,506	Hand Tong	8	-
					082	1,292	-	0	-
					055	308	-	0	-
					094	120	-	0	-

Table 18. Top 12 harvest rank NOAA code reporting areas in the Maryland portion of Chesapeake Bay with the total harvest during the 1999-2000 to 2016-2017 seasons and dominant gear time-series harvest.

NOAA	Description	Harvest Rank	% of Total Bay-Wide Time-Series Harvest	Total Time-Series NOAA Harvest (bushels)	Gear Used for Depletion Analysis	Gear-Specific Time-Series NOAA Harvest (bushels)	Gear-Specific Harvest as % of Total NOAA Harvest
537	Broad Creek	1	14	479,232	Hand Tong	341,158	71
039	Eastern Bay	2	26	394,418	Diver	240,291	61
292	Upper Tangier Sound	3	36	335,331	Patent Tong	157,361	47
192	LowerTangier Sound	4	45	295,027	Power Dredge	197,928	67
043	Fishing Bay	5	51	228,355	Power Dredge	202,362	89
168	Lower Patuxent River	6	56	149,240	Patent Tong	136,040	91
047	Honga River	7	60	147,627	Power Dredge	131,033	89
025	Upper Bay Mainstem	8	64	118,713	Patent Tong	102,009	86
072	Pocomoke Sound	9	67	112,755	Power Dredge	86,439	77
137	Lower Choptank River	10	70	107,989	Power Dredge	61,139	57
231	Middle Chester River	11	73	94,174	Hand Tong	65,027	69
053	Little Choptank River	12	76	87,563	Hand Tong	72,562	83

Table 19. Harvest by season, Number of NOAA codes with harvest, Number of Estimates Generated, and Percent of NOAA codes with reported harvest and estimates.

Harvest Season	Total Reported Harvest	Number of NOAAs with harvest	Number of Estimates Generated	% of NOAAs with harvest
1999-2000	345,850	39	7	18
2000-2001	316,630	39	16	53
2001-2002	109,175	39	16	59
2002-2003	47,141	39	10	38
2003-2004	19,028	39	5	25
2004-2005	57,558	39	7	22
2005-2006	130,323	39	14	41
2006-2007	154,236	39	15	44
2007-2008	66,807	39	12	38
2008-2009	87,358	39	12	34
2009-2010	114,236	39	15	43
2010-2011	103,608	39	18	55
2011-2012	101,398	39	14	40
2012-2013	330,064	39	18	51
2013-2014	417,784	39	21	60
2014-2015	375,244	39	21	57
2015-2016	380,163	39	21	60
2016-2017	213,397	39	26	72

Table 20. Total harvest during the 1999-2000 to 2016 -2017 seasons by region and mean exploitation rate for each region.

Region	Region Harvest Rank	Region Total Time-Series Harvest	Region % of Cumulative Time Series	Region Mean Exploitation
Tangier Sound	1	1,253,771	37%	0.35
Choptank River	2	845,525	25%	0.39
Eastern Bay/Chester River	3	643,549	19%	0.33
Chesapeake Bay Mainstem	4	320,398	10%	0.37
Patuxent River	5	306,846	9%	0.31
Western Shore	6	29,439	1%	-

Table 21. Distribution of estimates of exploitation rate of oysters in the Maryland portion of Chesapeake Bay by dominant gear.

Gear used to Develop Estimates	Number of NOAA Codes	Number of Estimates	Percent of NOAA Codes	Median Number of Years of Estimates	Mean Exploitation Rate	Mean Initial Abundance
Power Dredge	13	123	45%	10	0.42	24,651
Hand Tong	10	70	25%	7	0.33	49,042
Patent Tong	5	55	20%	11	0.32	69,166
Diver	5	27	10%	3	0.36	24,651

Table 22. Mean exploitation fraction during the 1999-2000 through 2016-2017 seasons by gear for oysters harvested in the Maryland portion of Chesapeake Bay.

Gear Used to Develop Estimates	Time-Series Mean Exploitation Rate
Power Dredge	0.28
Hand Tong	0.17
Patent Tong	0.16
Diver	0.12

Table 23. Pair-wise comparisons of gear-specific exploitation rates for oysters harvested in the Maryland portion of Chesapeake Bay.

			Gear-Specific Exploitation Rate			
Gear 1	Gear 2	n	Gear 1 mean	Gear 2 mean	mean difference	P
Diver	Hand Tong	60	0.09	0.13	-0.04	0.065
Hand Tong	Patent Tong	30	0.04	0.12	-0.08	0.003
Hand Tong	Power Dredge	45	0.10	0.23	0.14	<0.001
Patent Tong	Power Dredge	50	0.08	0.19	-0.12	<0.001

Table 24. Comparison of the year associated with the minimum value for estimated market abundance from the assessment model (N minimum year) and the minimum index of market oysters from the standardized fall dredge survey time series (Density minimum year) by region and NOAA Code.

NOAA Code	NOAA Name	N minimum year	Density minimum year	Difference in years
Tangier Sound Region				
5	Big Annemessex River	2000	1999	1
43	Fishing Bay	2005	2005	0
47	Honga River	2005	2006	1
57	Manokin River	2007	2006	1
62	Nanticoke River	2003	2003	0
72	Pocomoke Sound	2005	2006	1
96	Wicomico River (East)	2006	2006	0
192	Tangier Sound South	2016	2016	0
292	Tangier Sound North	2006	2006	0
Choptank River Region				
53	Little Choptank River	2002	2002	0
137	Lower Choptank River	2002	2002	0
237	Mid Choptank River	2003	2003	0
337	Upper Choptank River	2004	2005	1
437	Harris Creek	2003	2003	0
537	Broad Creek	2003	2003	0
637	Tred Avon River	2002	2002	0
Eastern Bay Region				
39	Eastern Bay	2009	2011	2
60	Miles River	2009	2011	2
99	Wye River	2011	2011	0
131	Lower Chester River	2017	2009	8
231	Mid Chester River	2017	2011	6
331	Upper Chester River	2017	2010	7
Chesapeake Bay Mainstem Region				
25	Upper Bay	2013	2011	2
27	South Mid-Bay	2002	2004	2
127	North Mid-Bay	2017	2011	6
129	Lower Bay East	2016	2008	8
229	Lower Bay West	2002	2002	0
Patuxent River and Potomac River Region				
168	Lower Patuxent River	2002	2002	0
268	Mid Patuxent River	2002	2003	1
368	Upper Patuxent River	2003	2002	1
78	St. Mary's River	2002	2002	0
86	Smith Creek	2002	2011	9

Table 24 Continued

NOAA Code	NOAA Name	N minimum year	Density minimum year	Difference in years
174	Breton & St. Clements Bays	2007	2004	3
274	Wicomico River (West)	2014	2010	4
Western Shore Region				
82	Severn River	2011	2008	3
88	South River	2007	2011	4

13.0 FIGURES

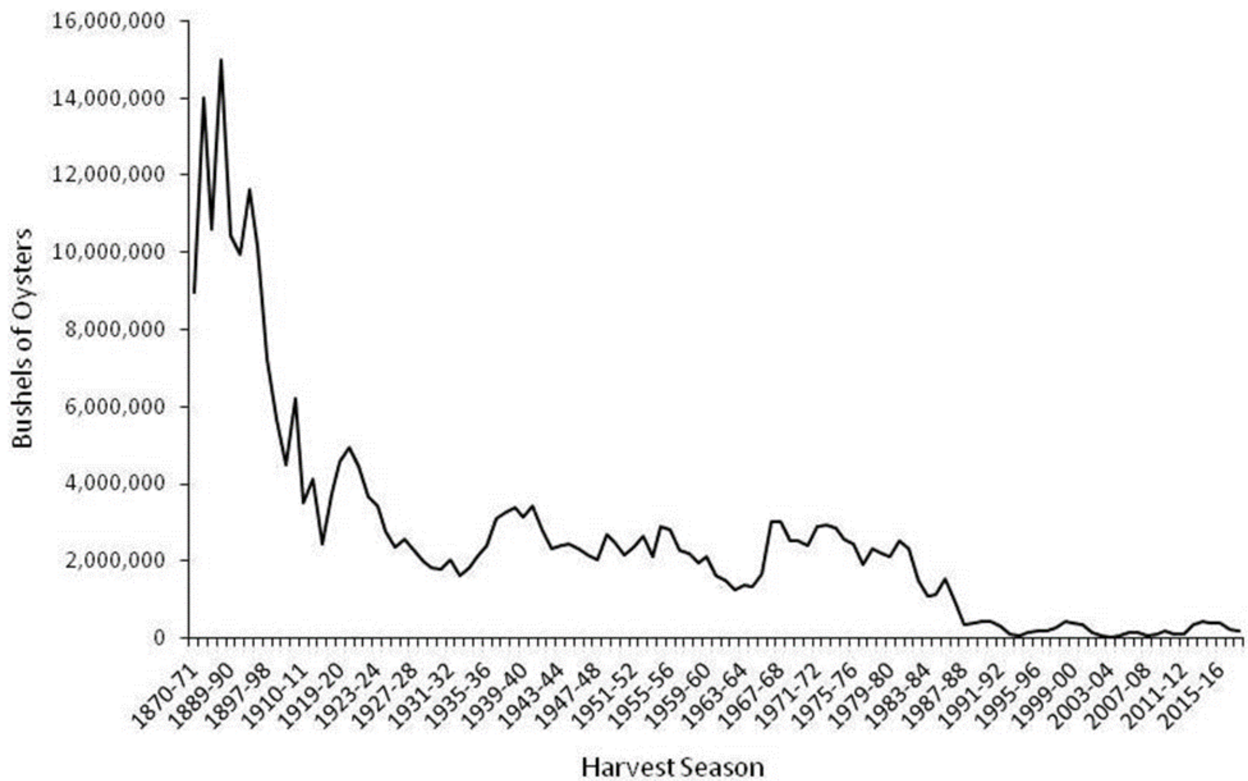

Figure 1. The harvest of oysters (bushels) from the Maryland portion of Chesapeake Bay from the 1870-71 through the 2017-2018 harvest seasons.

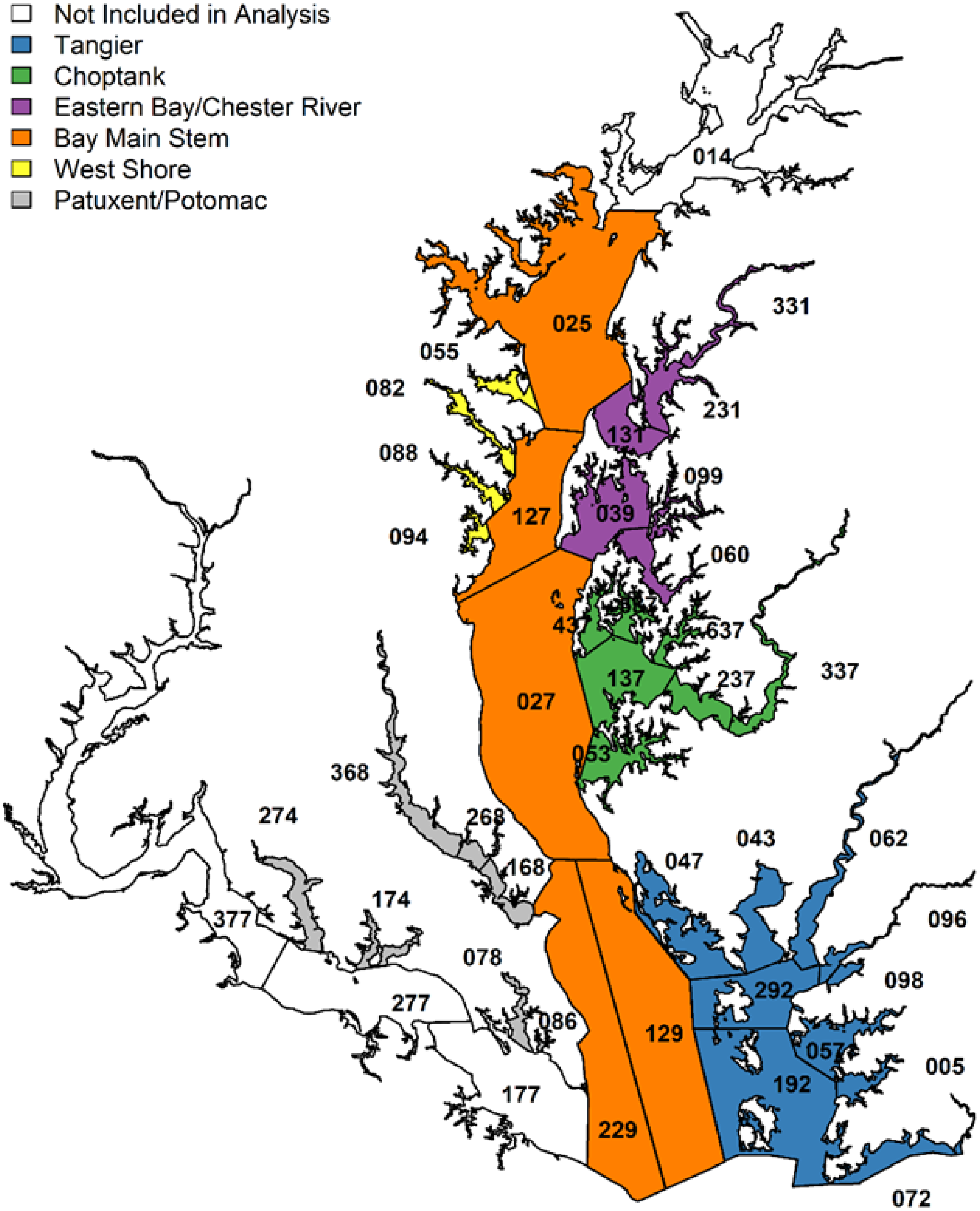

Figure 2. NOAA code harvest reporting areas in the Maryland portion of Chesapeake Bay.

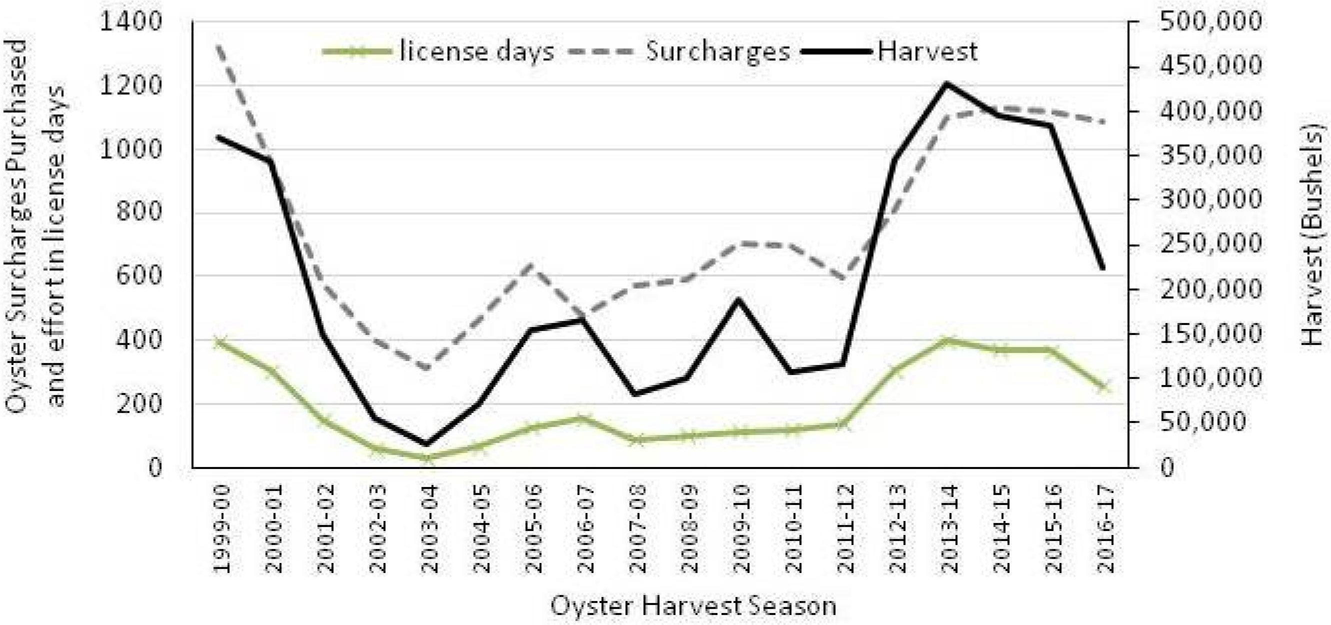

Figure 3. Effort in the oyster fishery as represented by license days, the number of surcharges sold each year and the bushels harvested from the Maryland portion of Chesapeake Bay during the 1999-2000 through 2016-2017 seasons.

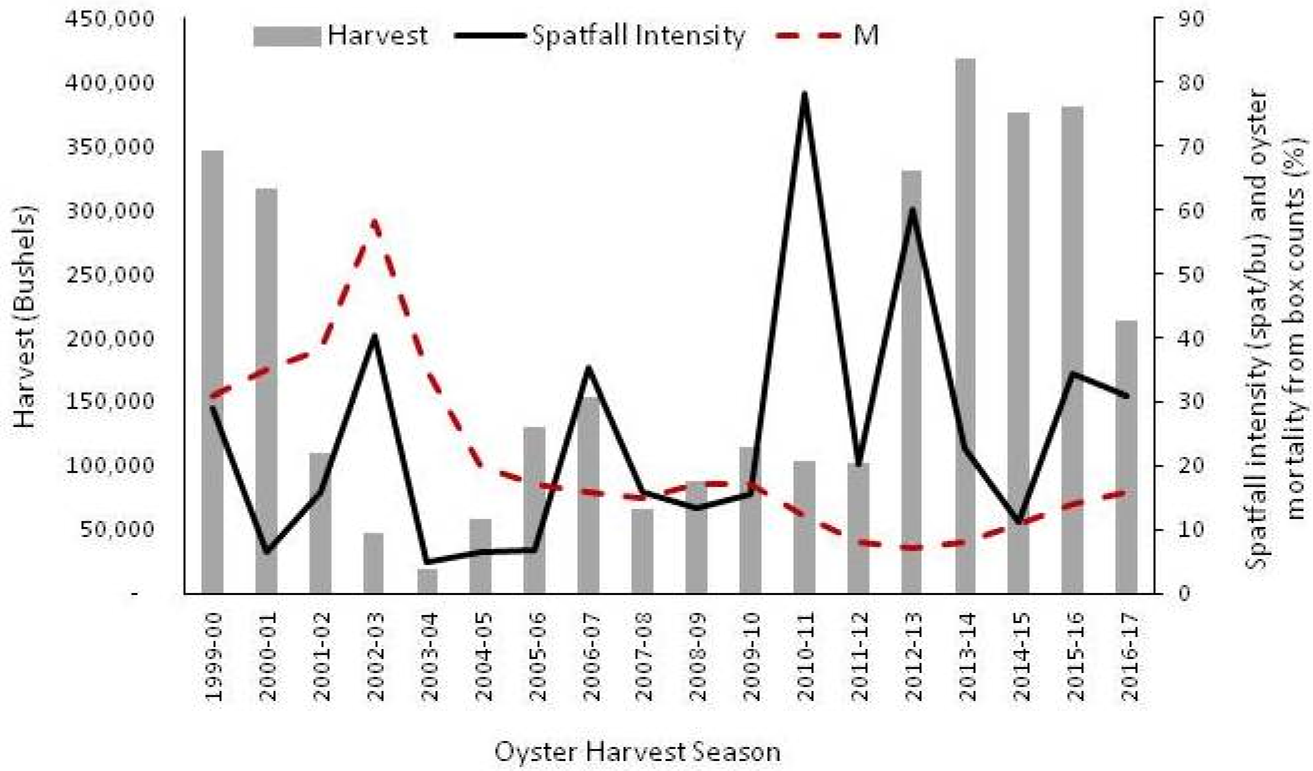

Figure 4. Oyster harvest from the Maryland portion of Chesapeake Bay along with an index of spatfall and mortality from the Maryland Department of Natural Resources fall dredge survey for the 1999-2000 through 2016-2017 seasons.

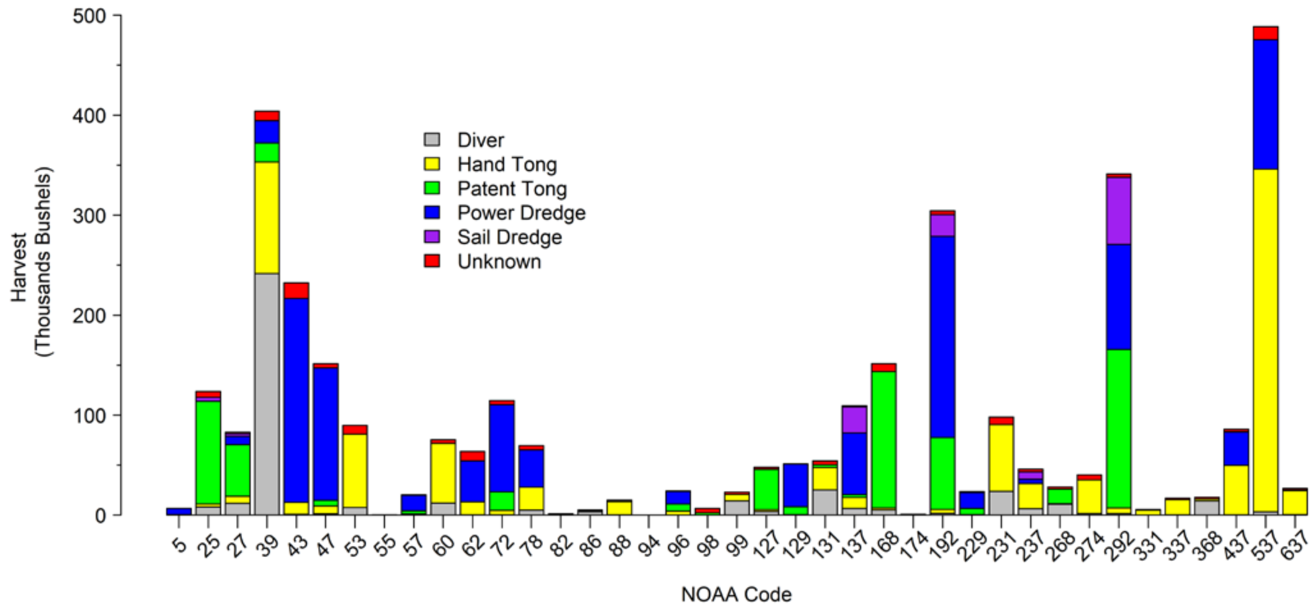

Figure 5. Oyster harvest by gear for each NOAA code reporting area in the Maryland portion of Chesapeake Bay. Harvest is totaled over the 1999-2000 through 2016-2017 seasons.

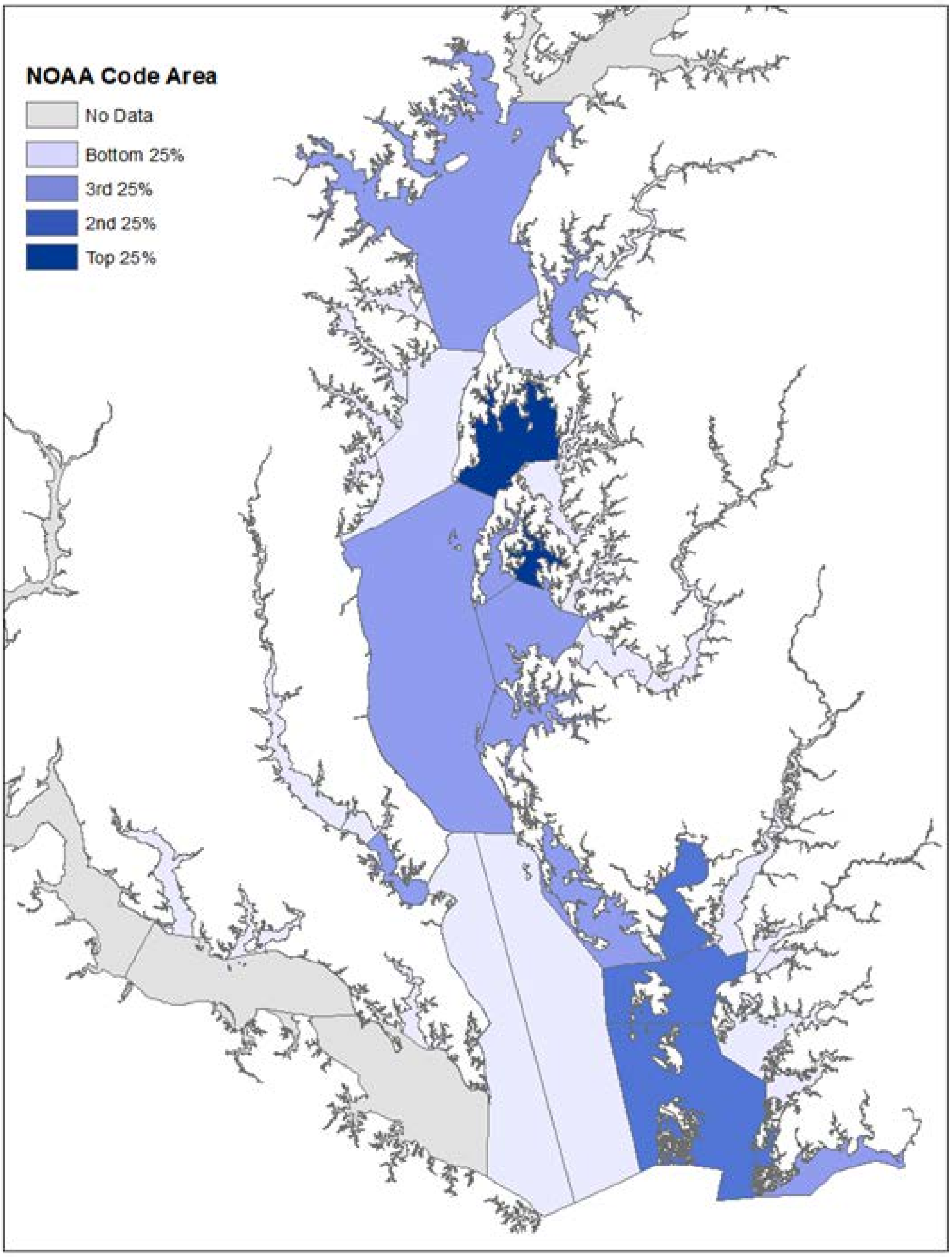

Figure 6. Map of the Maryland portion of Chesapeake Bay showing the spatial distribution of the total oyster harvest over the 1999-2000 through 2016-2017 seasons.

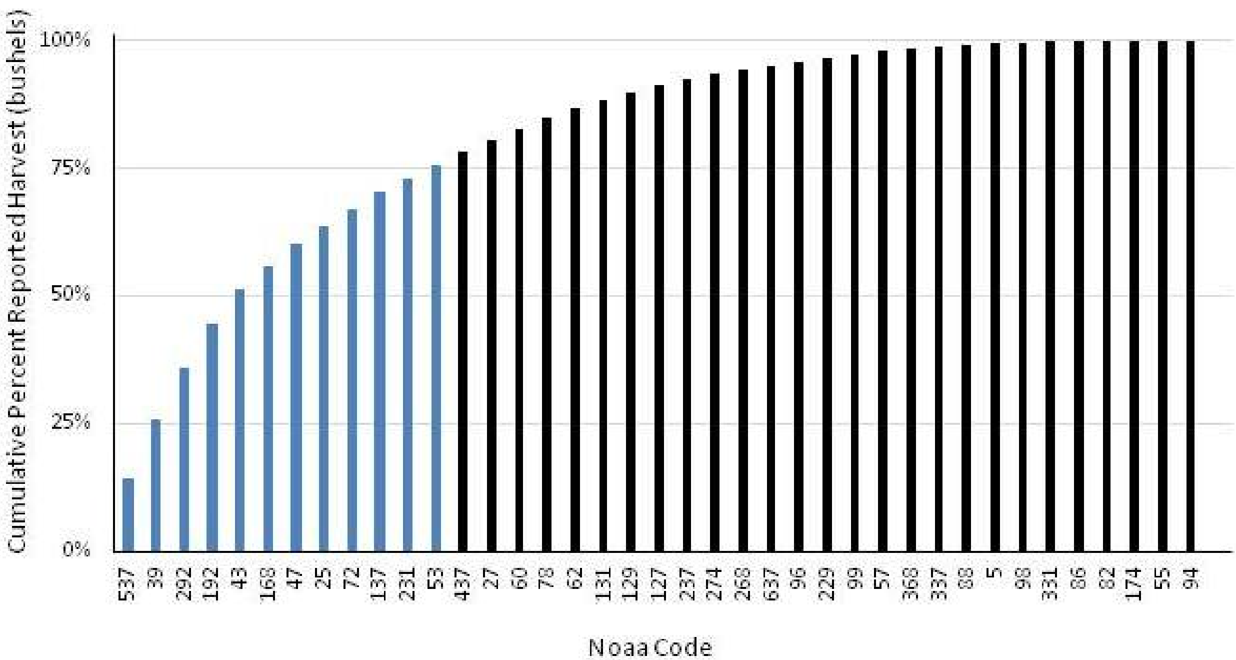

Figure 7. The cumulative distribution of the oyster harvest during the 1999-2000 through 2016-2017 seasons over the NOAA code harvest reporting areas in the Maryland portion of Chesapeake Bay.

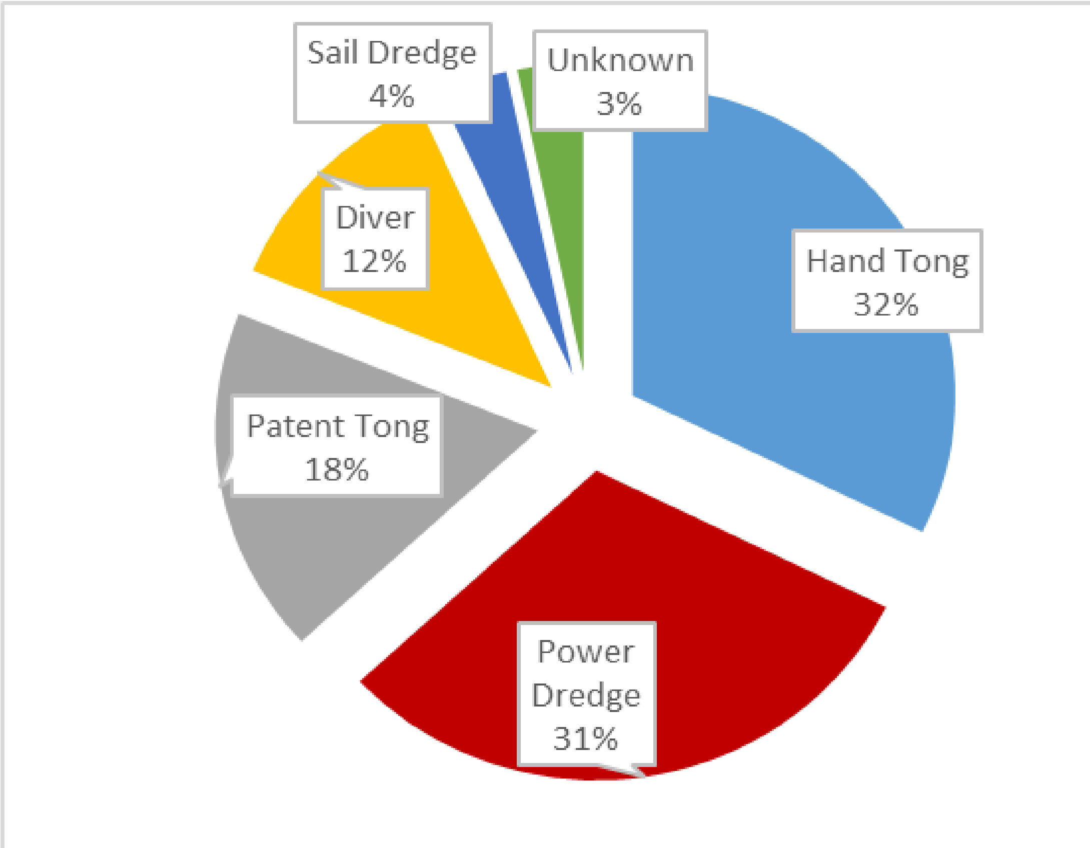

Figure 8. The fraction of oyster harvest by gear type in the Maryland portion of Chesapeake Bay during the 1999-2000 through 2016-2017 seasons.

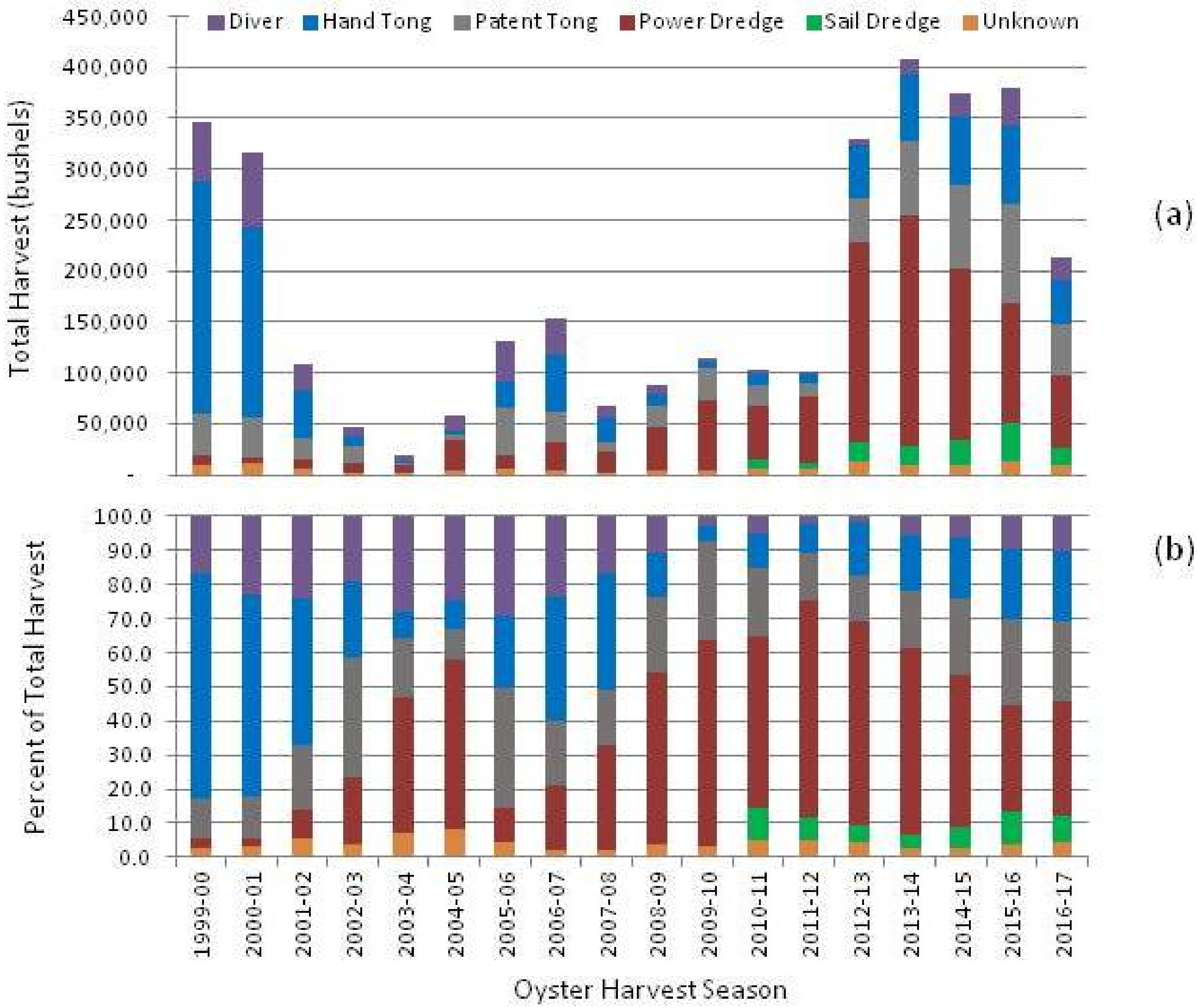

Figure 9. Annual oyster harvest by gear from the Maryland portion of Chesapeake Bay a) in bushels, b) as a percentage of the annual harvest during the 1999-2000 through 2016-2017 seasons.

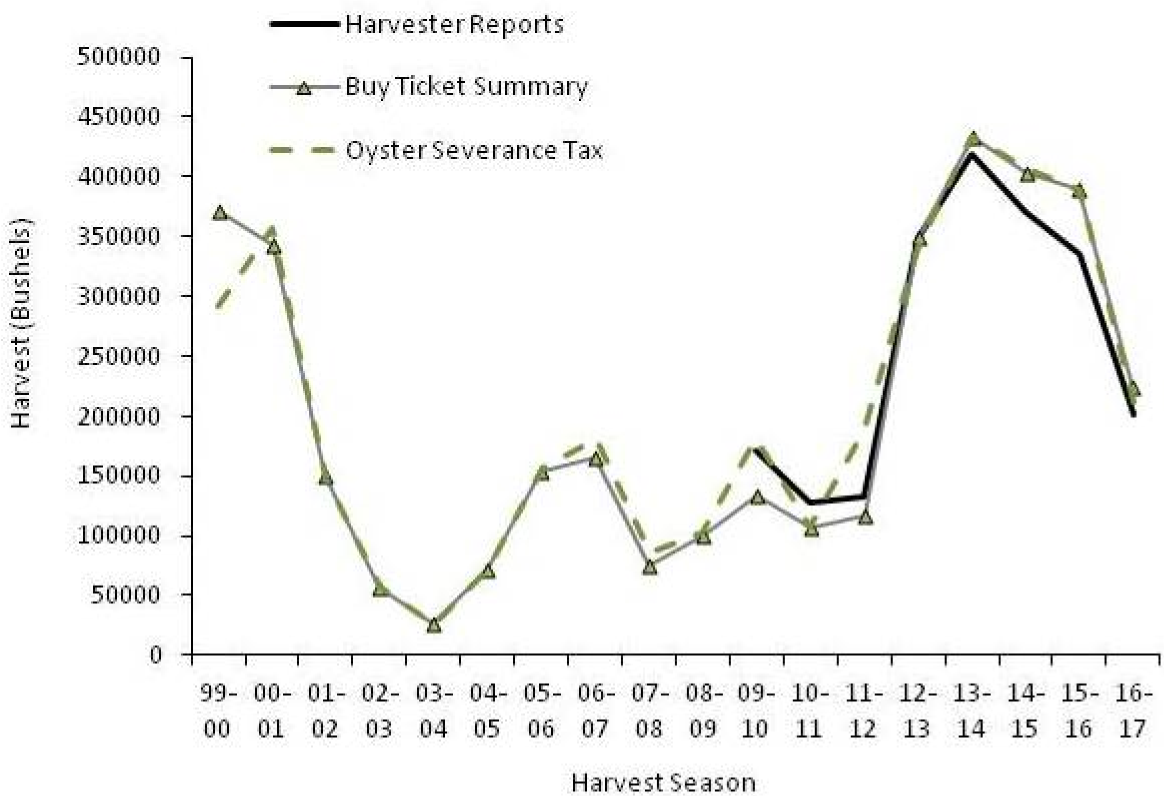

Figure 10. A comparison of three different sources of reported oyster harvest from the Maryland portion of Chesapeake Bay: harvester reports, buy tickets and the oyster severance tax for the 1999-2000 through 2016-2017 seasons.

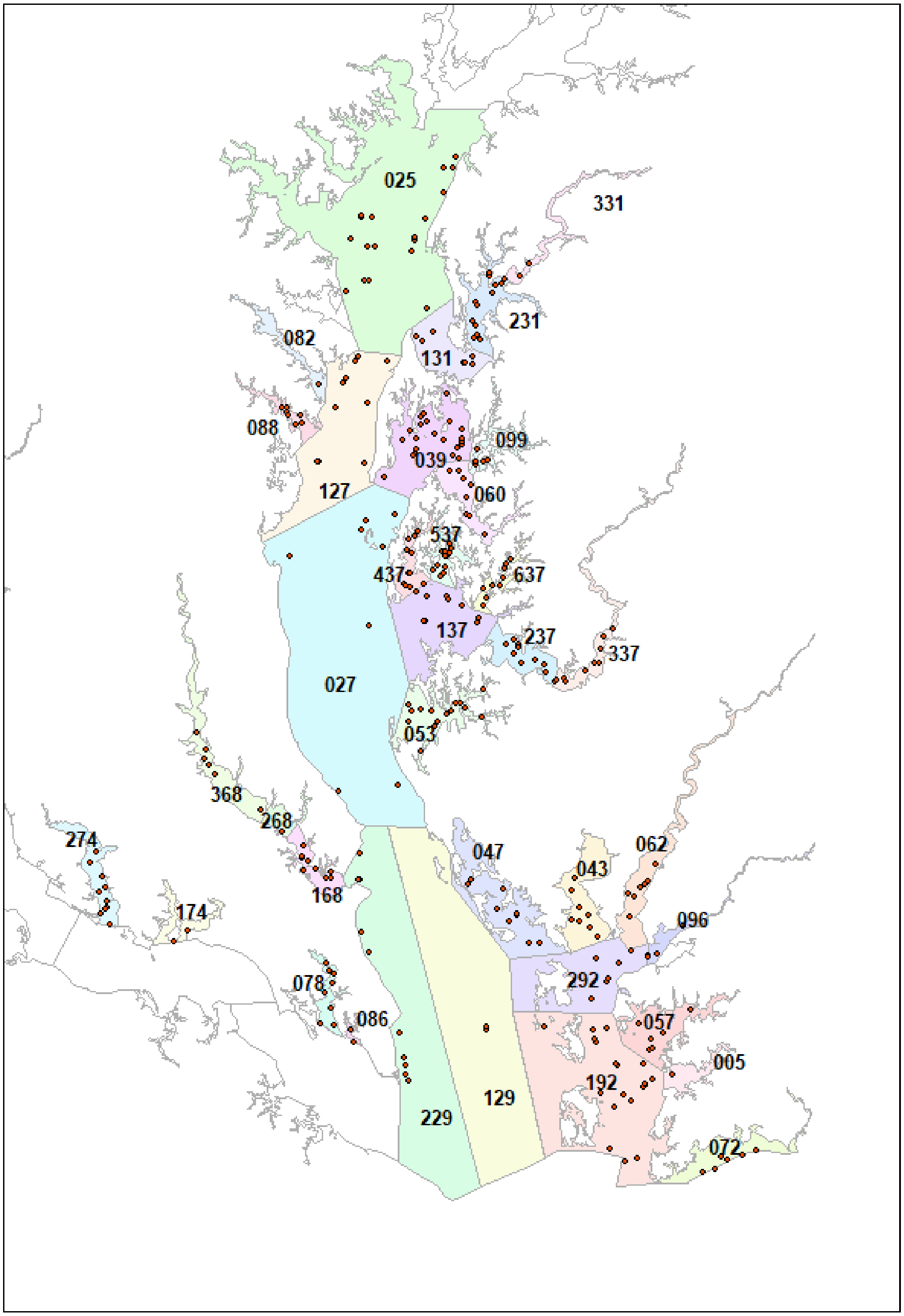

Figure 11. Map of the Maryland portion of Chesapeake Bay showing NOAA codes and sampling sites for the Maryland Department of Natural Resources fall dredge survey.

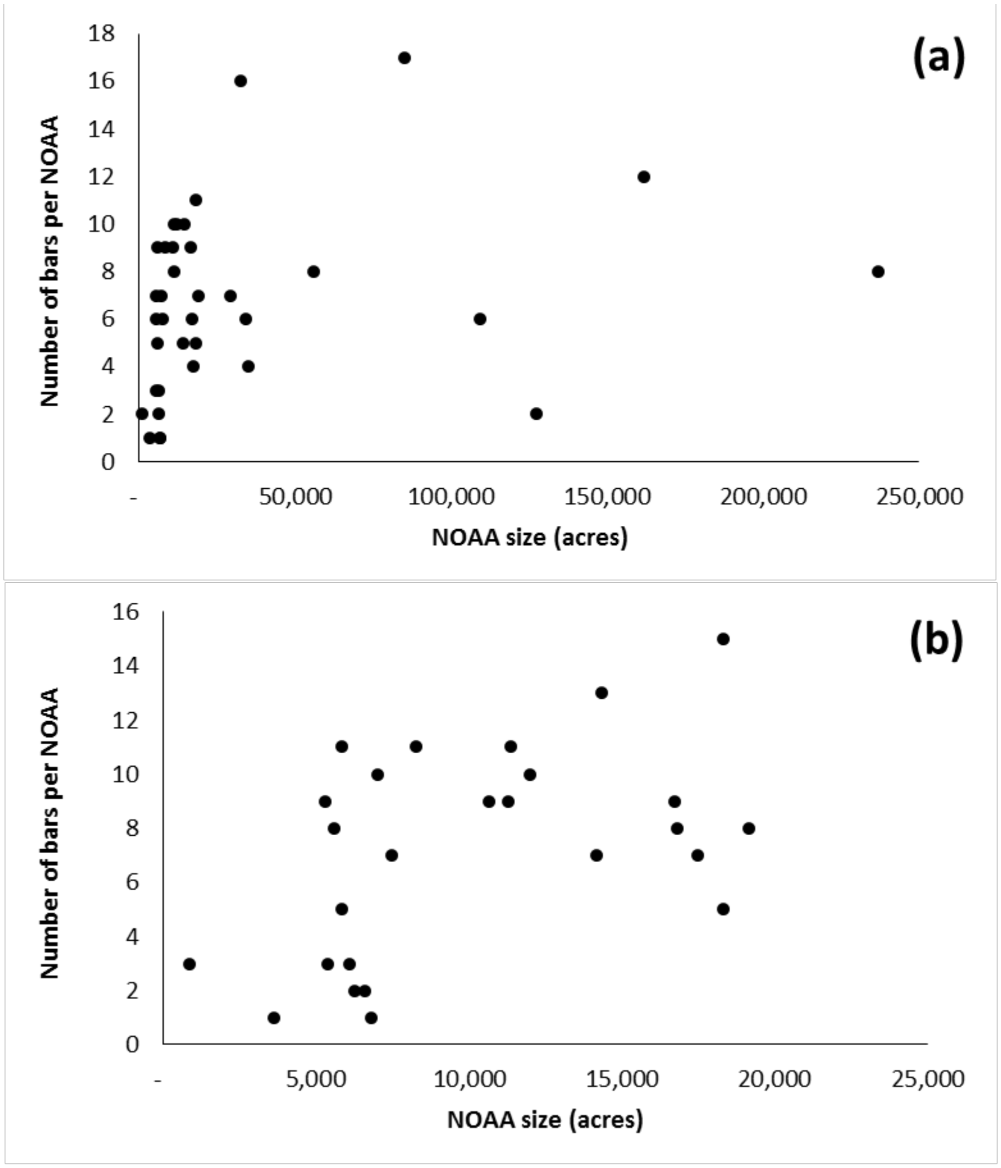

Figure 12. Size of Maryland Chesapeake Bay NOAA code vs. number of bars sampled by the Maryland fall dredge survey for (a) all NOAA codes (b) NOAA codes less than 25,000 acres in size.

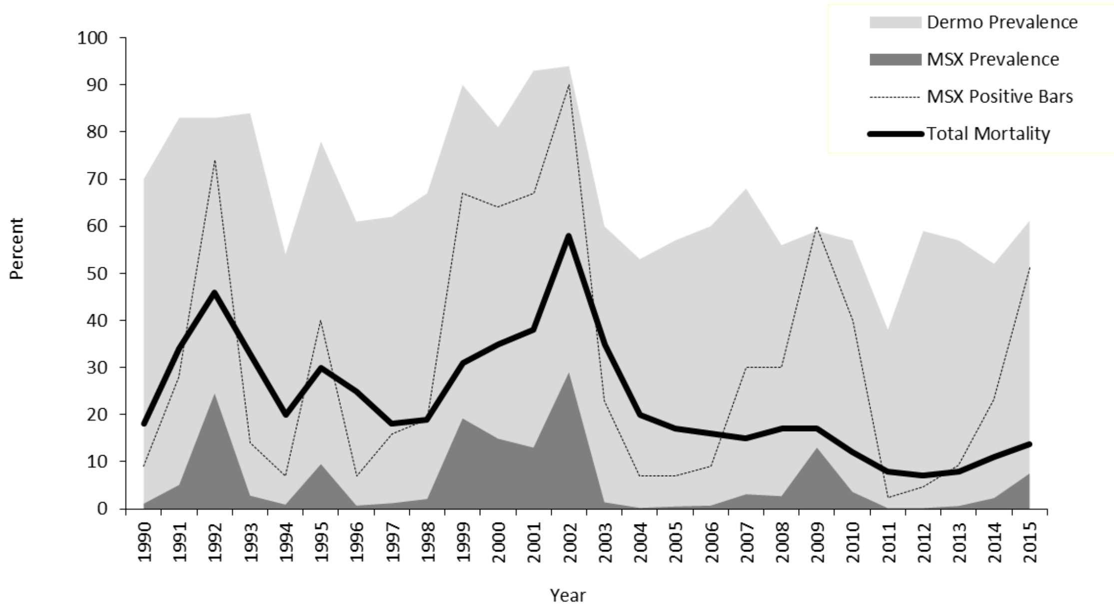

Figure 13. Measures of disease and total mortality, calculated from box count data, on 43 oyster bars sampled for disease by the Maryland fall dredge survey (1990-2015).

Figure 14. Total natural mortality for eastern oyster *Crassostrea virginica* in Maryland Chesapeake Bay (1999-2016) calculated from Maryland fall dredge survey box count data.

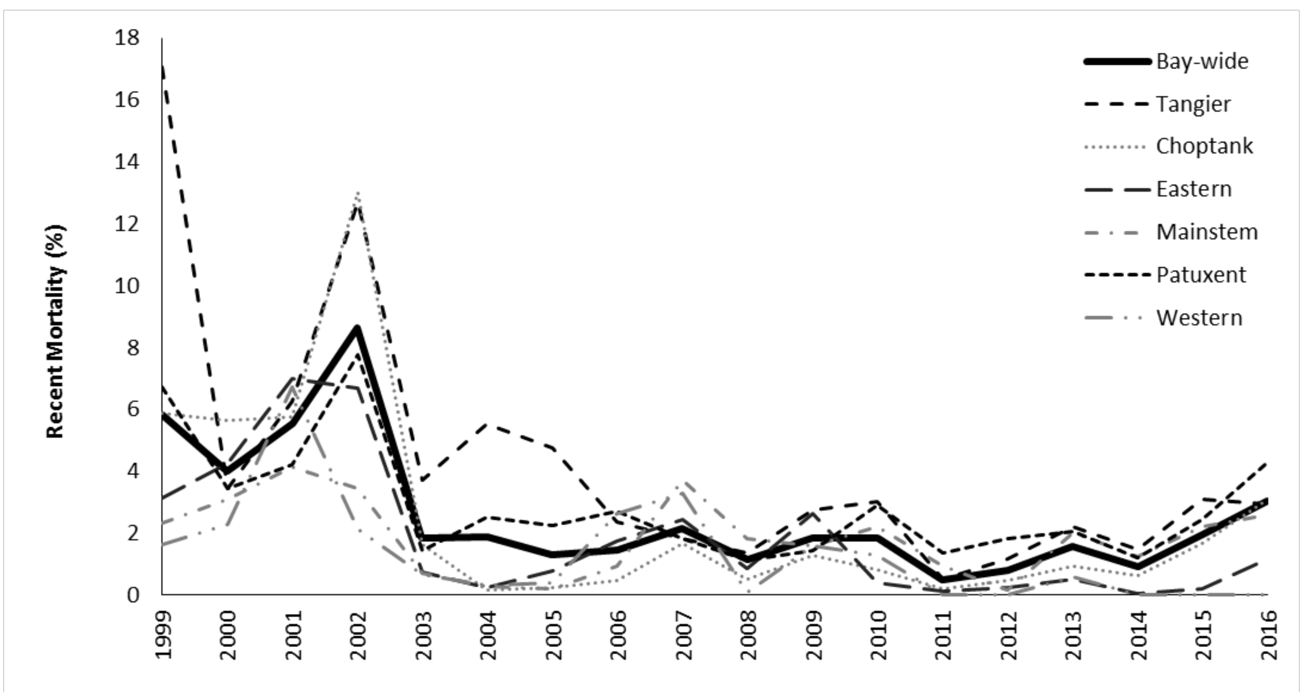

Figure 15. Recent natural mortality for eastern oyster *Crassostrea virginica* in Maryland Chesapeake Bay (1999-2016) calculated from Maryland fall dredge survey box count data.

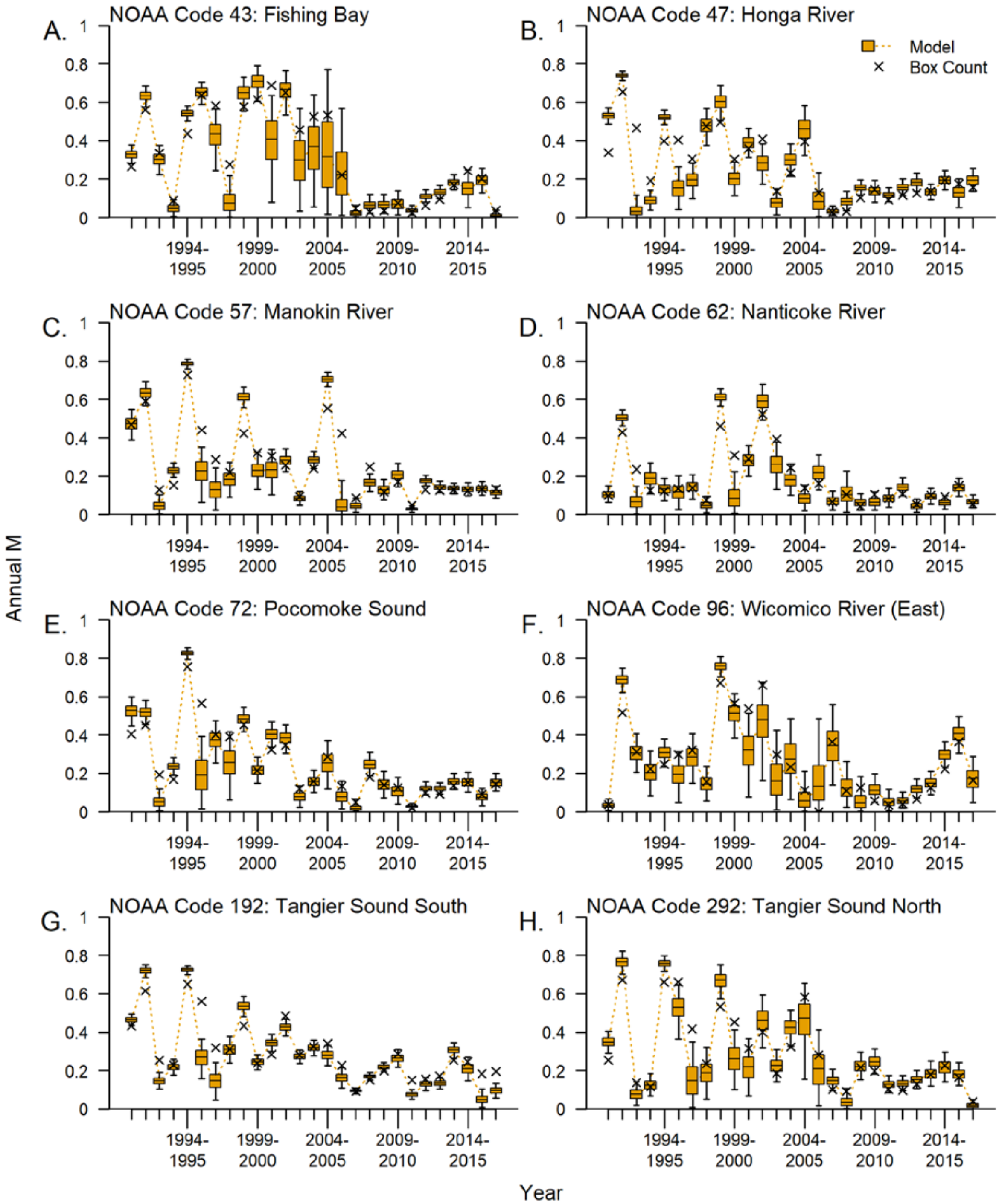

Figure 16. Natural mortality rate estimates (Annual M; fraction per year) for adult oysters from the model (boxplots) and the box count method (points) for individual NOAA codes of the Tangier Sound region. The box represents the interquartile range, the line the median, and the whiskers 95% credibility intervals. The dashed line connects the median values of the boxplots.

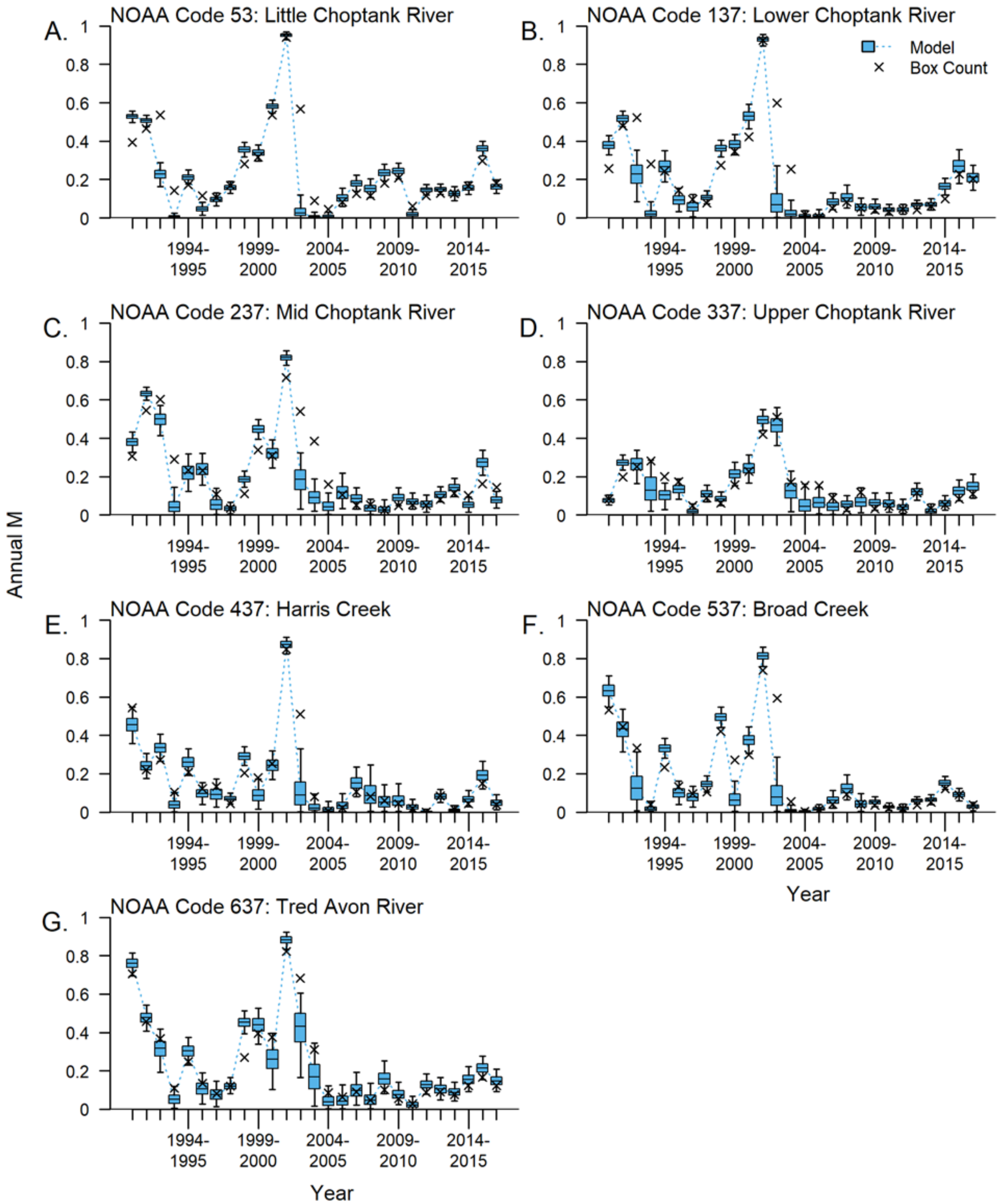

Figure 17. Natural mortality rate estimates for adult oysters from the Choptank River region. Symbol definitions are the same as Figure 16.

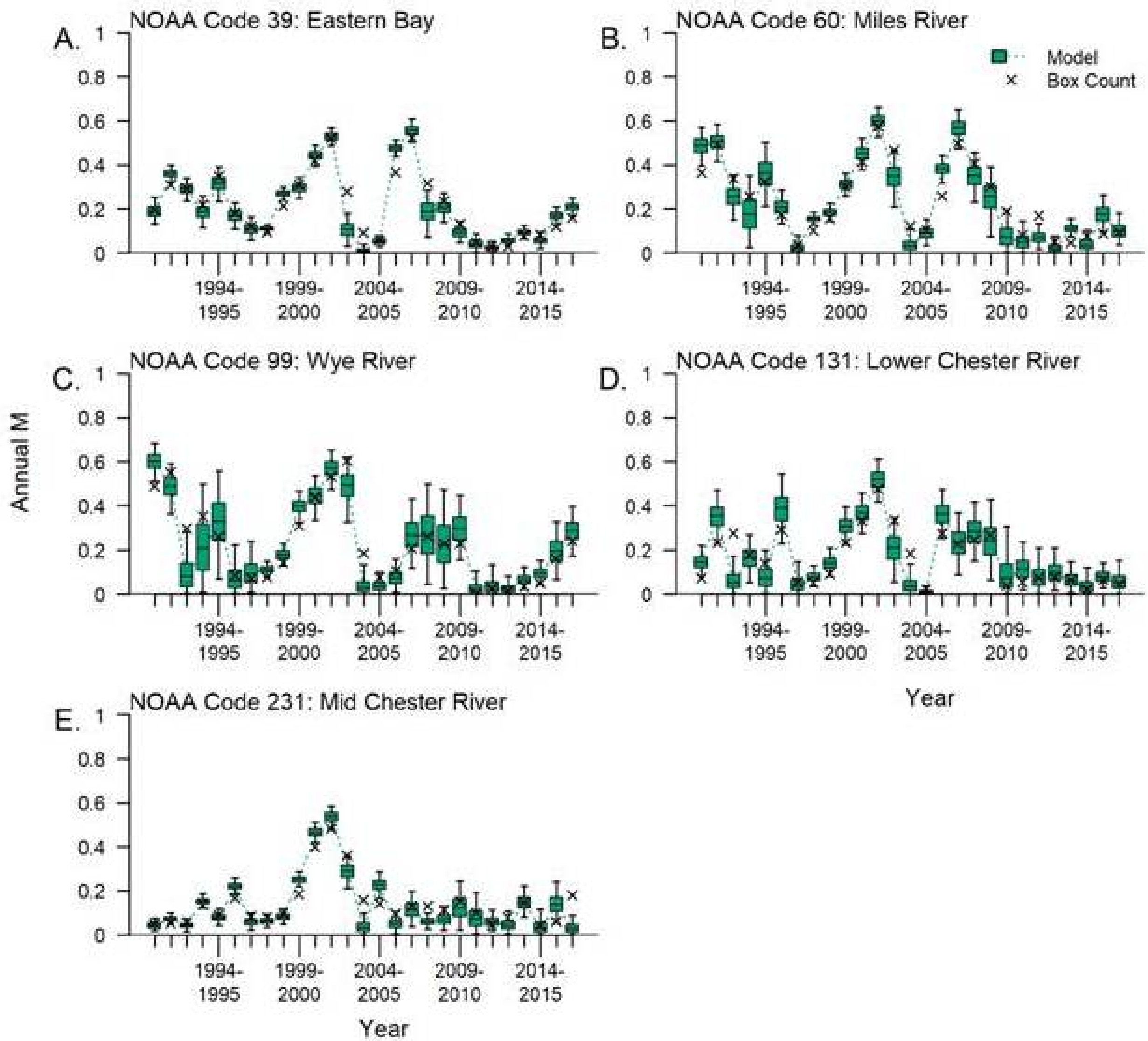

Figure 18. Natural mortality rate estimates for adult oysters from the Eastern Bay region. Symbol definitions are the same as Figure 16.

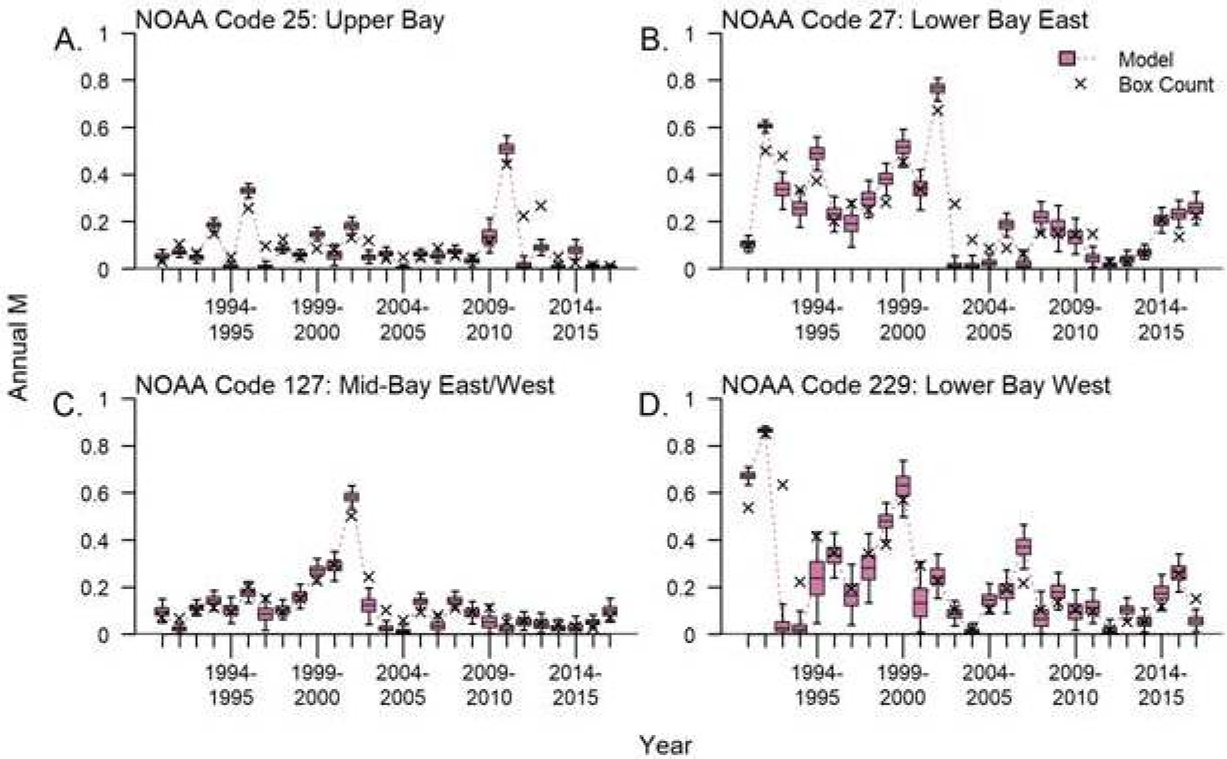

Figure 19. Natural mortality rate estimates for adult oysters from the Chesapeake Bay Mainstem region. Symbol definitions are the same as Figure 16.

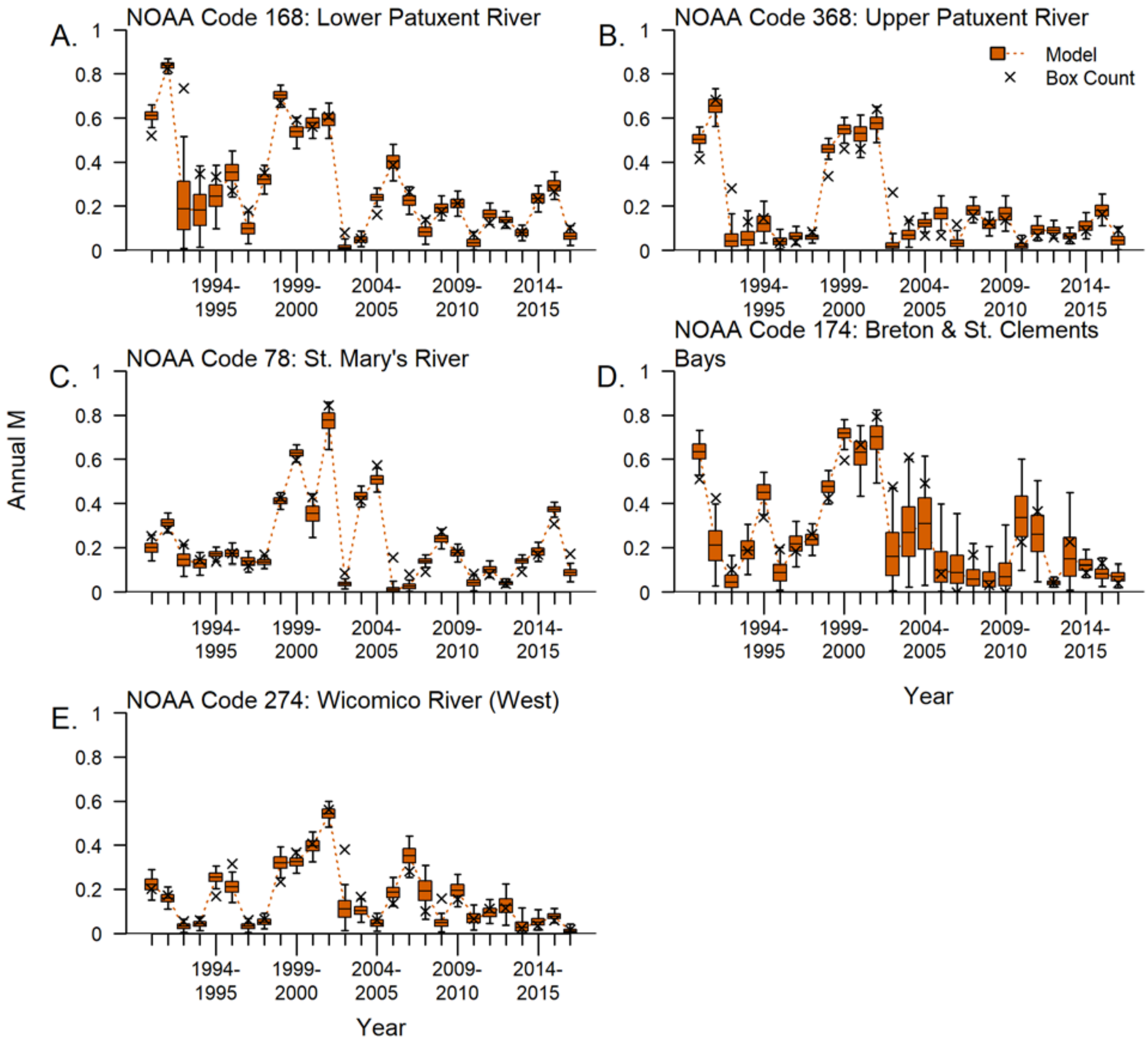

Figure 20. Natural mortality rate estimates for adult oysters from the Patuxent and Potomac Rivers region. Symbol definitions are the same as Figure 16.

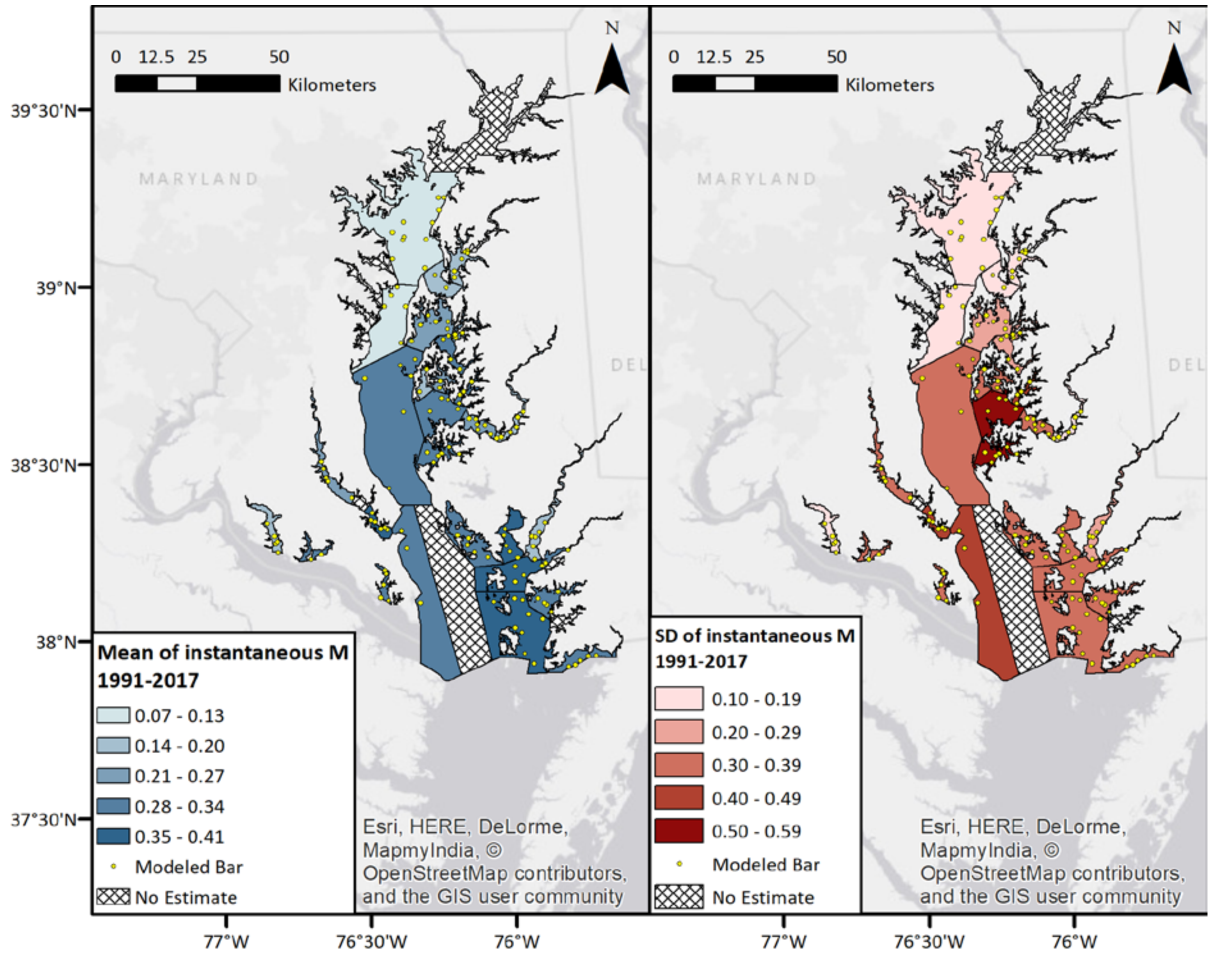

Figure 21. Mean and standard deviations of the median values of instantaneous natural mortality by NOAA code as estimated from the model. Darker colors indicate higher a higher mean or standard deviation over the time series. Yellow points mark the approximate locations of bars that were used in the model. Crosshatching indicates NOAA codes that were not modeled.

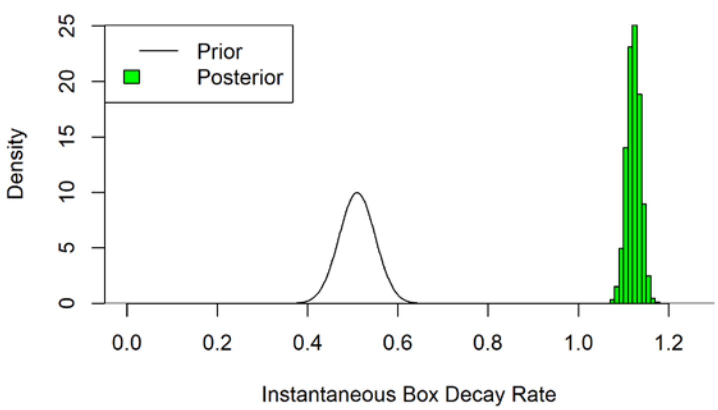

Figure 22. Prior (black line) and posterior (green histogram) distributions for the box decay (i.e., disarticulation) rate from the model.

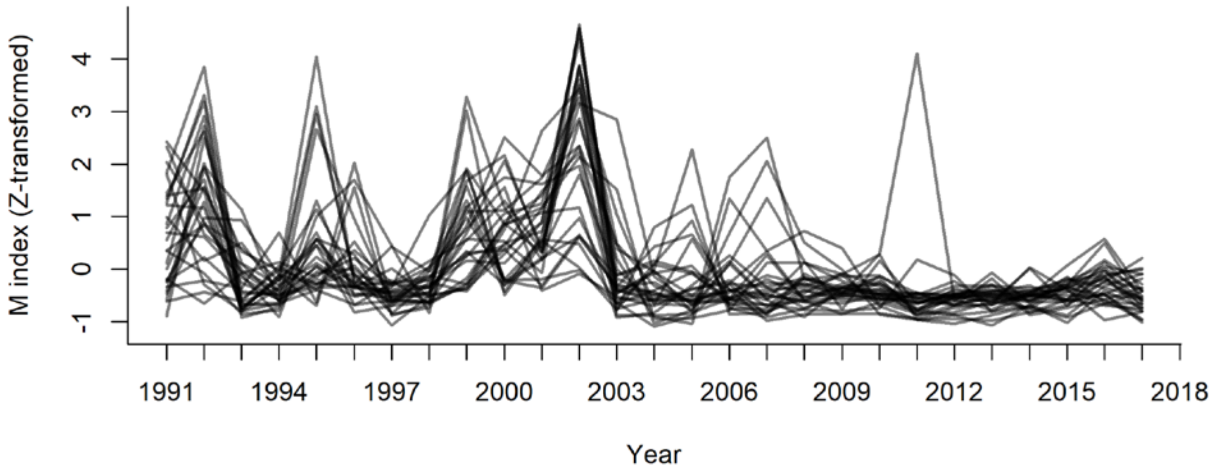

Figure 23. Standardized time series of instantaneous median natural mortality rates. Each line represents a time series of z-transformed median instantaneous natural mortality in a NOAA code.

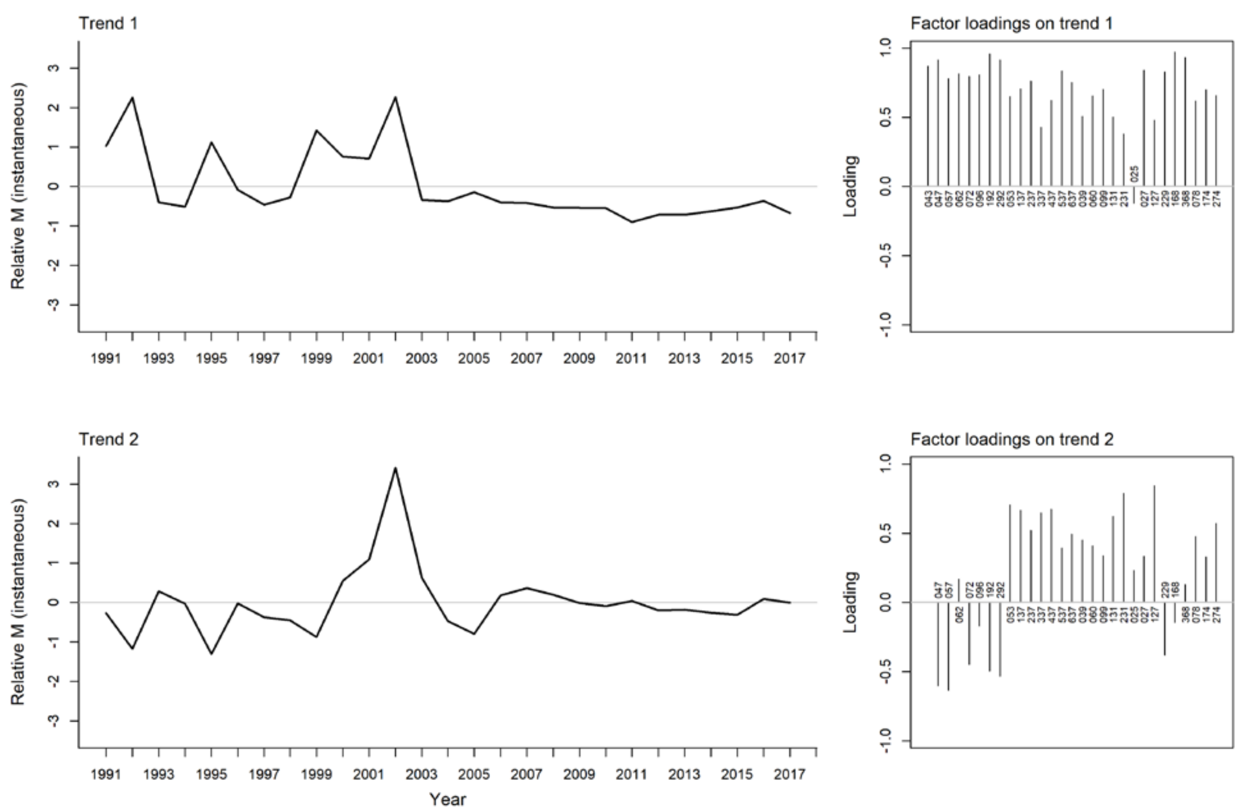

Figure 24.. Trends and loadings from dynamic factor analysis with 2 trends. The labels on the factor loadings are NOAA codes.

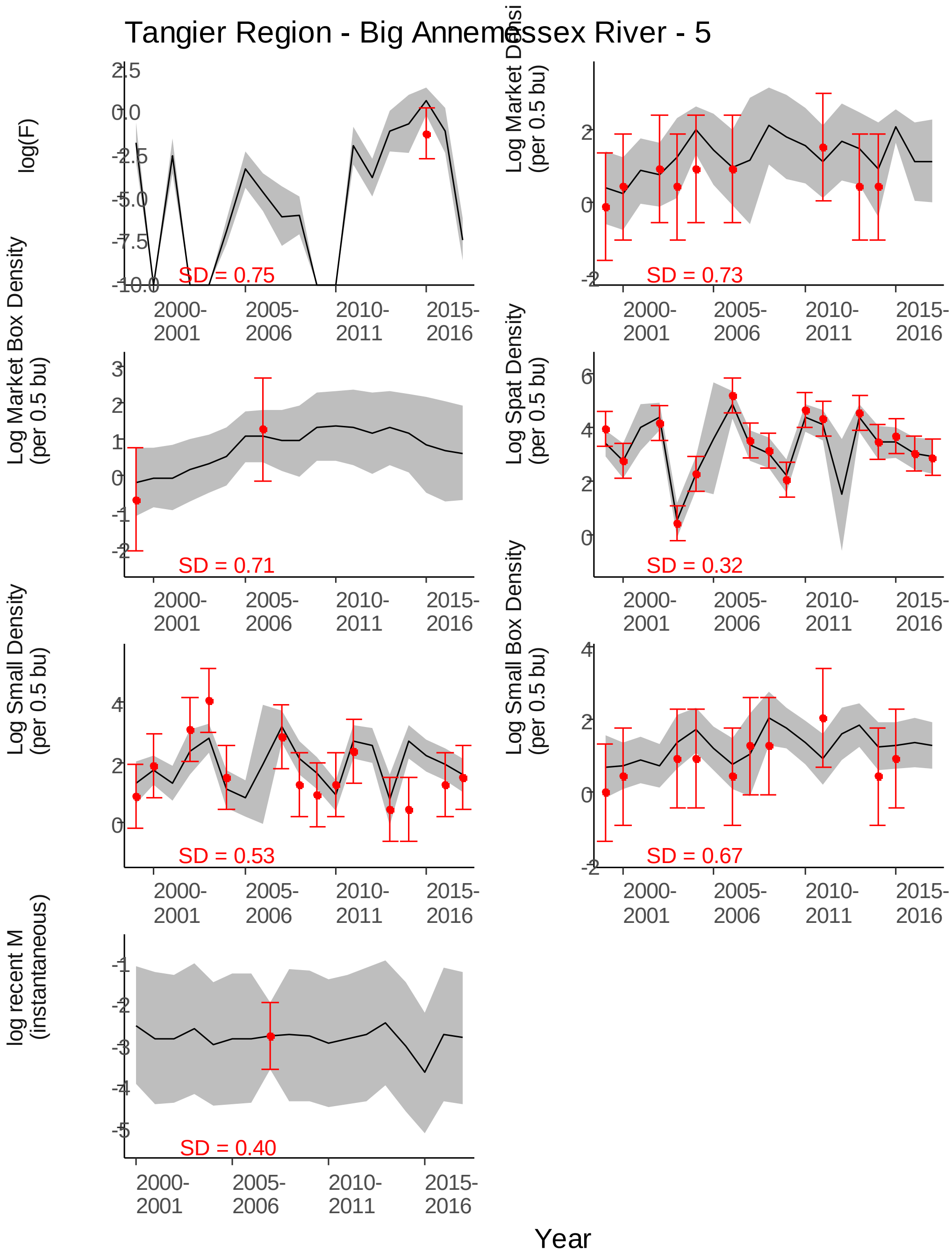

Figure 25. Estimated (line) and observed (points) of: log fishing mortality rate (F), log relative density (number per 0.5 Maryland bushels (bu)) of live market, market box, live small, small box, and spat, and log recent natural mortality (M) index during 1999-2000 in the Big Annemessex River (NOAA code 5). Whiskers indicate approximate 95% confidence intervals (CIs) on the observations (given the standard deviations (SDs) used in model fitting), and the shaded areas indicate approximate 95% CIs of the model estimates.

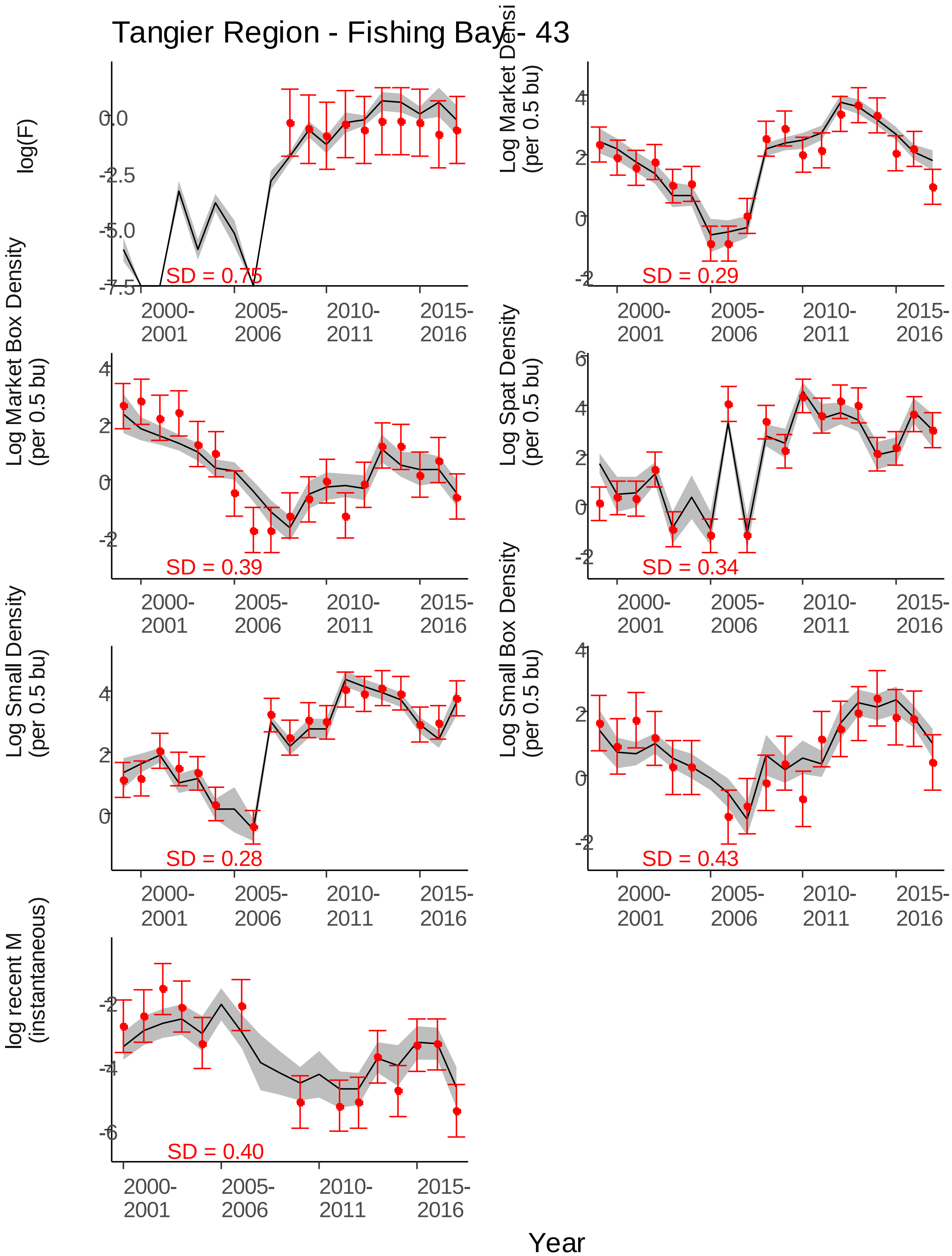

Figure 26. . Estimated (line) and observed (points) values for Fishing Bay (NOAA code 43). Variable and symbol definitions are the same as Figure 25.

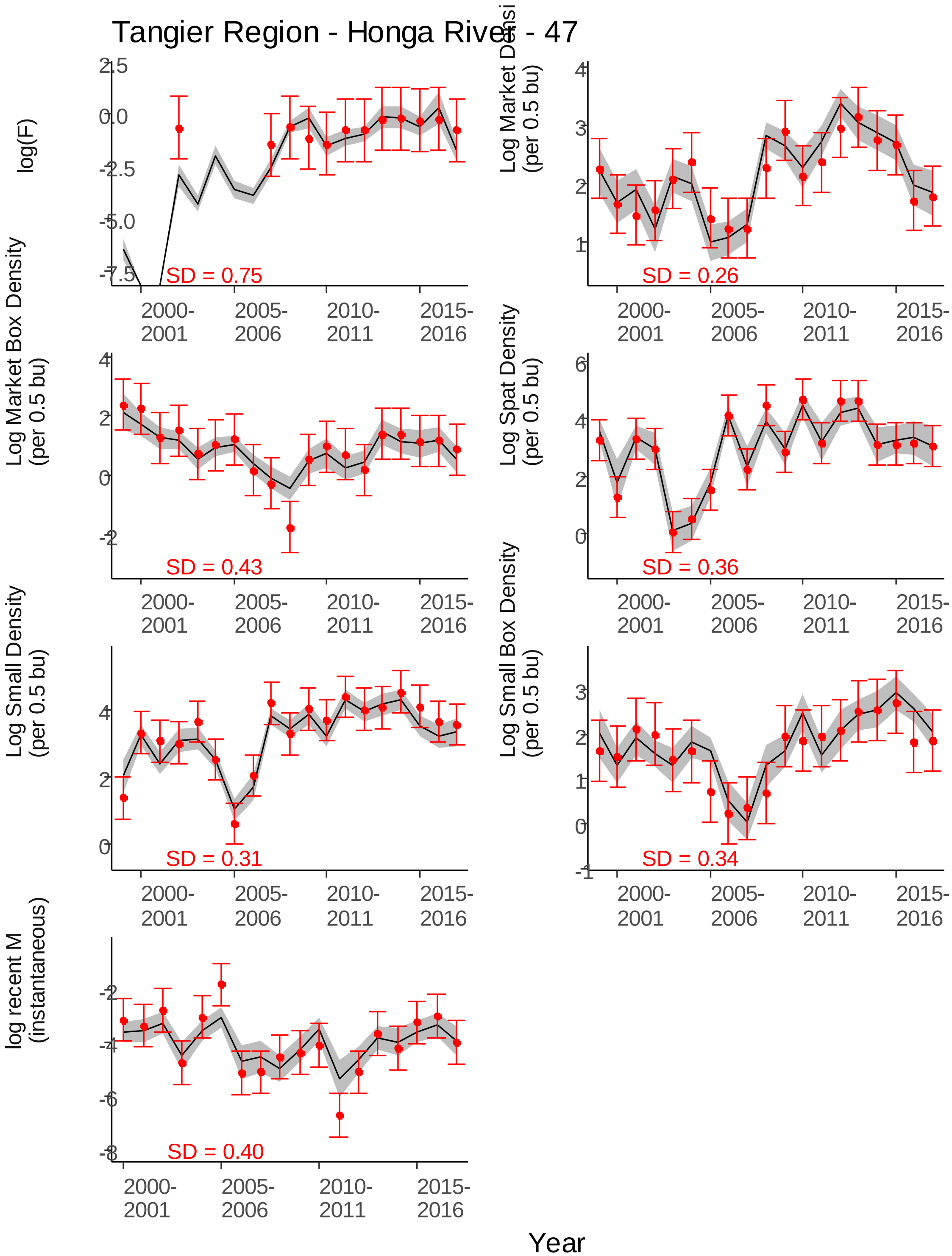

Figure 27. Estimated (line) and observed (points) values for the Honga River (NOAA code 47). Variable and symbol definitions are the same as Figure 25.

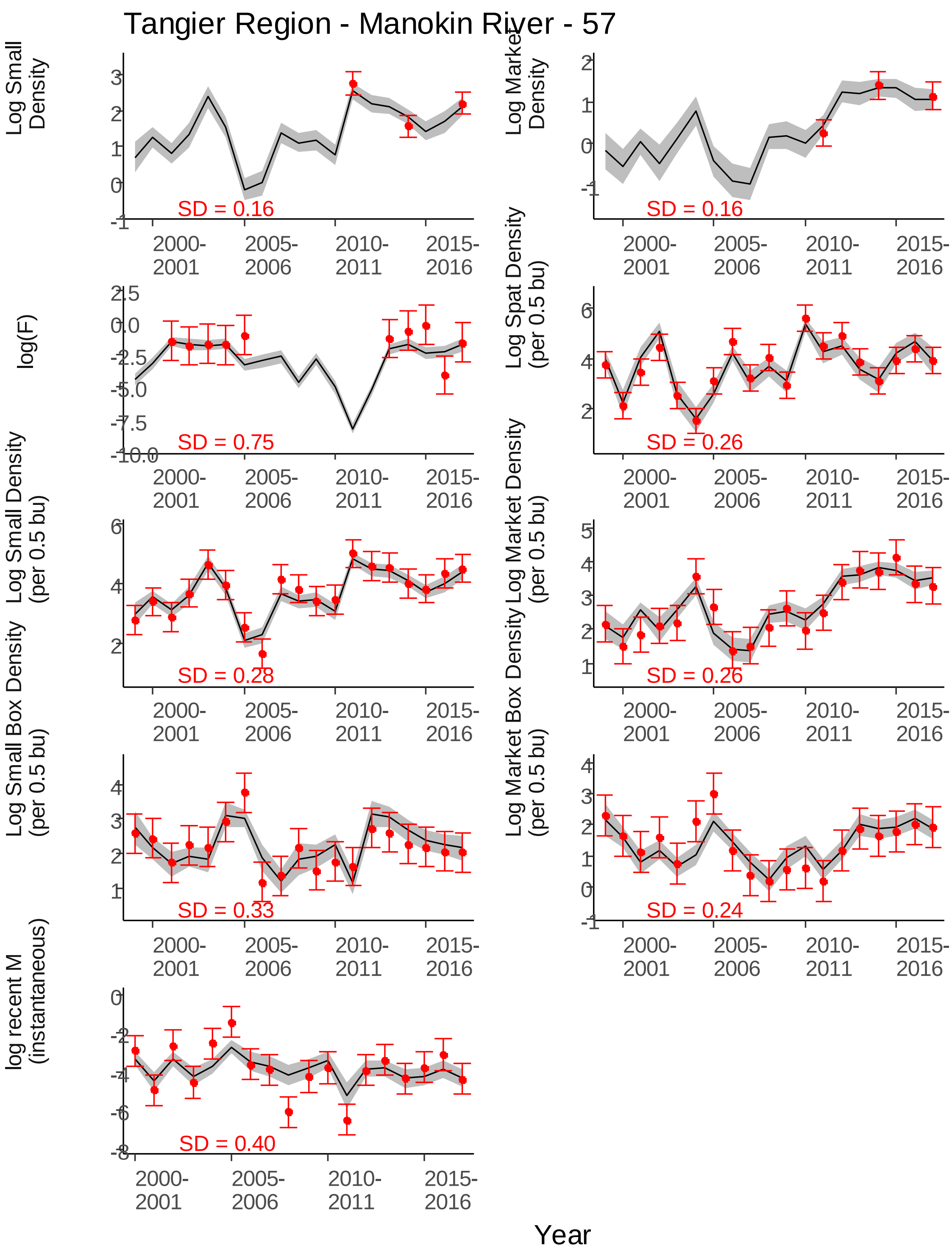

Figure 28. Estimated (line) and observed (points) values for the Manokin River (NOAA code 57). The top two panels indicate estimated and observed density (number m^{-2}) of small and market oysters. Variable and symbol definitions are the same as Figure 25.

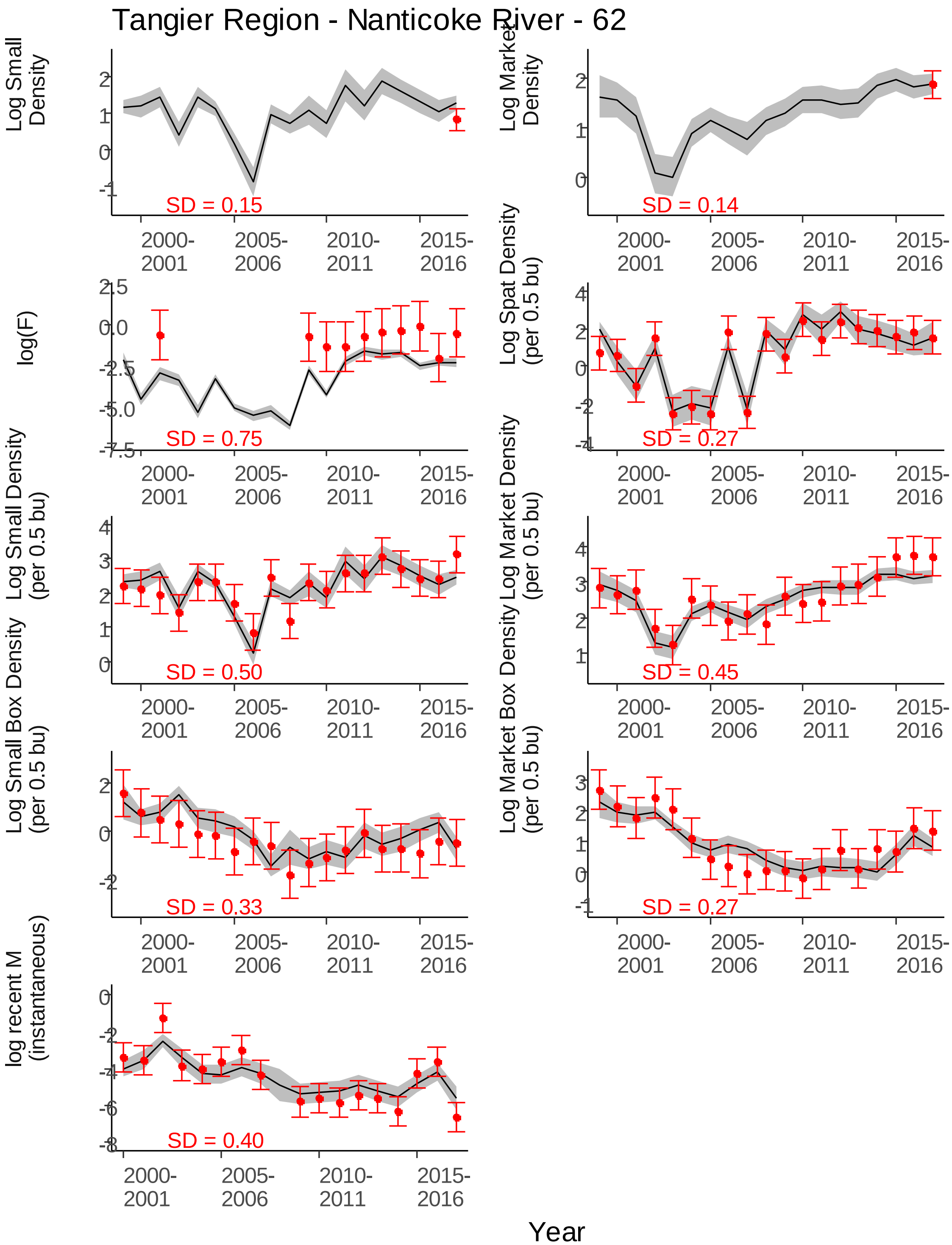

Figure 29. Estimated (line) and observed (points) values for the Nanticoke River (NOAA code 62). Variable and symbol definitions are the same as Figures 25 and 28.

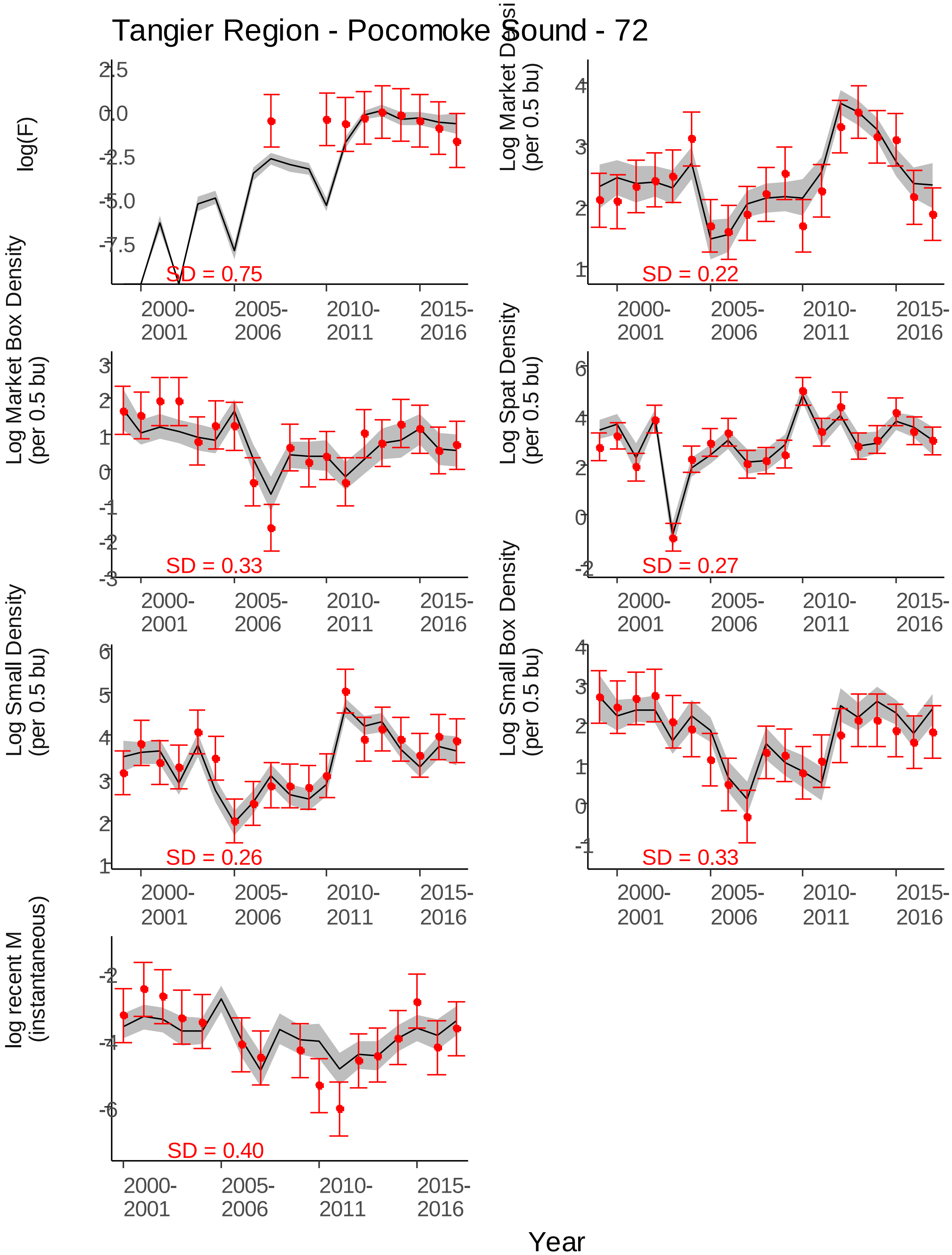

Figure 30. Estimated (line) and observed (points) values for the Pocomoke Sound (NOAA code 72). Variable and symbol definitions are the same as Figure 25.

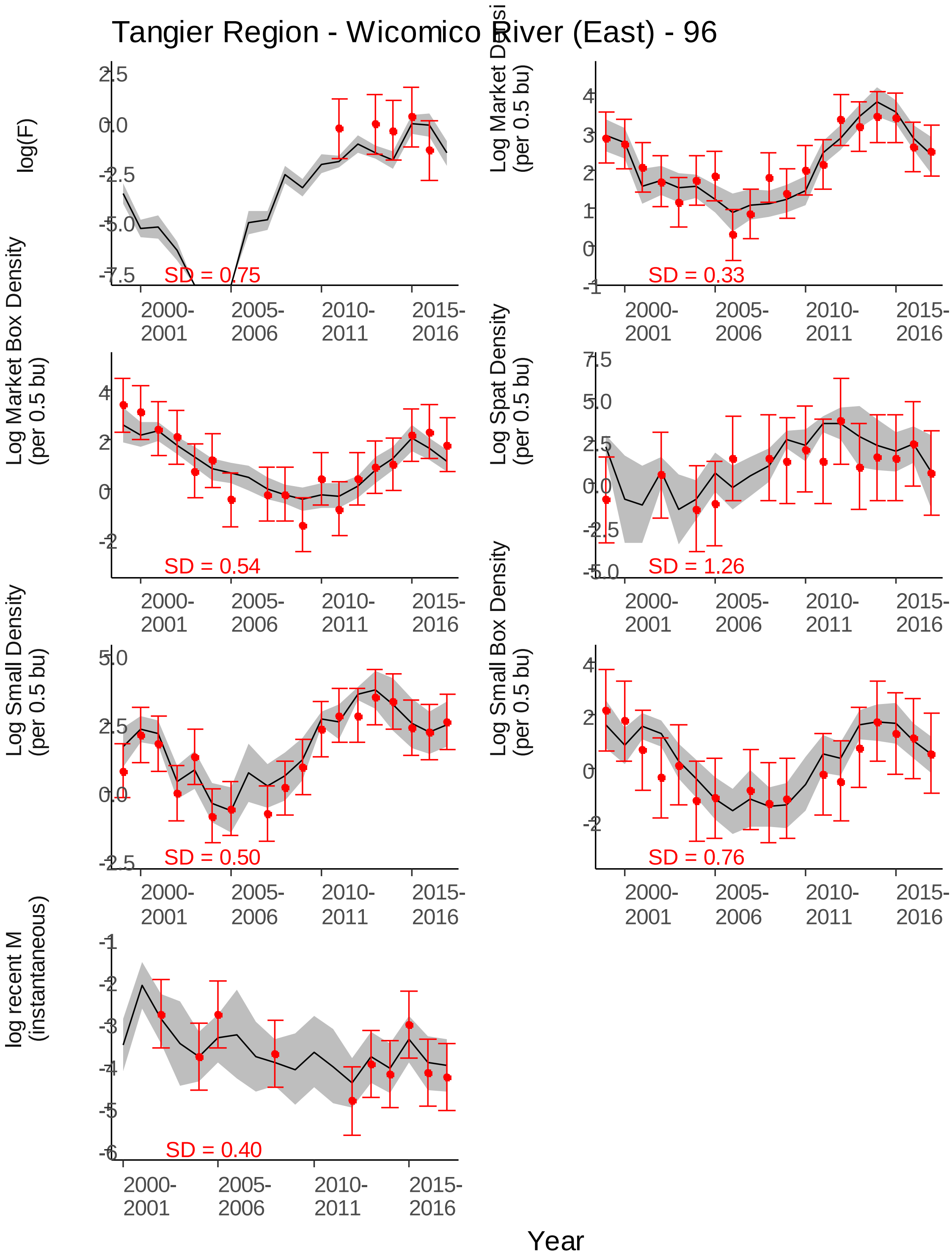

Figure 31. Estimated (line) and observed (points) values for the Wicomico River (NOAA code 96). Variable and symbol definitions are the same as Figure 25.

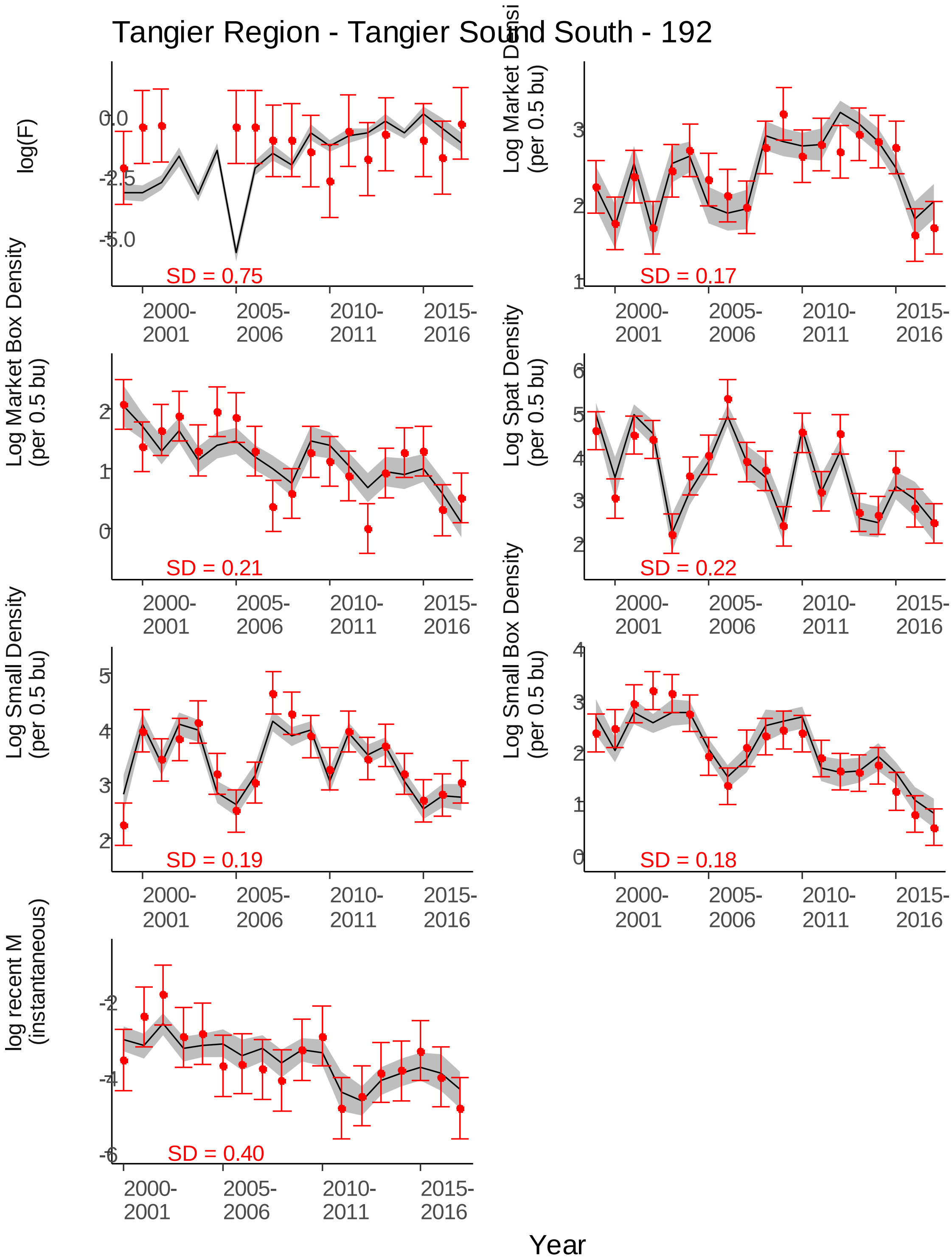

Figure 32. Estimated (line) and observed (points) values for lower Tangier Sound (NOAA code 192). Variable and symbol definitions are the same as Figure 25.

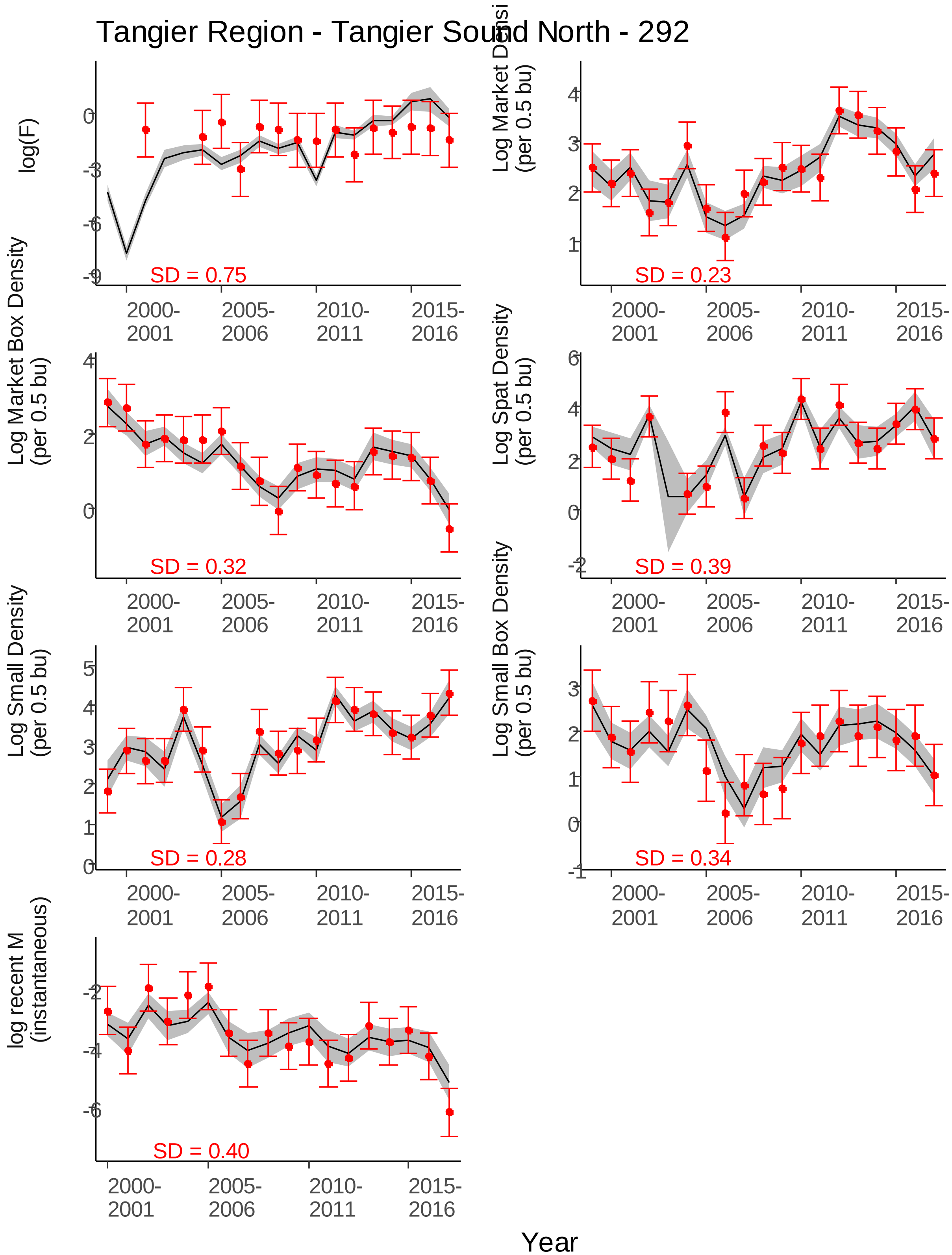

Figure 33. Estimated (line) and observed (points) values for upper Tangier Sound (NOAA code 292). Variable and symbol definitions are the same as Figure 25.

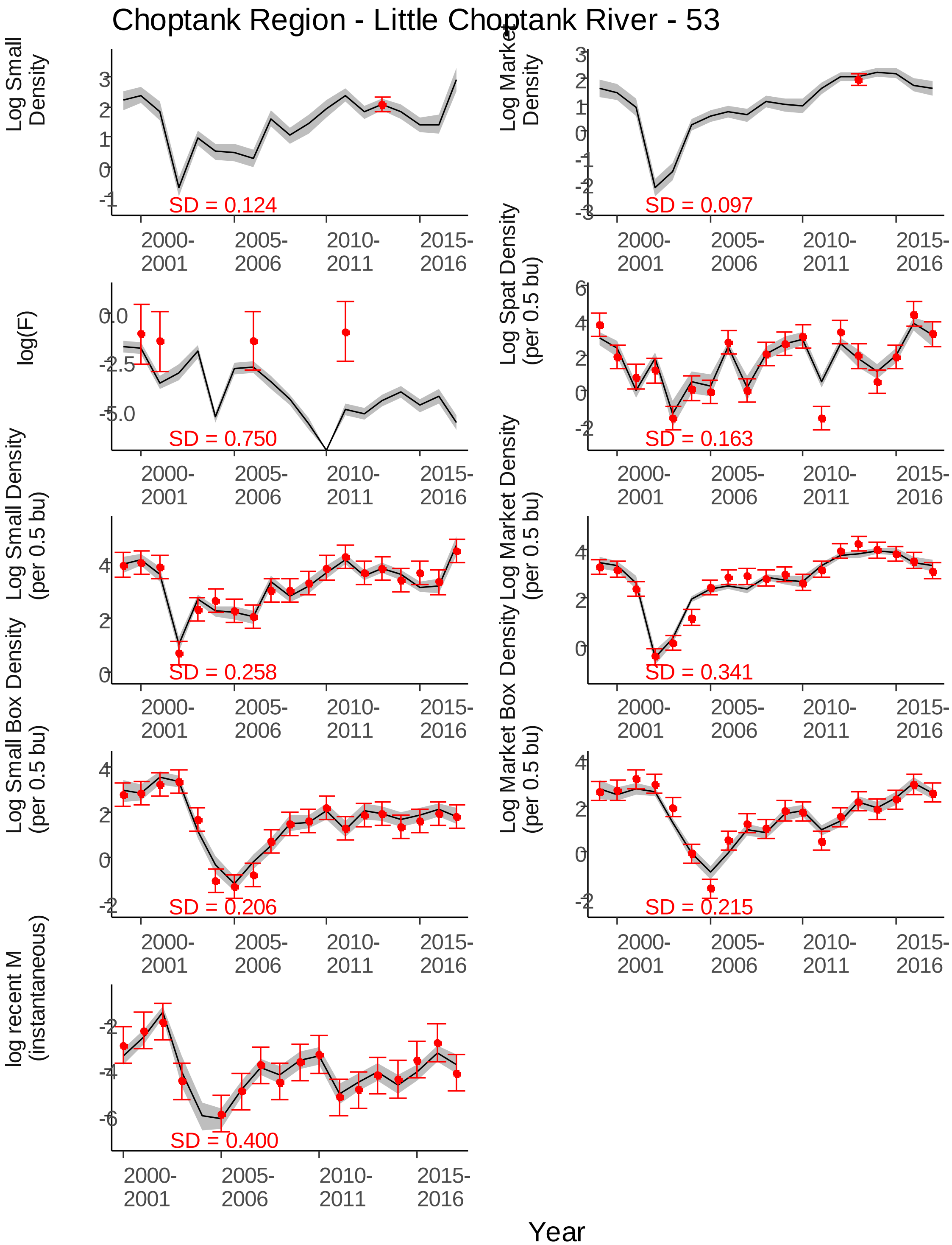

Figure 34. Estimated (line) and observed (points) for the Little Choptank River (NOAA code 53). Variable and symbol definitions are the same as Figures 25 and 28.

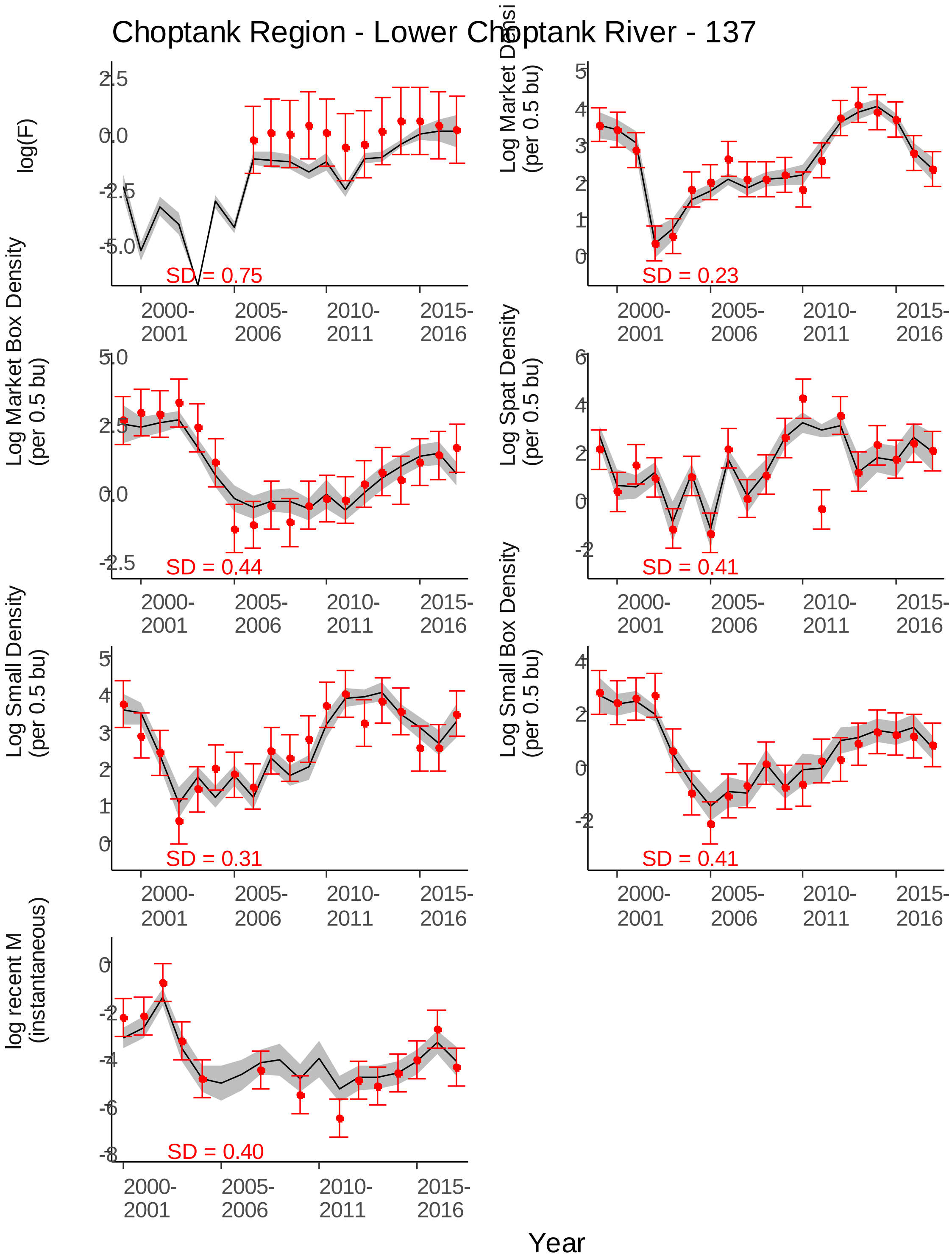

Figure 35. Estimated (line) and observed (points) for the Lower Choptank River (NOAA code 137). Variable and symbol definitions are the same as Figure 25.

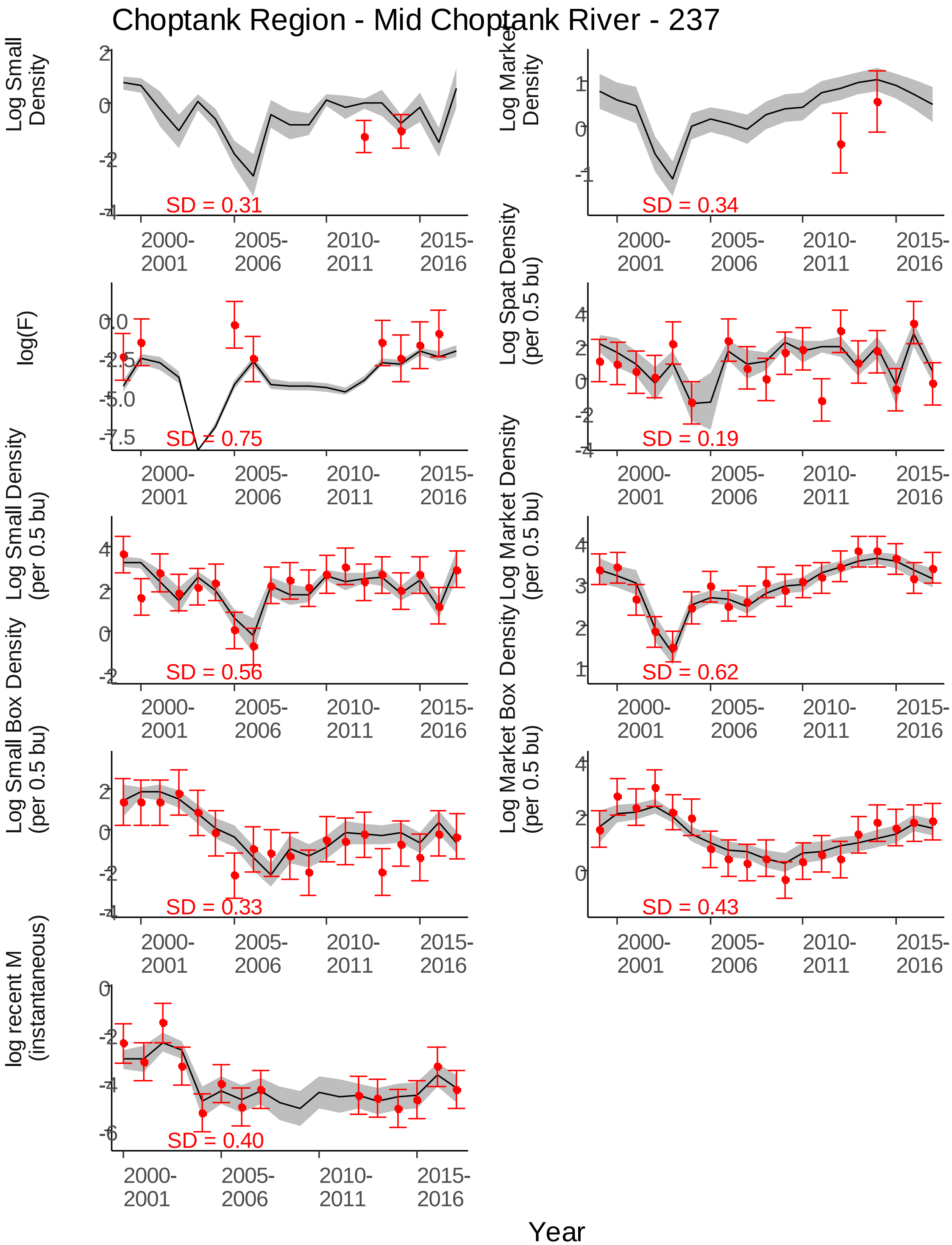

Figure 36. Estimated (line) and observed (points) for the middle Choptank River (NOAA code 237). Variable and symbol definitions are the same as Figures 25 and 28.

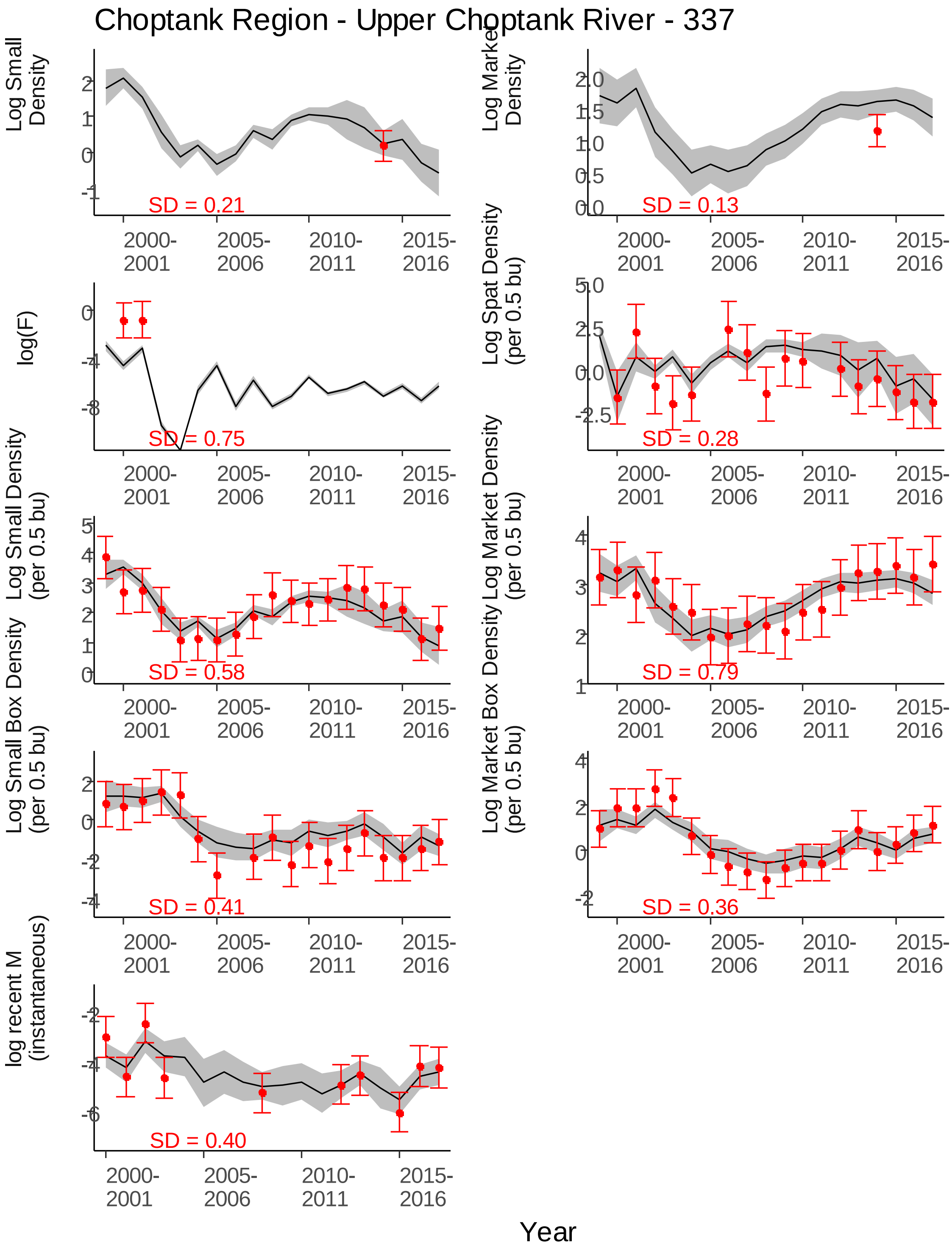

Figure 37. Estimated (line) and observed (points) for the upper Choptank River (NOAA code 337). Variable and symbol definitions are the same as Figures 25 and 28.

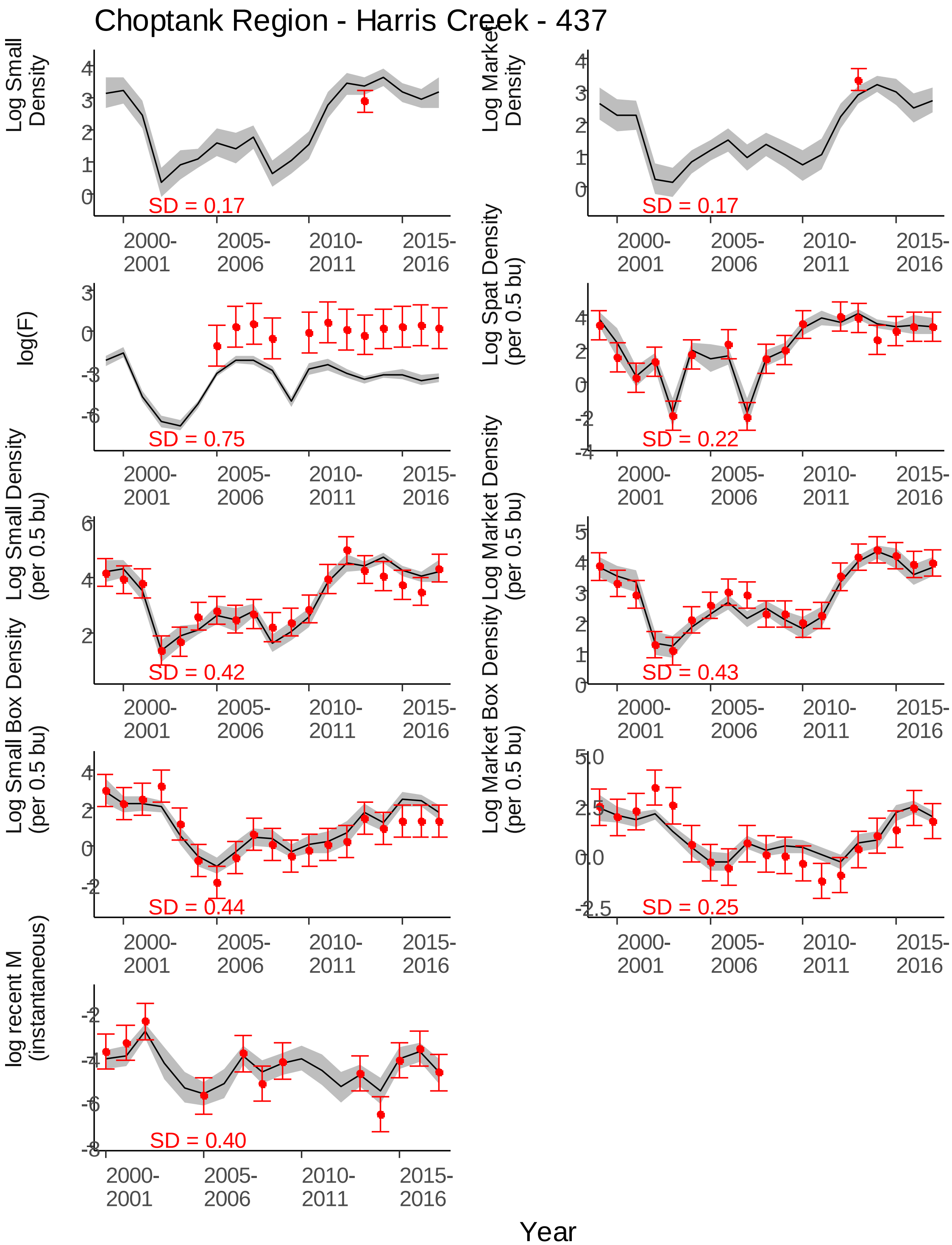

Figure 38. Estimated (line) and observed (points) for Harris Creek (NOAA code 437). Variable and symbol definitions are the same as Figures 25 and 28.

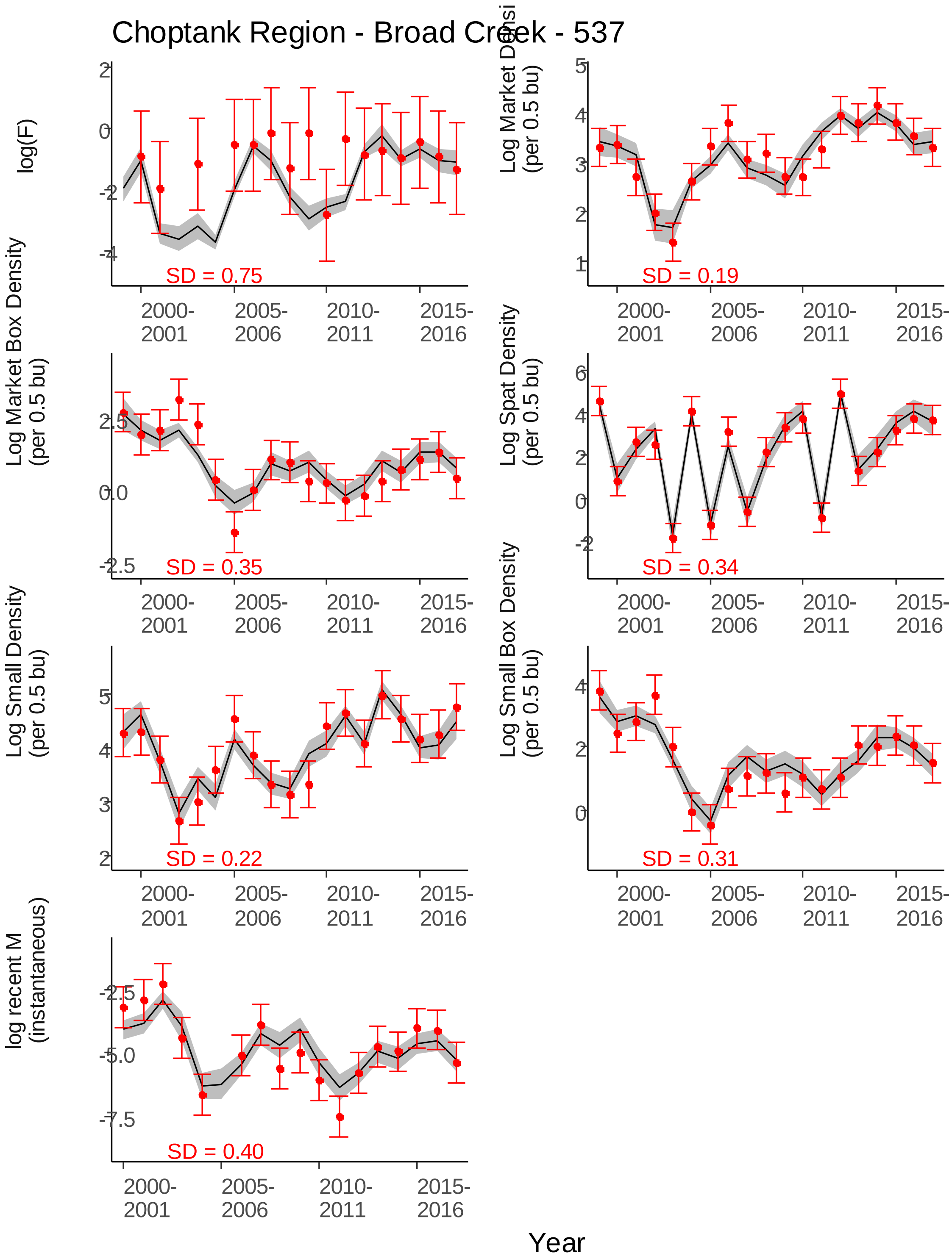

Figure 39. Estimated (line) and observed (points) for Broad Creek (NOAA code 537). Variable and symbol definitions are the same as Figure 25.

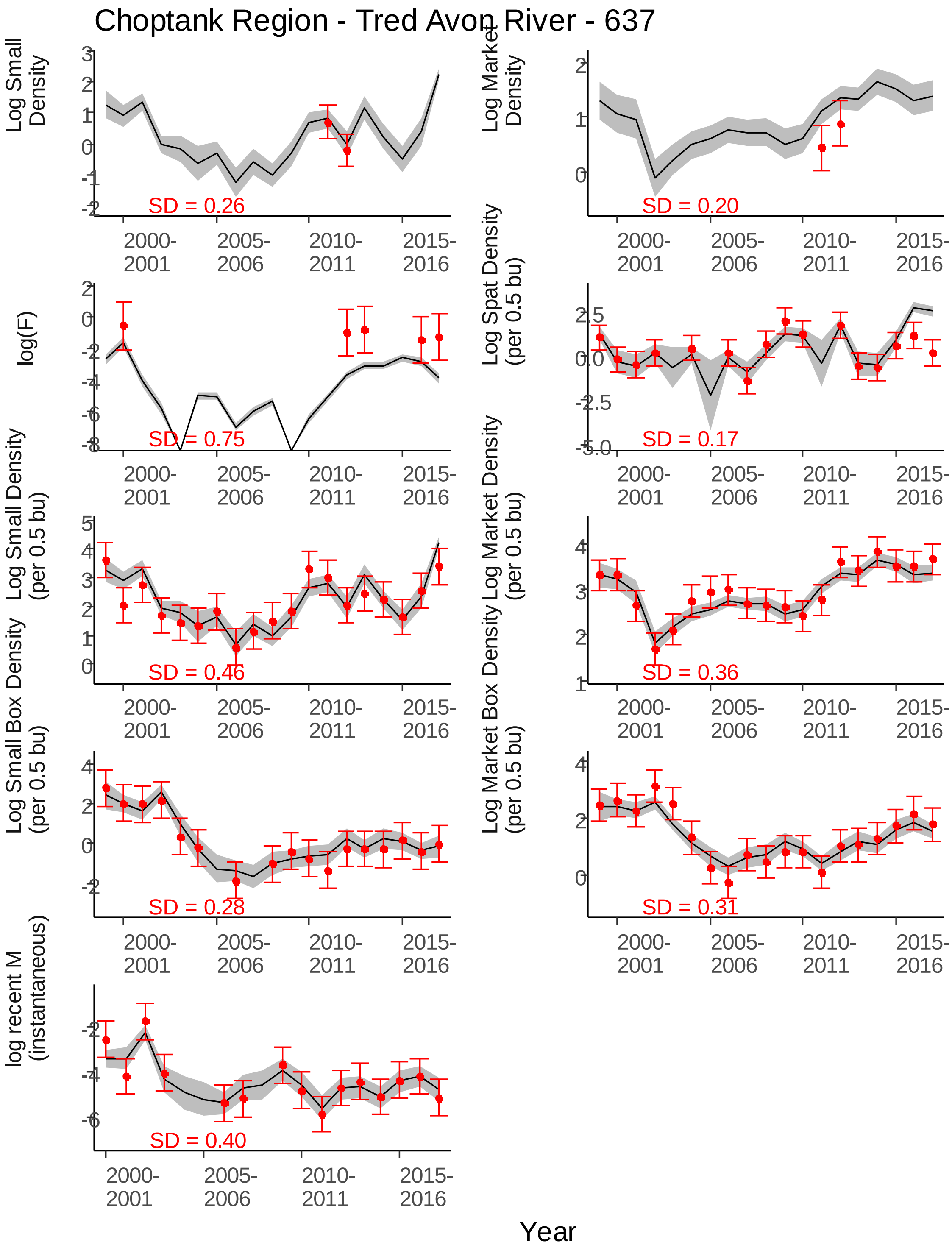

Figure 40. Estimated (line) and observed (points) for the Tred Avon River (NOAA code 637). Variable and symbol definitions are the same as Figures 25 and 28.

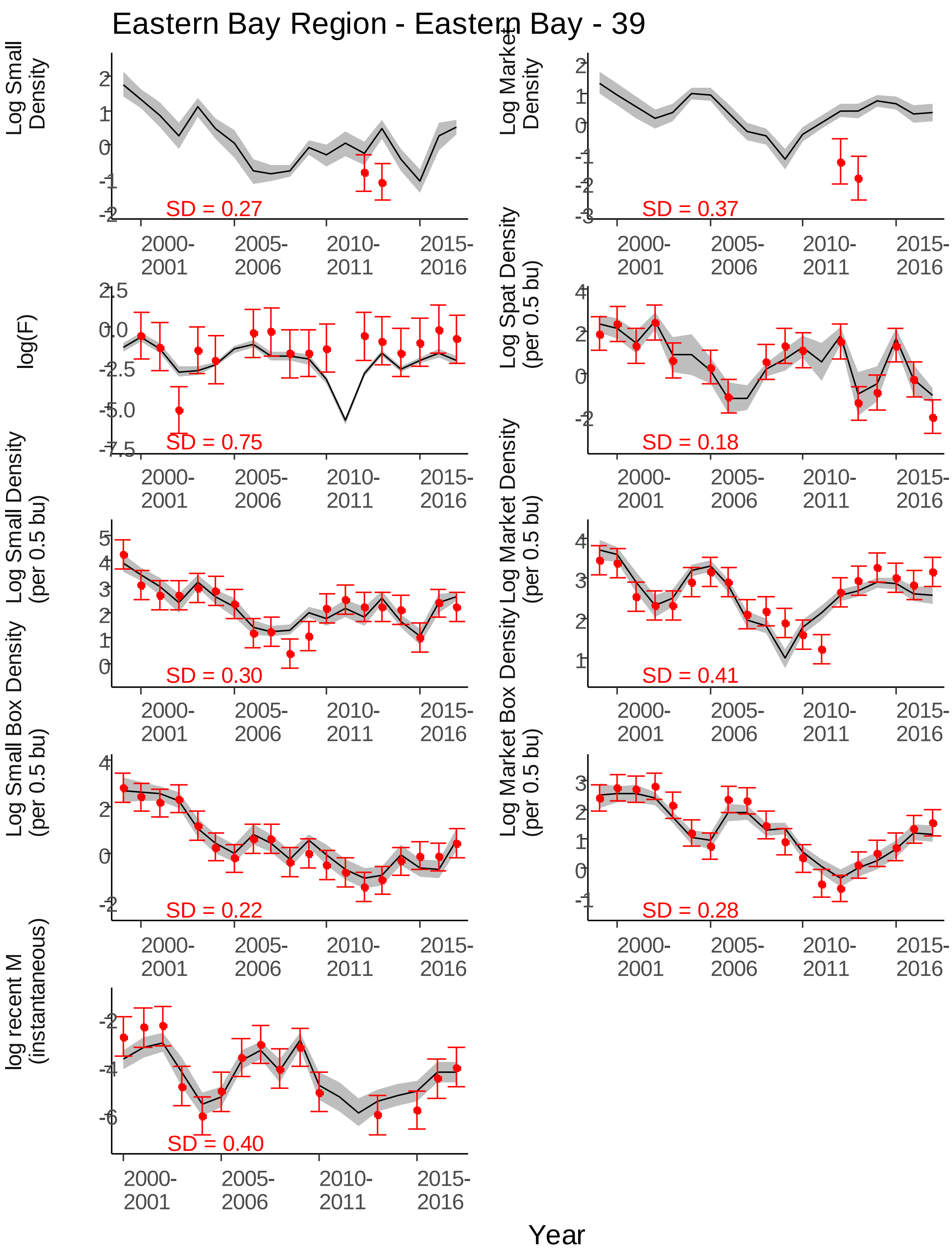

Figure 41. Estimated (line) and observed (points) for Eastern Bay (NOAA code 39). Variable and symbol definitions are the same as Figures 25 and 28.

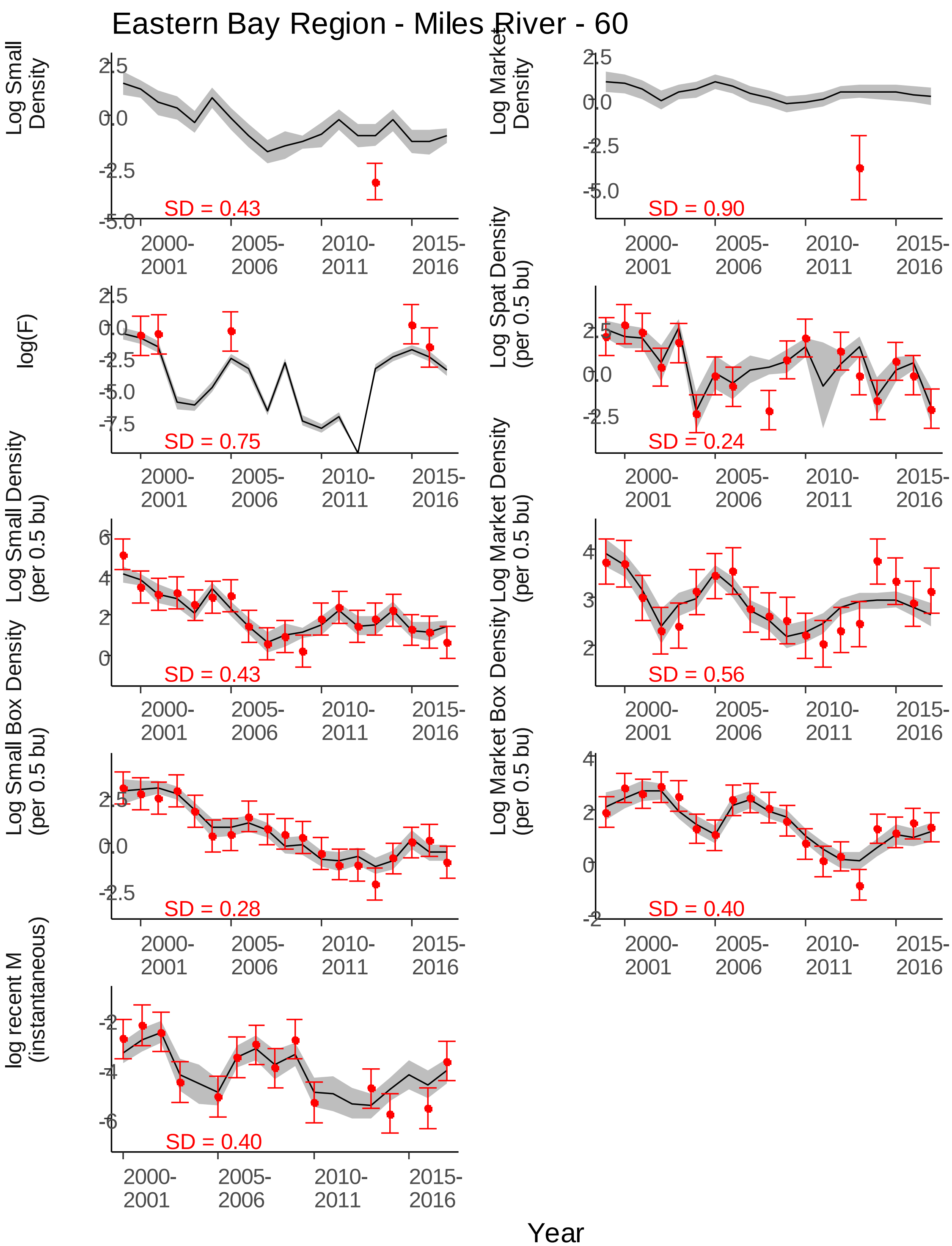

Figure 42. Estimated (line) and observed (points) for the Miles River (NOAA code 60). Variable and symbol definitions are the same as Figures 25 and 28.

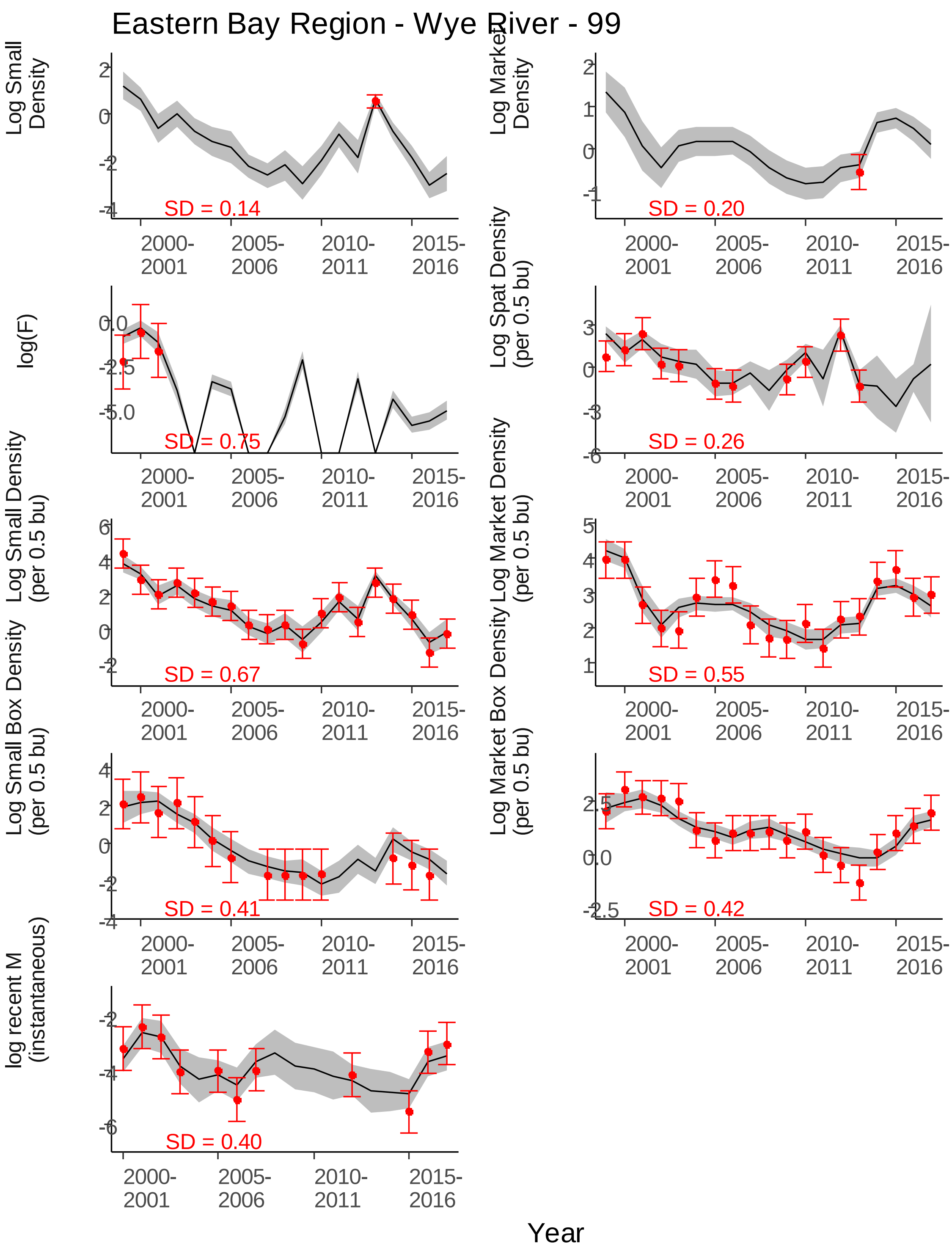

Figure 43. Estimated (line) and observed (points) for the Wye River (NOAA code 99). Variable and symbol definitions are the same as Figures 25 and 28.

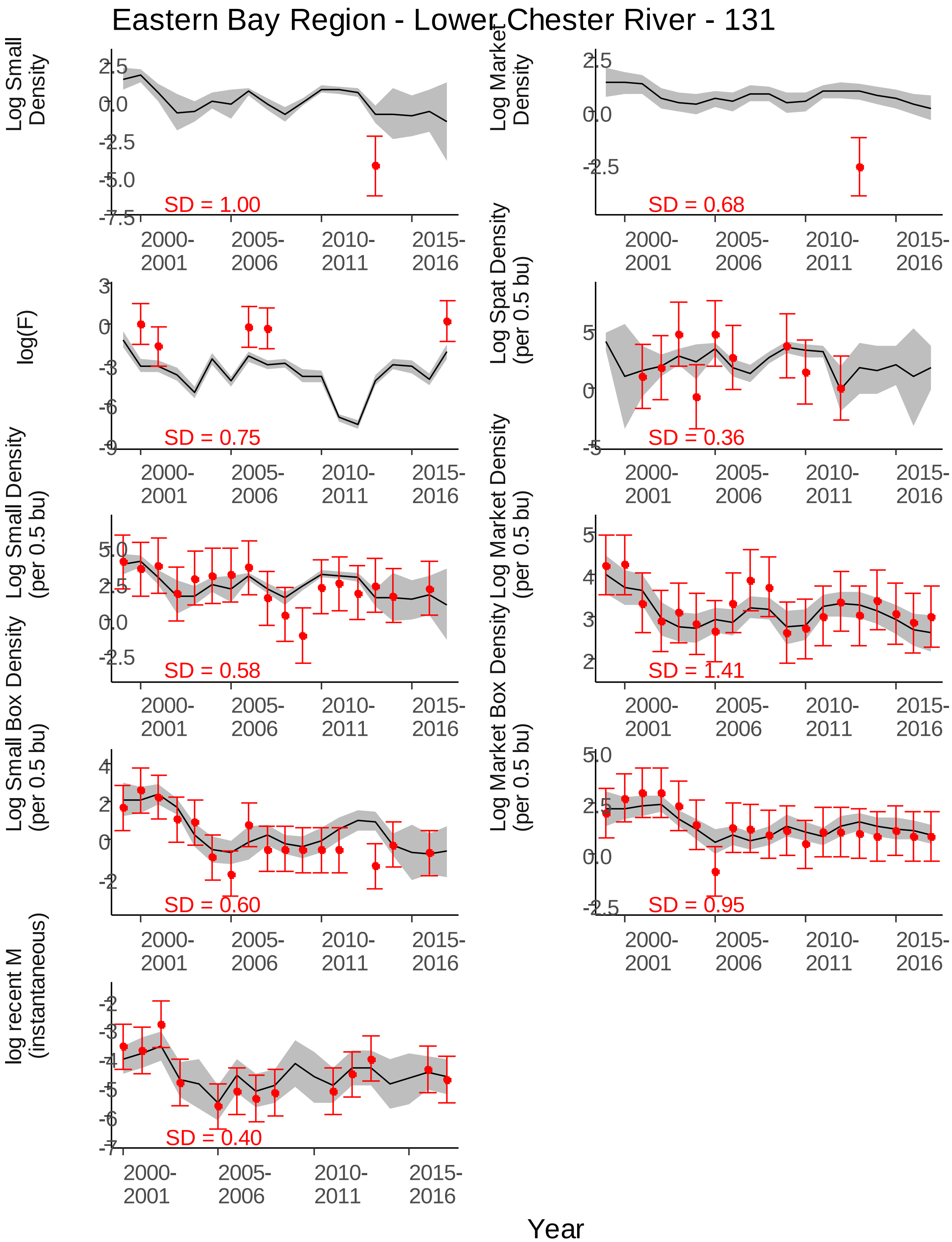

Figure 44. Estimated (line) and observed (points) for the lower Chester River (NOAA code 131). Variable and symbol definitions are the same as Figures 25 and 28.

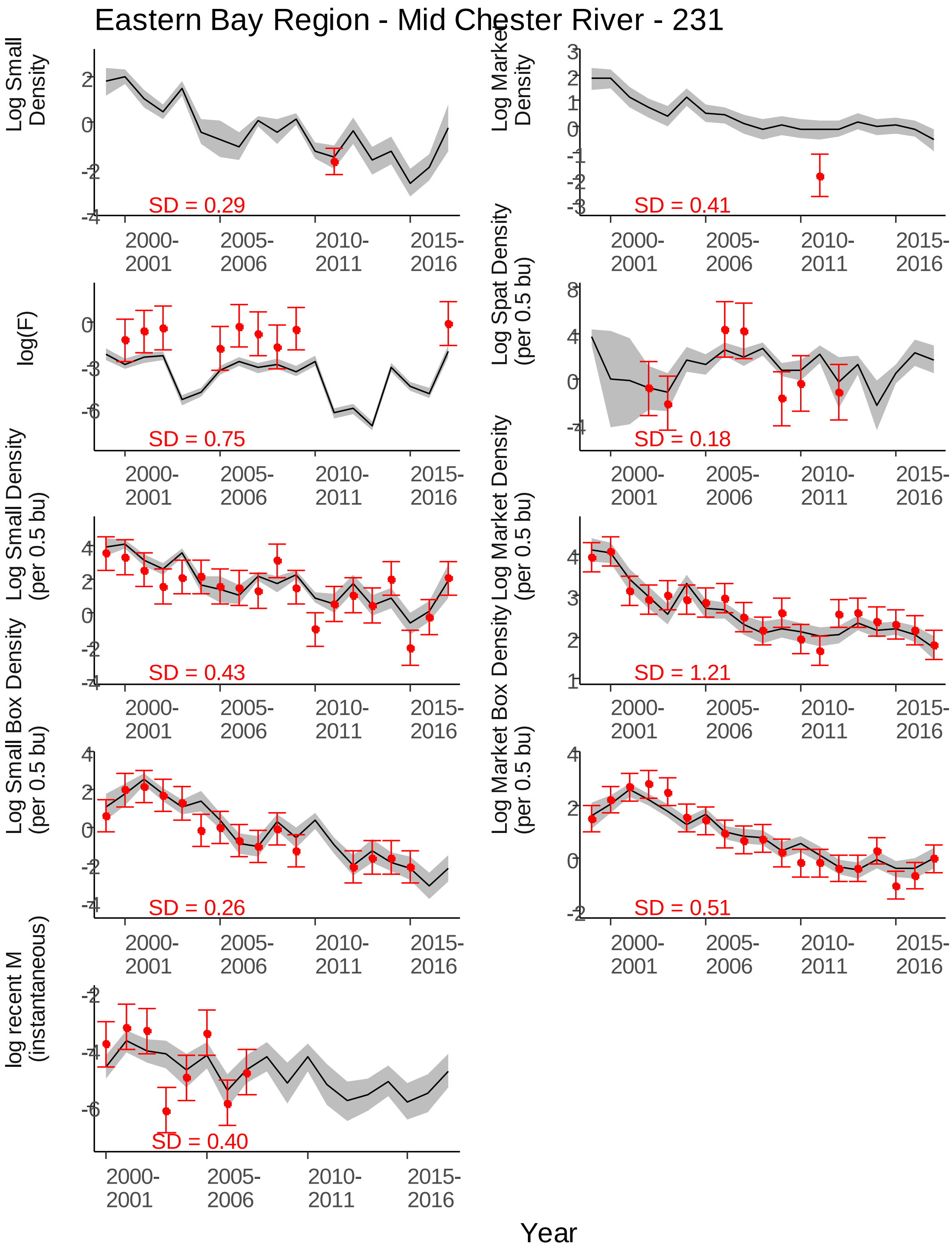

Figure 45. Estimated (line) and observed (points) for the middle Chester River (NOAA code 231). Variable and symbol definitions are the same as Figures 25 and 28.

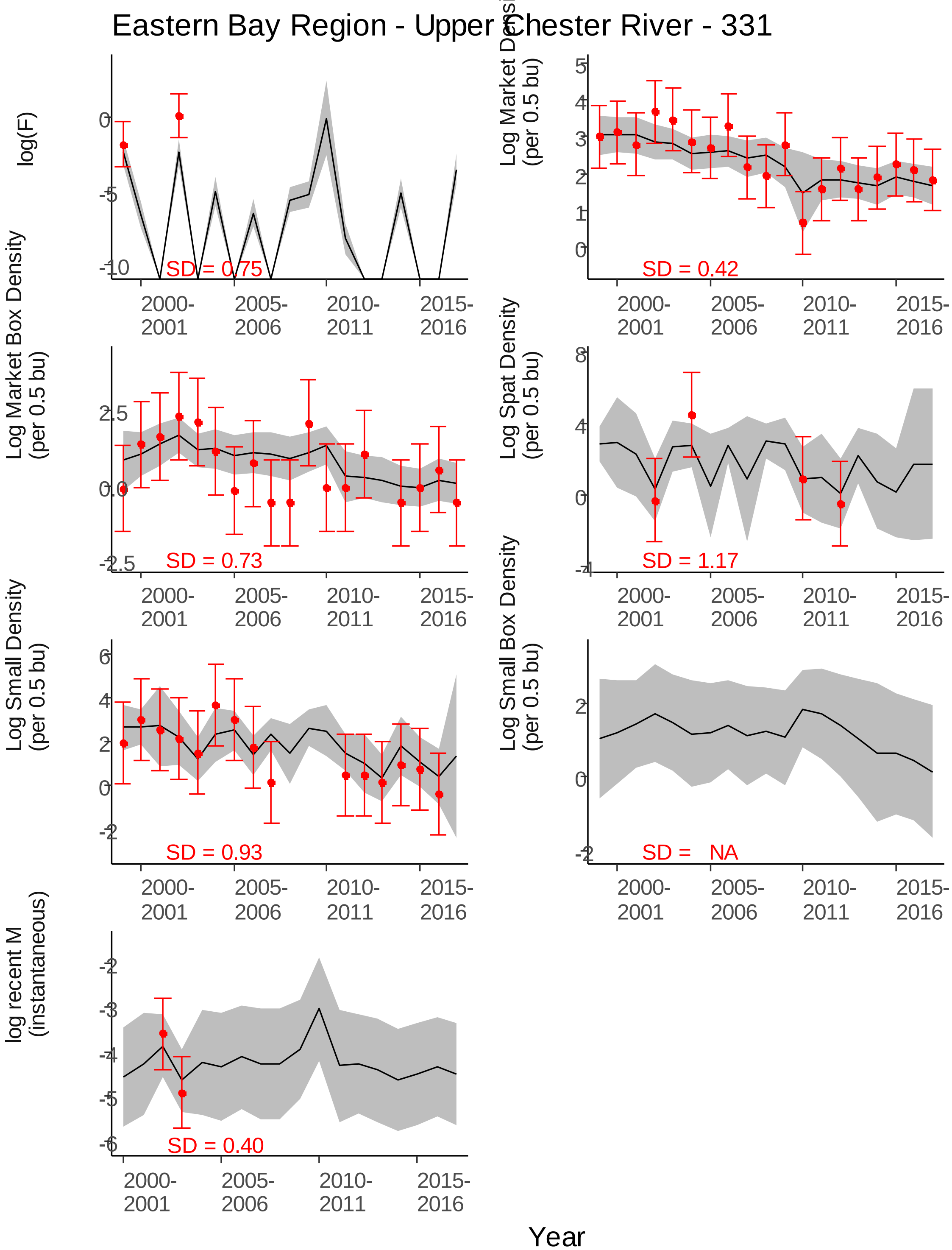

Figure 46. Estimated (line) and observed (points) for the upper Chester River (NOAA code 331). Variable and symbol definitions are the same as Figure 25.

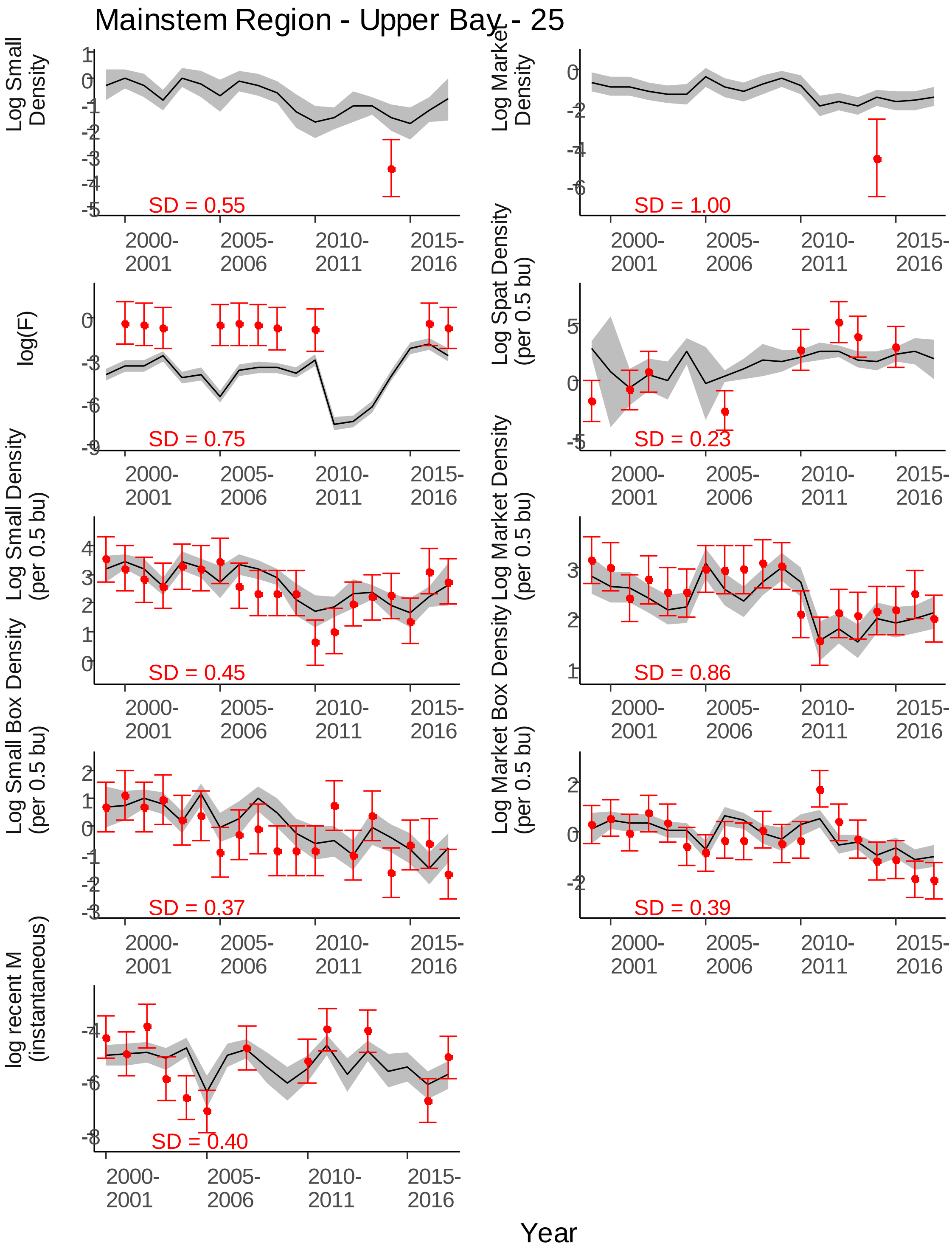

Figure 47. Estimated (line) and observed (points) for the Upper Bay (NOAA code 25). Variable and symbol definitions are the same as Figures 25 and 28.

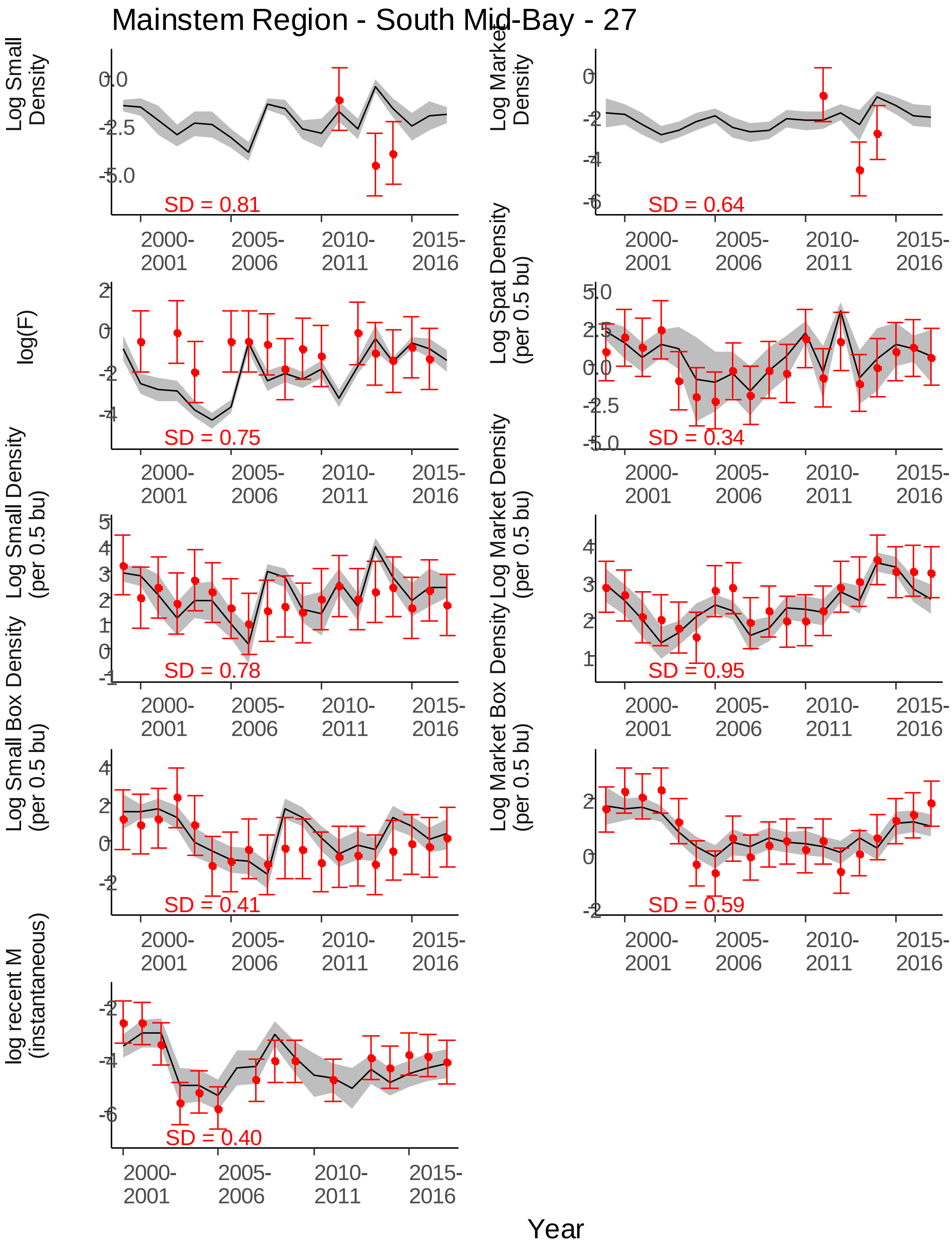

Figure 48. Estimated (line) and observed (points) for the South Mid-Bay (NOAA code 27). Variable and symbol definitions are the same as Figures 25 and 28.

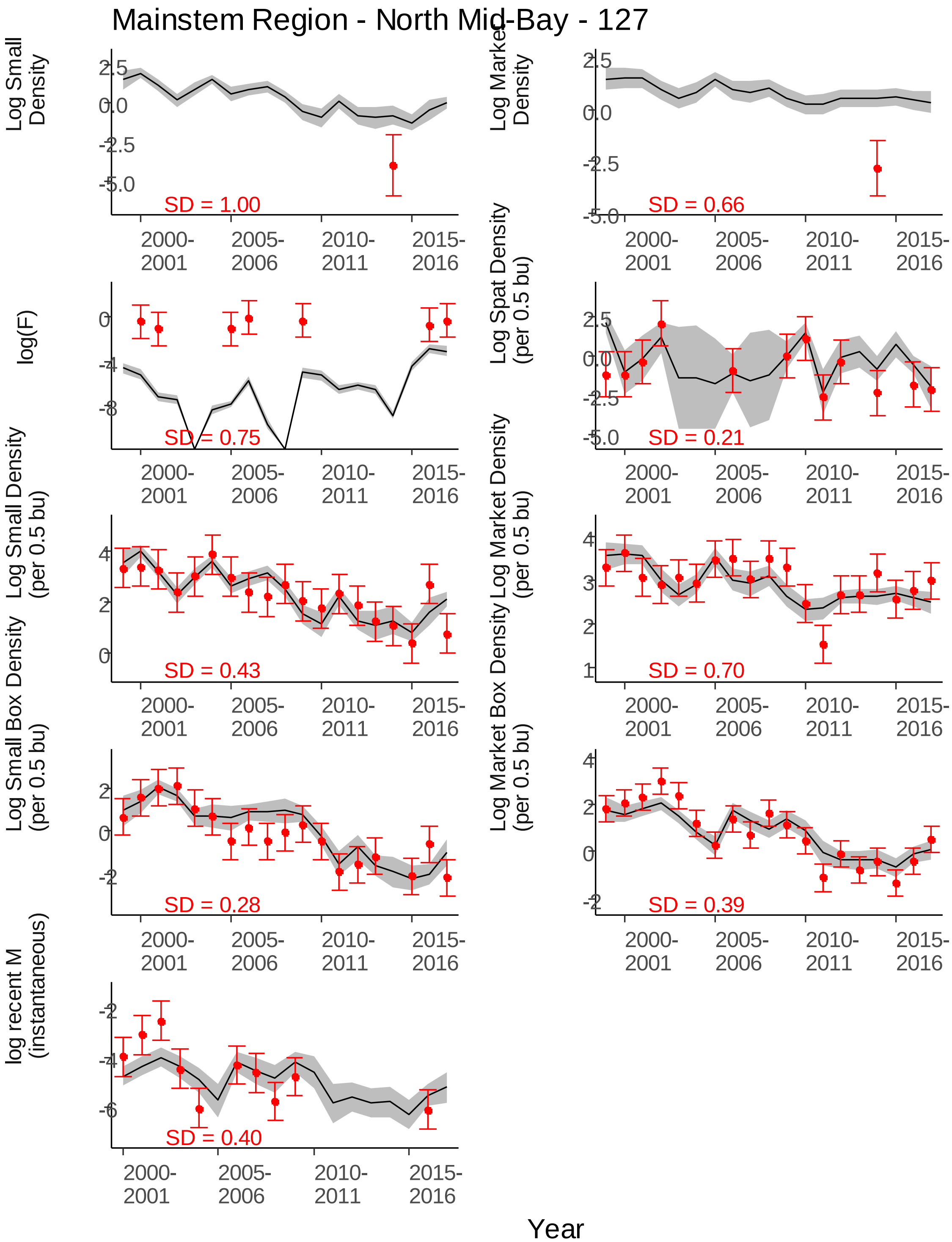

Figure 49. Estimated (line) and observed (points) for the North Mid-Bay (NOAA code 127). Variable and symbol definitions are the same as Figures 25 and 28.

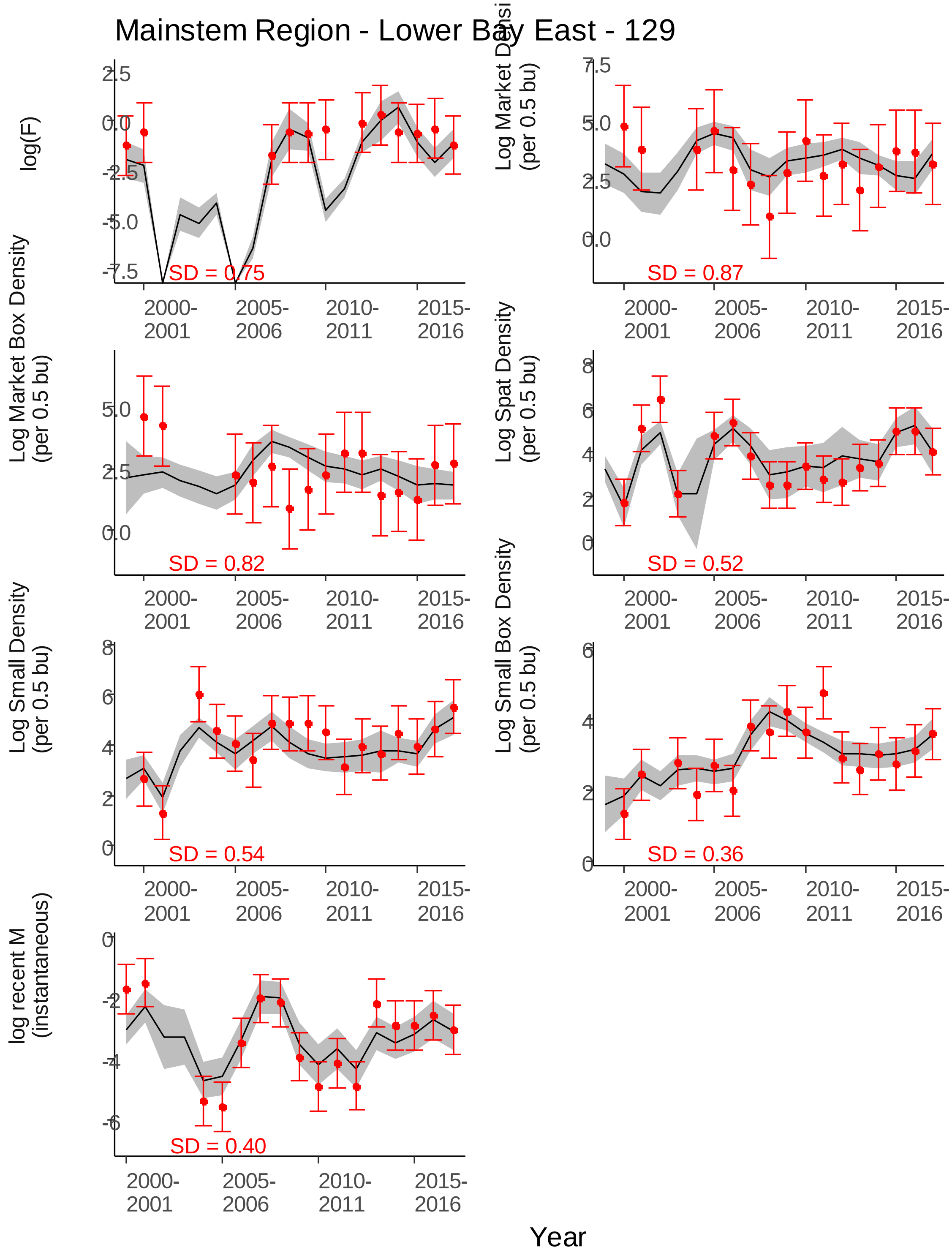

Figure 50. Estimated (line) and observed (points) for the Lower Bay East (NOAA code 129). Variable and symbol definitions are the same as Figure 25.

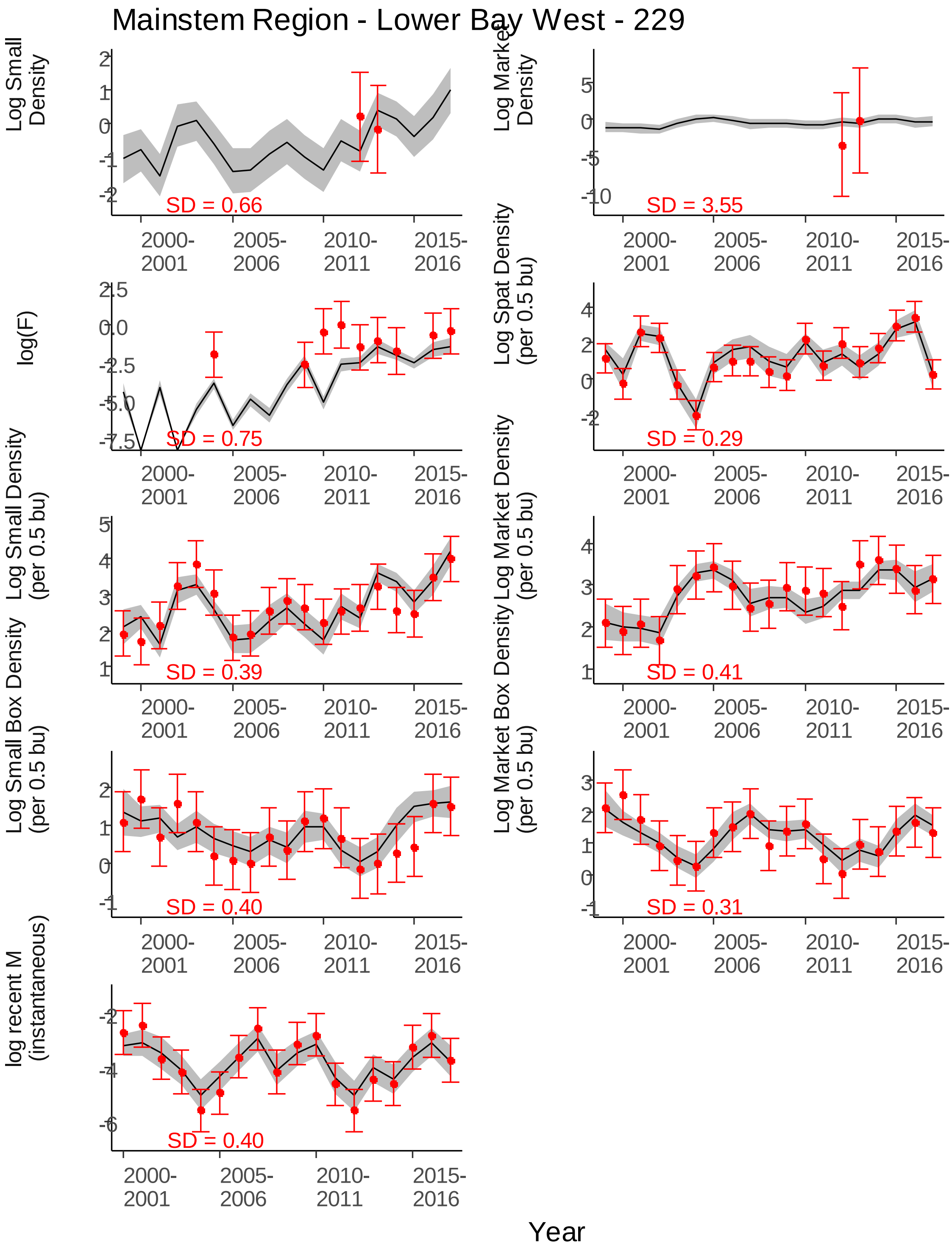

Figure 51. Estimated (line) and observed (points) for the Lower Bay West (NOAA code 229). Variable and symbol definitions are the same as Figures 25 and 28.

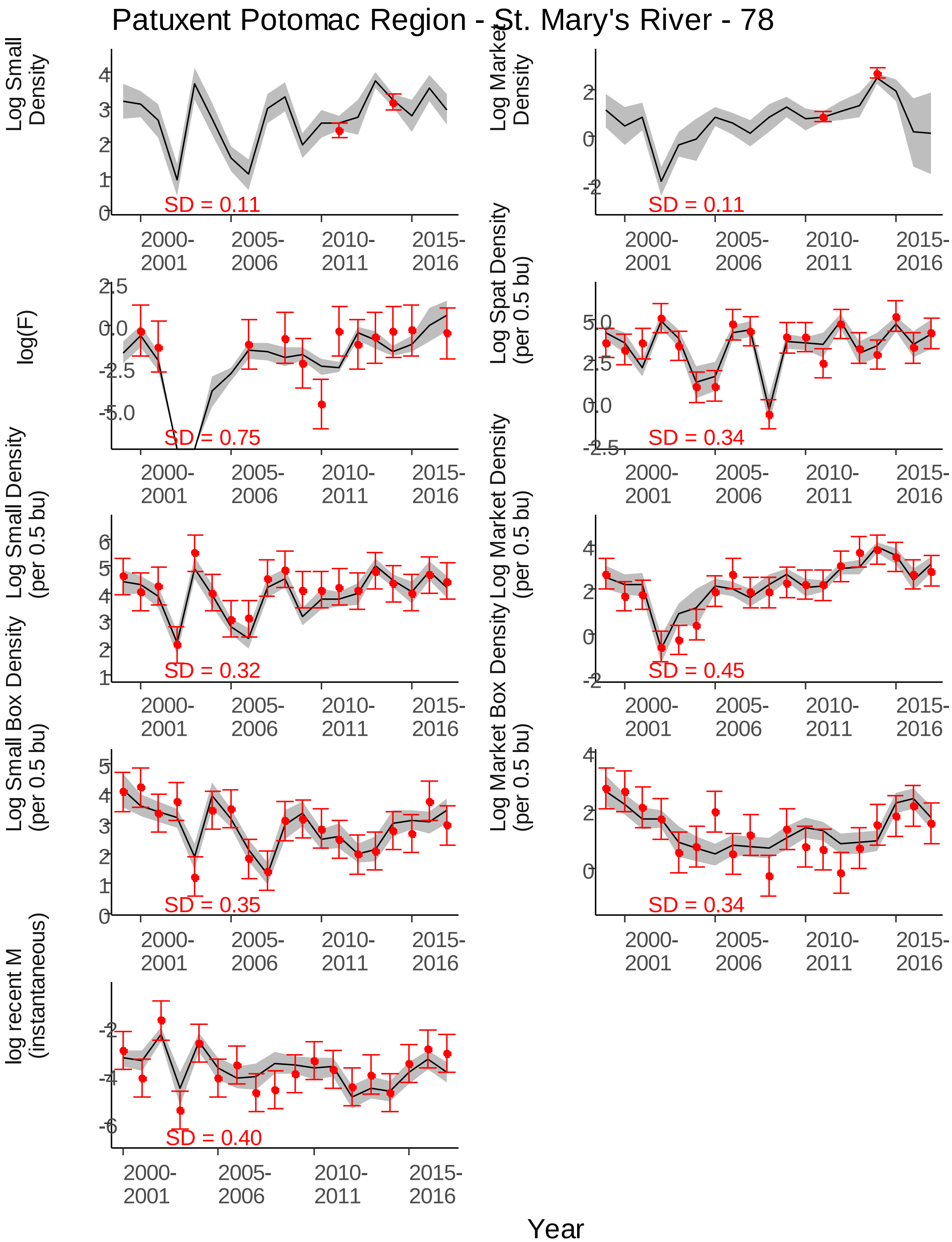

Figure 52. Estimated (line) and observed (points) for the St. Mary's River (NOAA code 78). Variable and symbol definitions are the same as Figures 25 and 28.

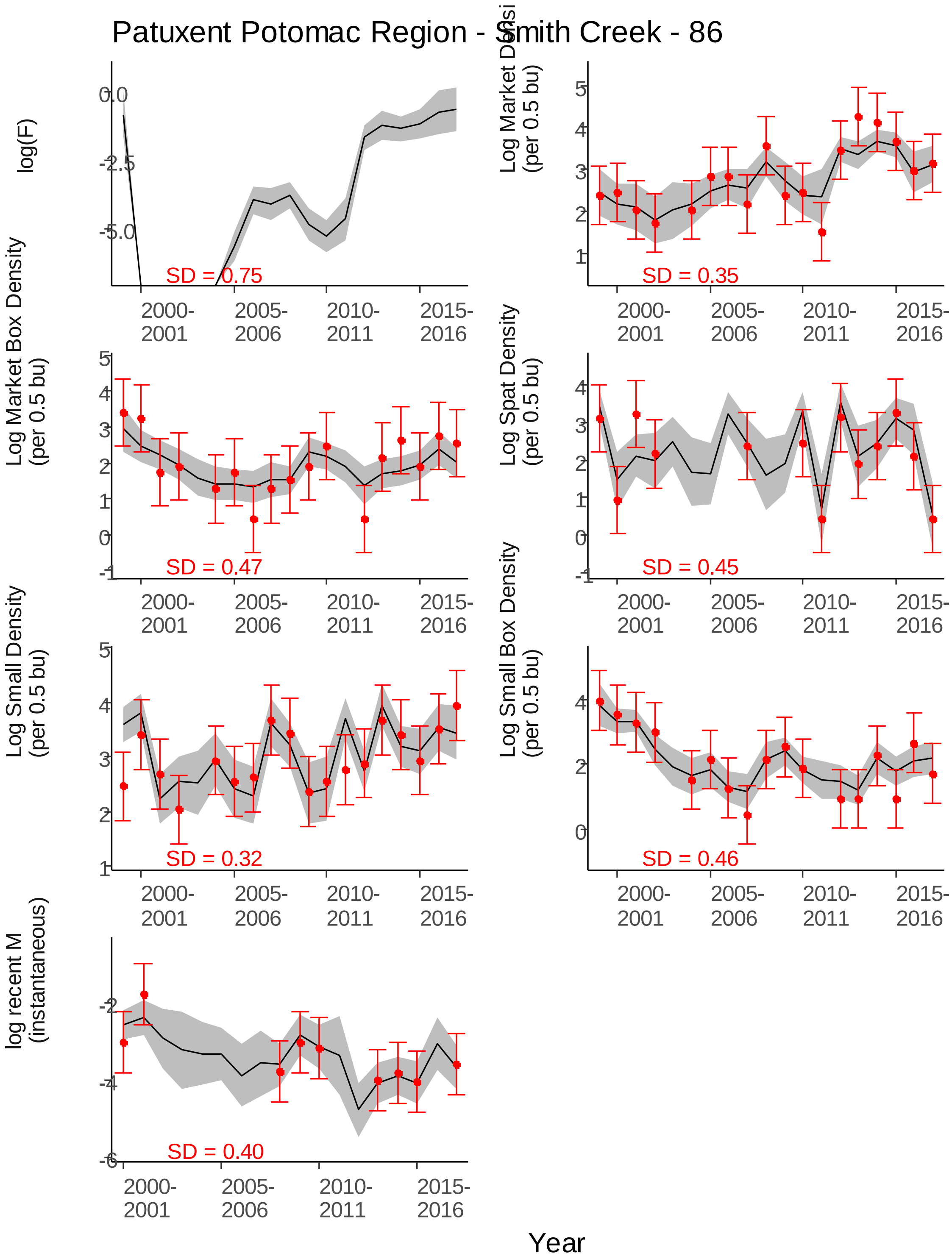

Figure 53. Estimated (line) and observed (points) for Smith Creek (NOAA code 86). Variable and symbol definitions are the same as Figures 25 and 28.

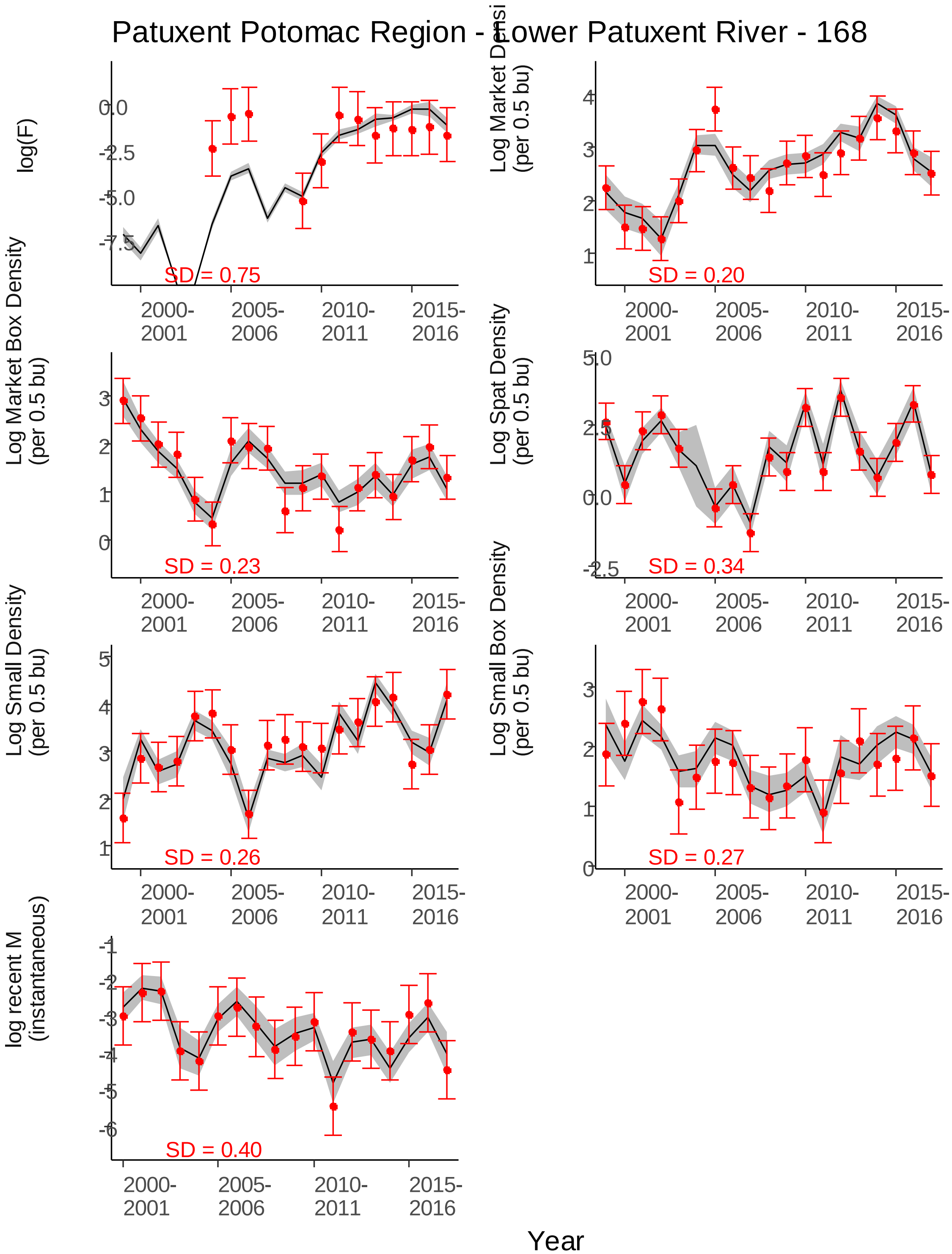

Figure 54. Estimated (line) and observed (points) for the lower Patuxent River (NOAA code 168). Variable and symbol definitions are the same as Figure 25.

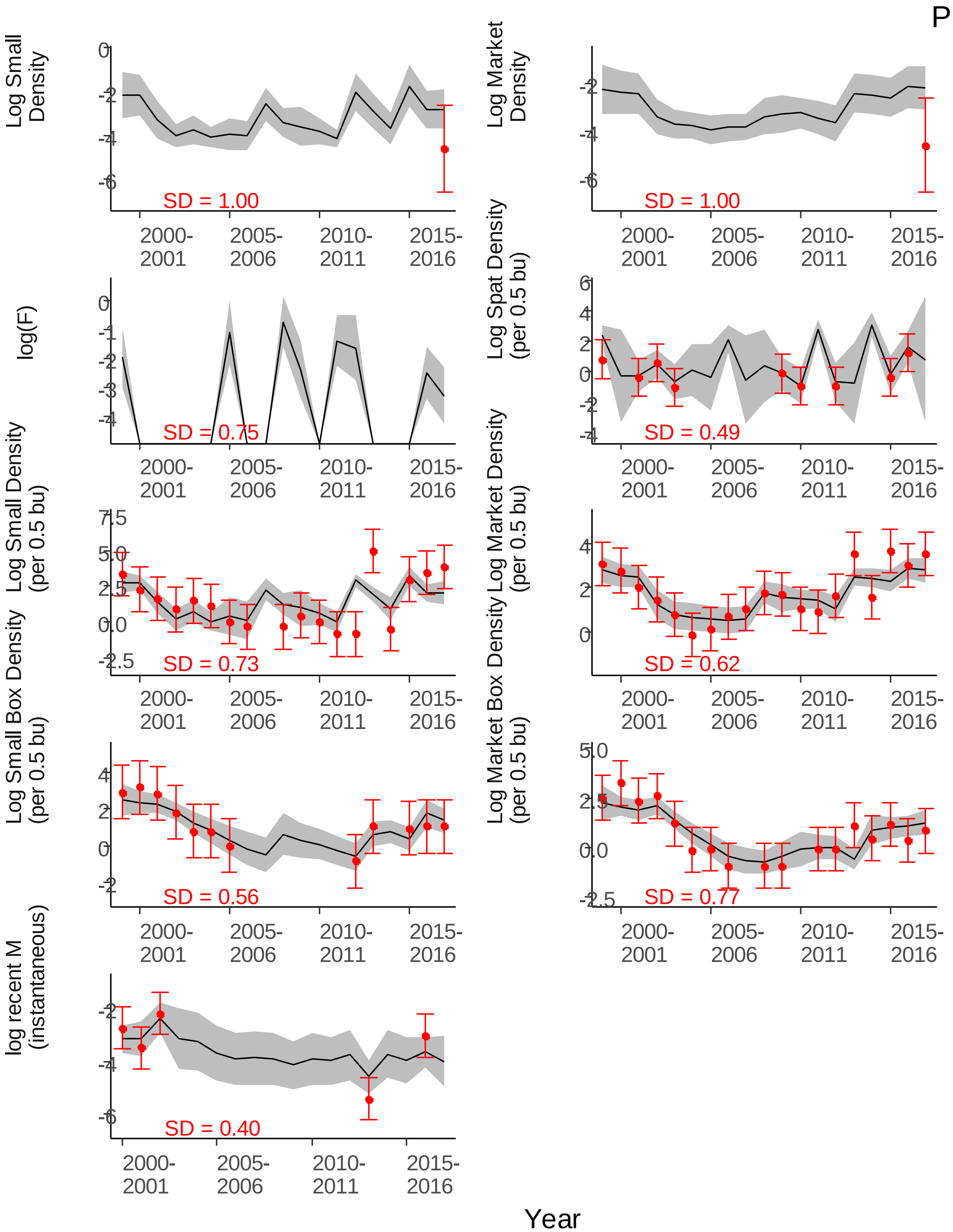

Figure 55. Estimated (line) and observed (points) for Breton and St. Clements Bays (NOAA code 174). Variable and symbol definitions are the same as Figures 25 and 28.

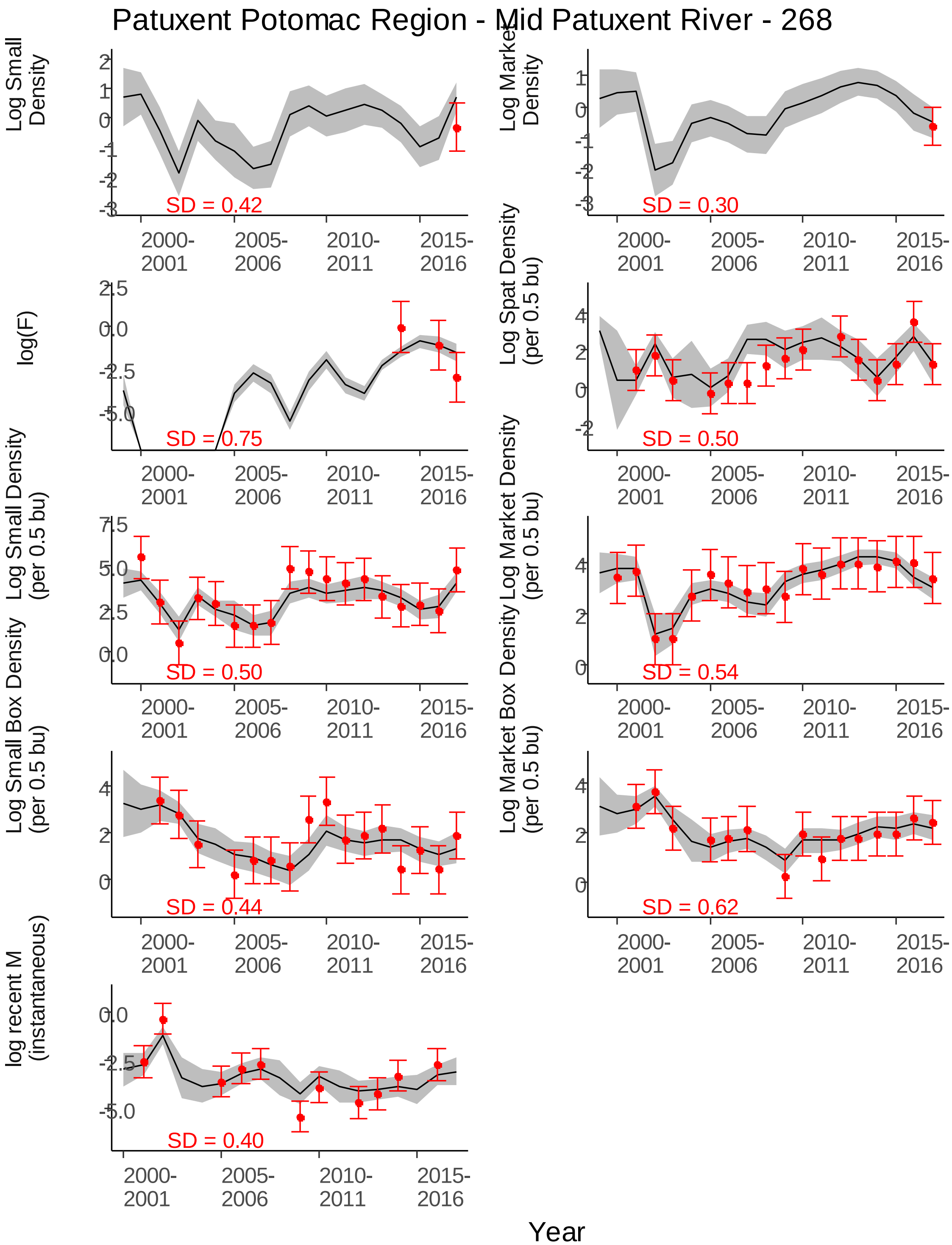

Figure 56. Estimated (line) and observed (points) for the middle Patuxent River (NOAA code 268). Variable and symbol definitions are the same as Figures 25 and 28.

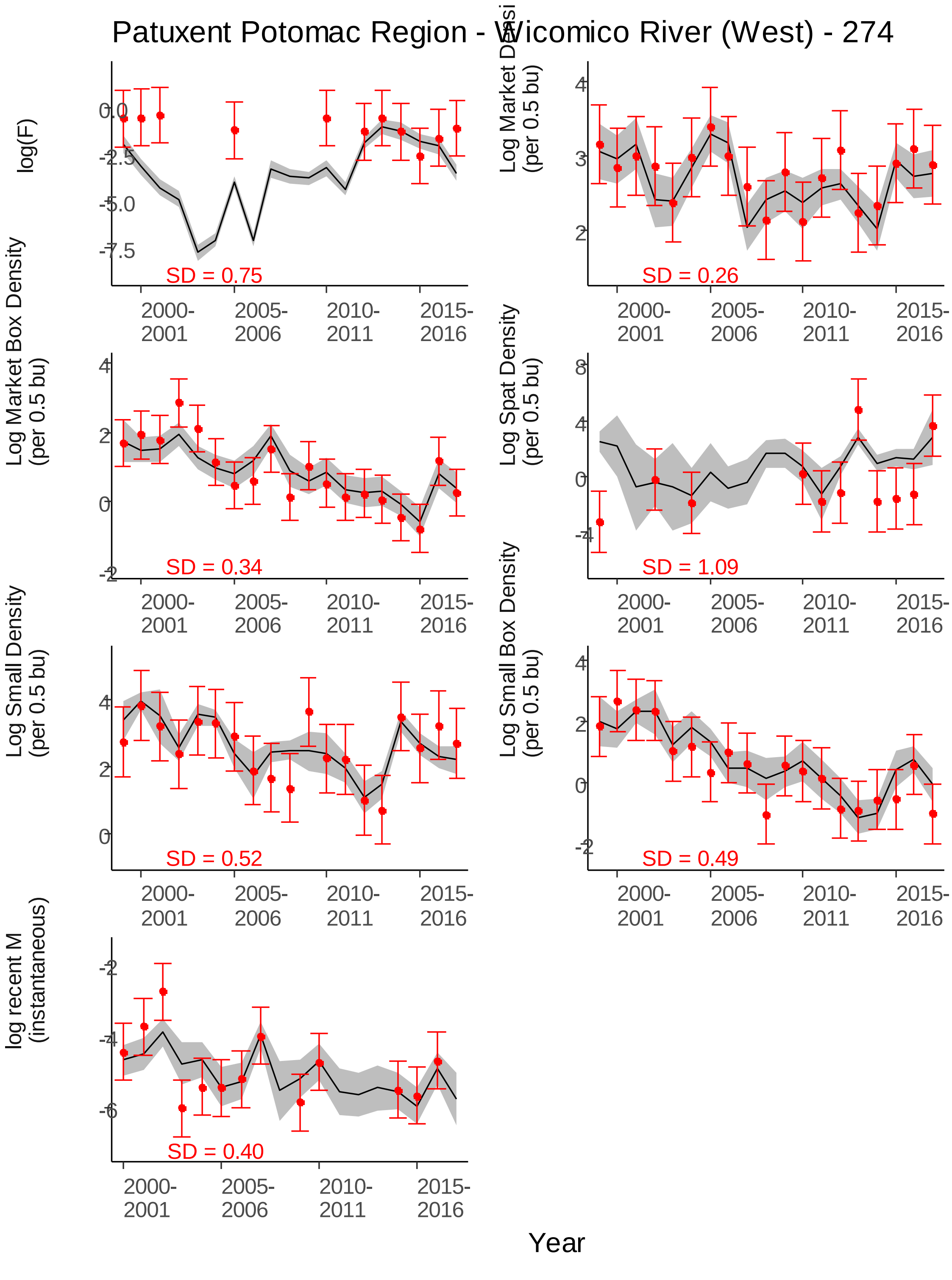

Figure 57. Estimated (line) and observed (points) for the upper Wicomico River (NOAA code 274). Variable and symbol definitions are the same as Figure 25.

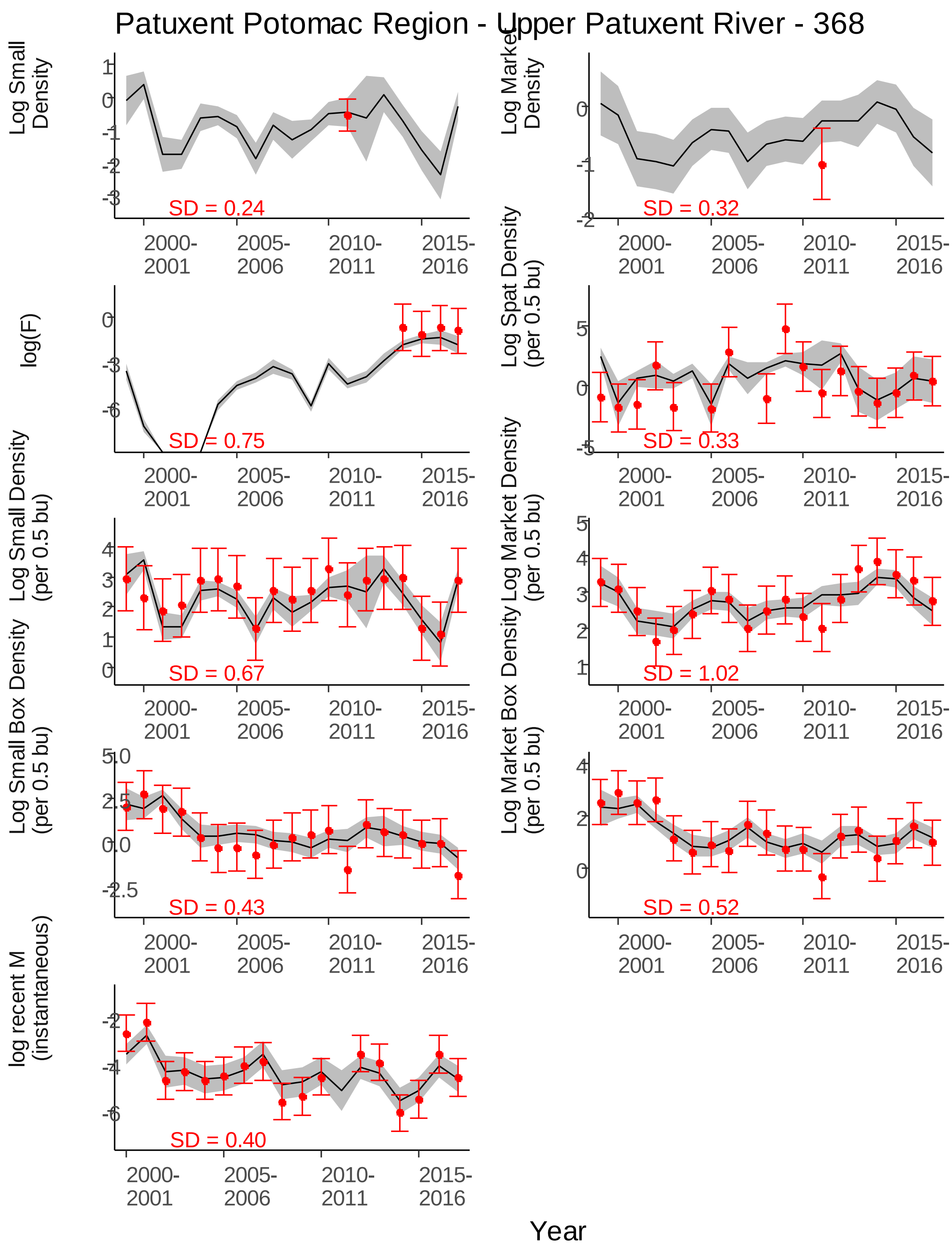

Figure 58. Estimated (line) and observed (points) for the upper Patuxent River (NOAA code 368). Variable and symbol definitions are the same as Figures 25 and 28.

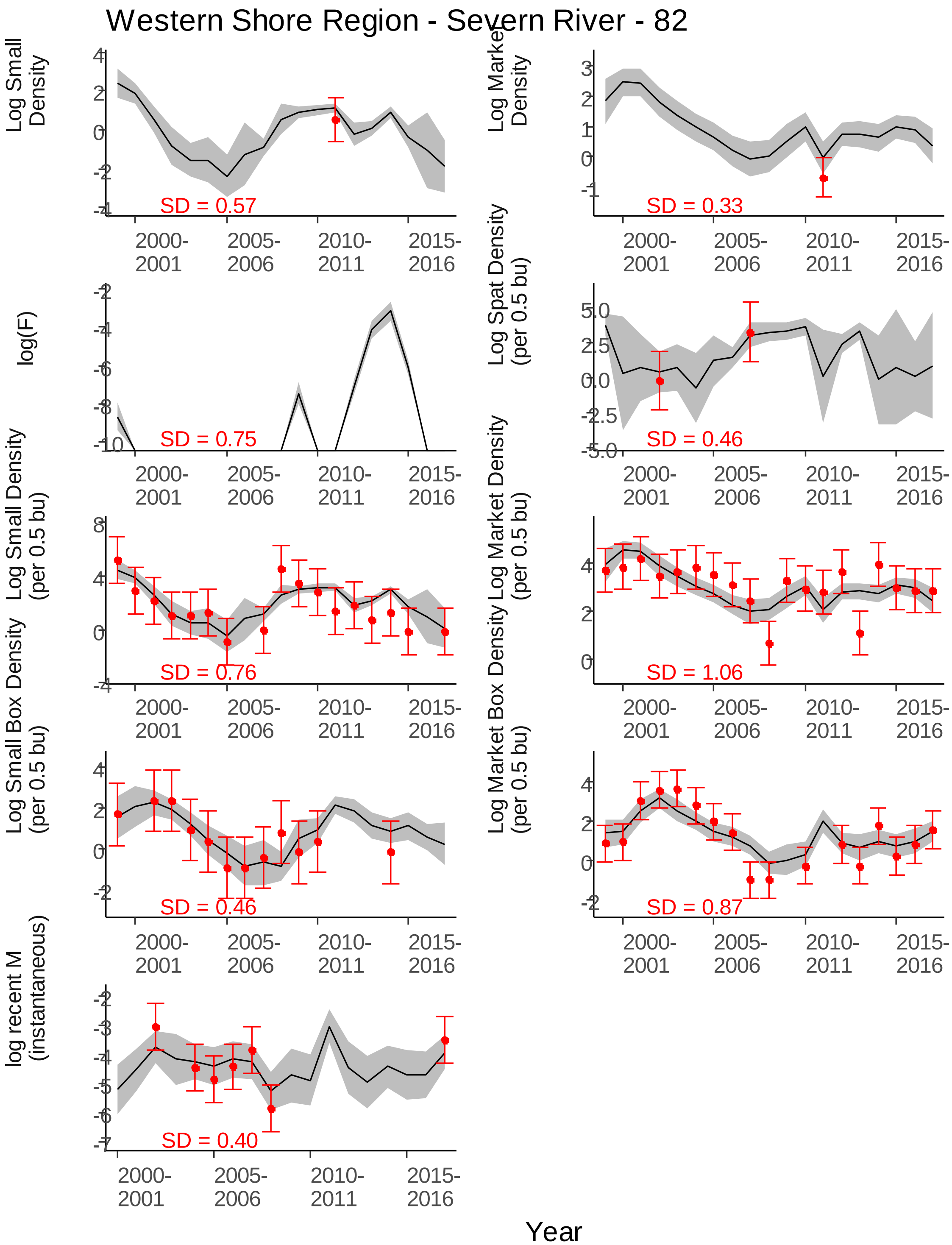

Figure 59. Estimated (line) and observed (points) for the Severn River (NOAA code 82). Variable and symbol definitions are the same as Figures 25 and 28.

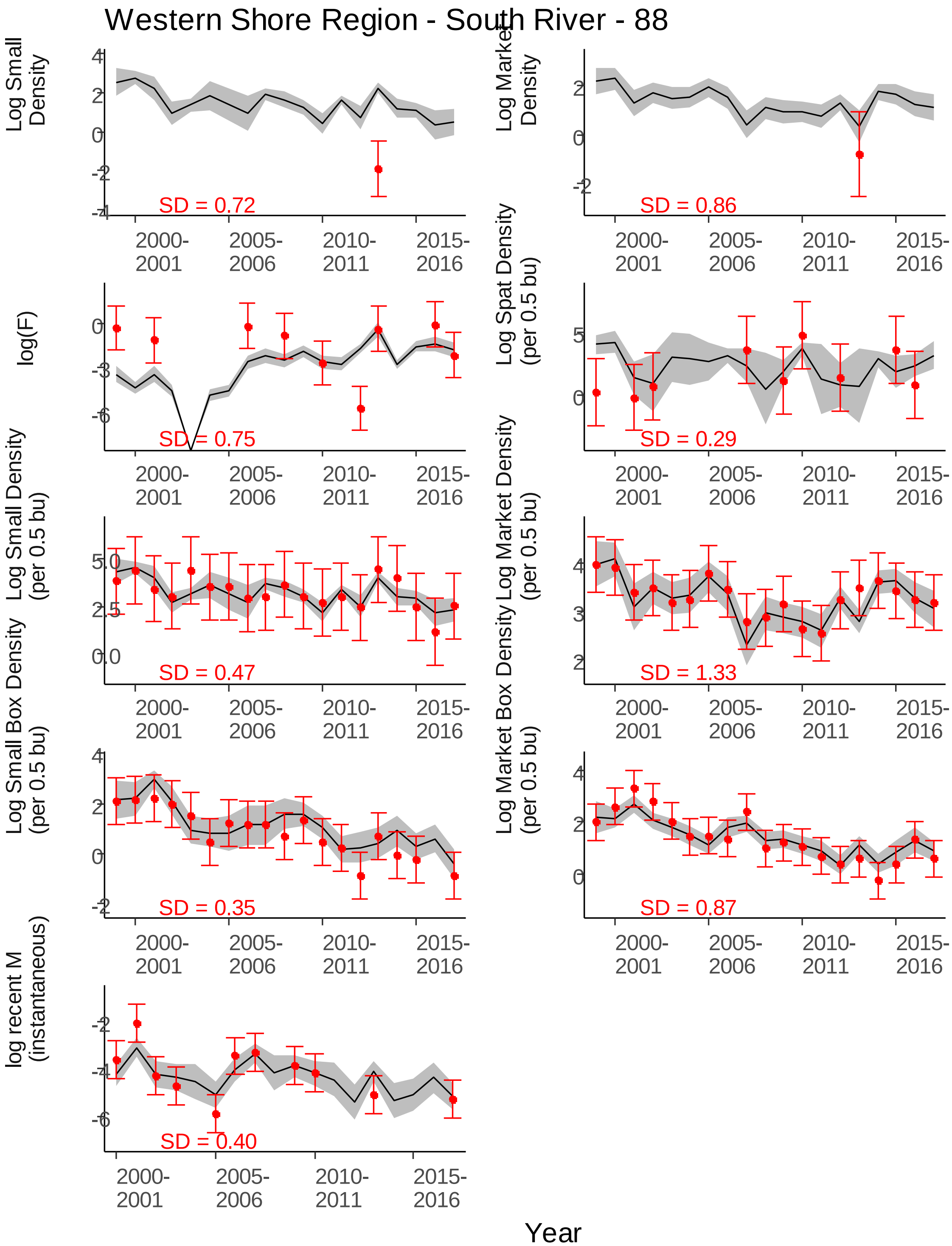

Figure 60. Estimated (line) and observed (points) for the South River (NOAA Code 88). Variable and symbol definitions are the same as Figures 25 and 28.

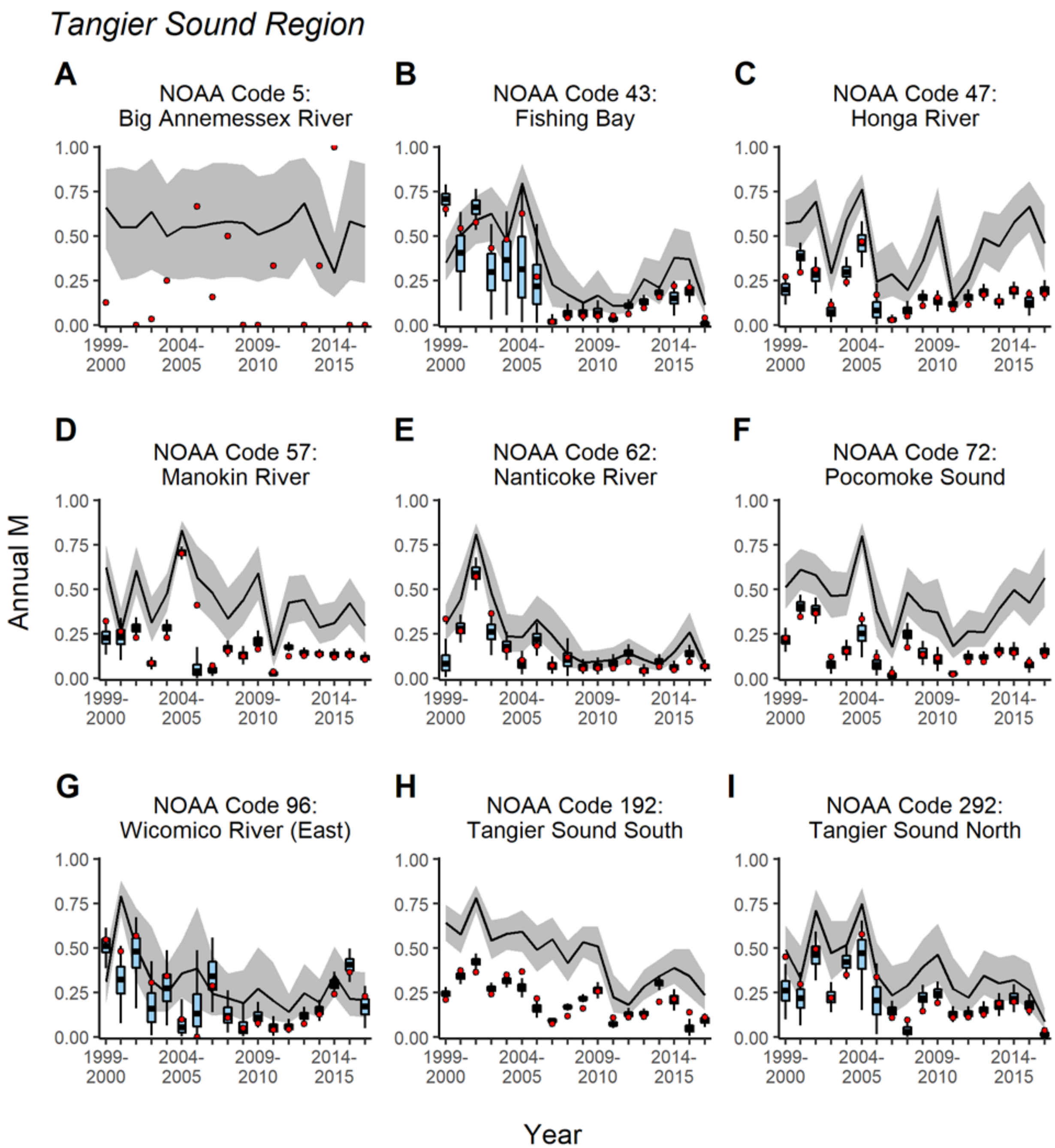

Figure 61. Annual natural mortality (M; fraction per year) by NOAA code for adult oysters in the Tangier Sound region as estimated by the assessment model (black line, approximate 95% confidence intervals shaded in gray), the box count method (red points), and the natural mortality model (boxplots shaded in light blue; the box represents the interquartile range, the line the median, and the whiskers 95% credibility intervals). The year labels correspond with the assessment model year, and the second year on these labels corresponds with the calendar year of when the natural mortality occurred. Natural mortality from the natural mortality model was not estimated for NOAA code 5 because there was not sufficient data.

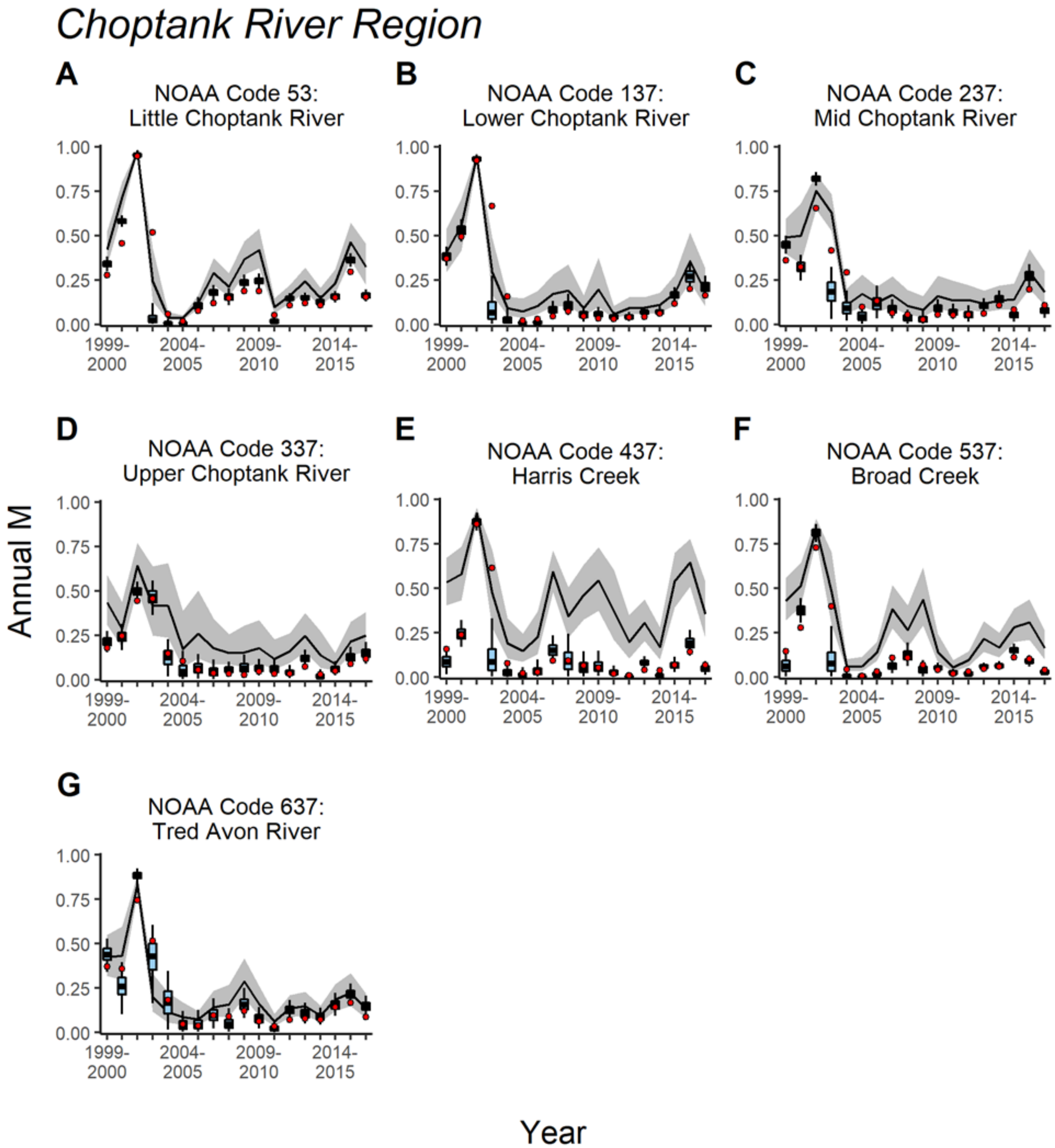

Figure 62. Annual natural mortality (M; fraction per year) by NOAA code for adult oysters in the Choptank region. Symbol descriptions as in Figure 61.

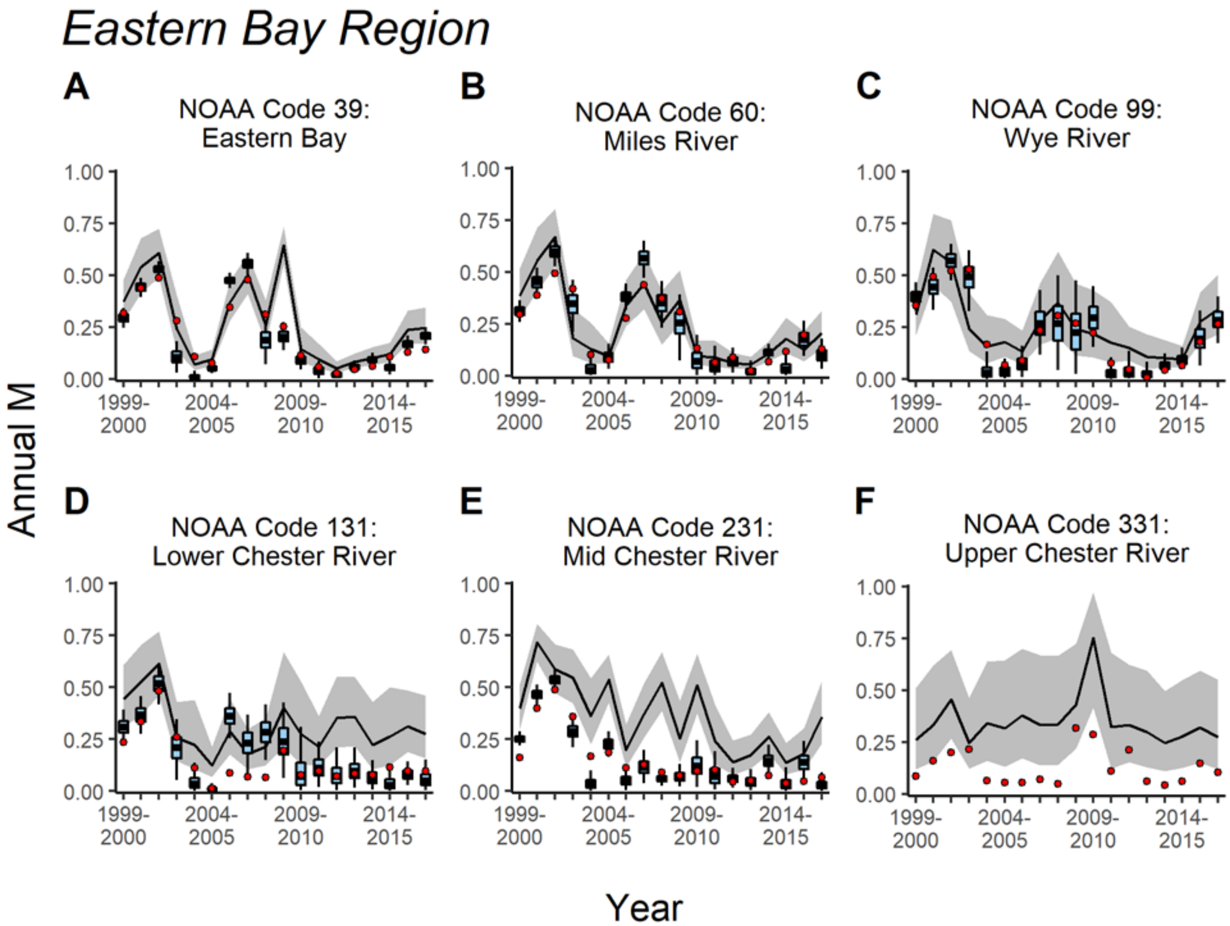

Figure 63. Annual natural mortality (M; fraction per year) by NOAA code for adult oysters in the Eastern Bay region. Symbol descriptions as in Figure 61. Natural mortality from the natural mortality model was not calculated for NOAA code 331 because there was not sufficient data.

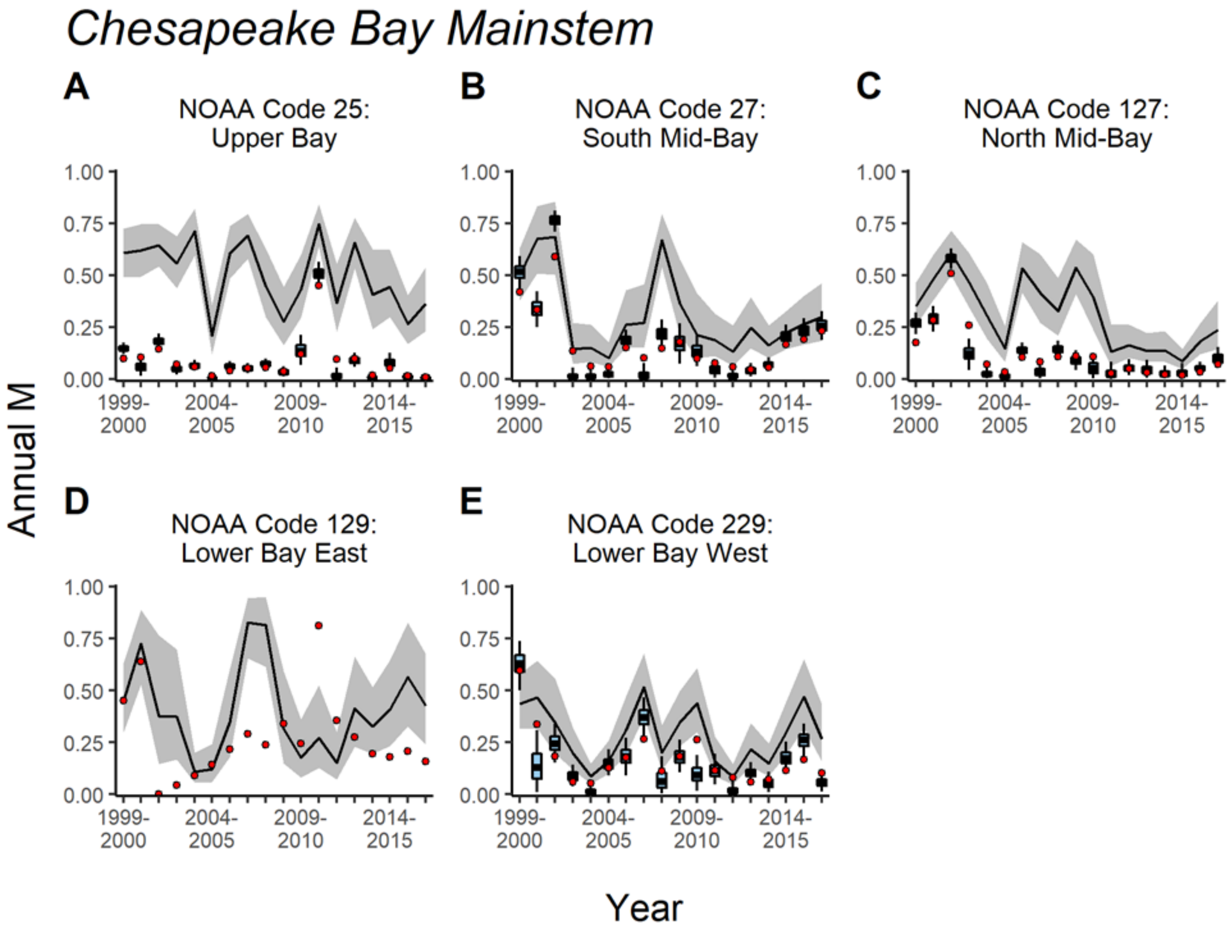

Figure 64. Annual natural mortality (M; fraction per year) by NOAA code for adult oysters in the Chesapeake Bay Mainstem region. Symbol descriptions as in Figure 61. Natural mortality from the natural mortality model was not calculated for NOAA code 129 because there was not sufficient data.

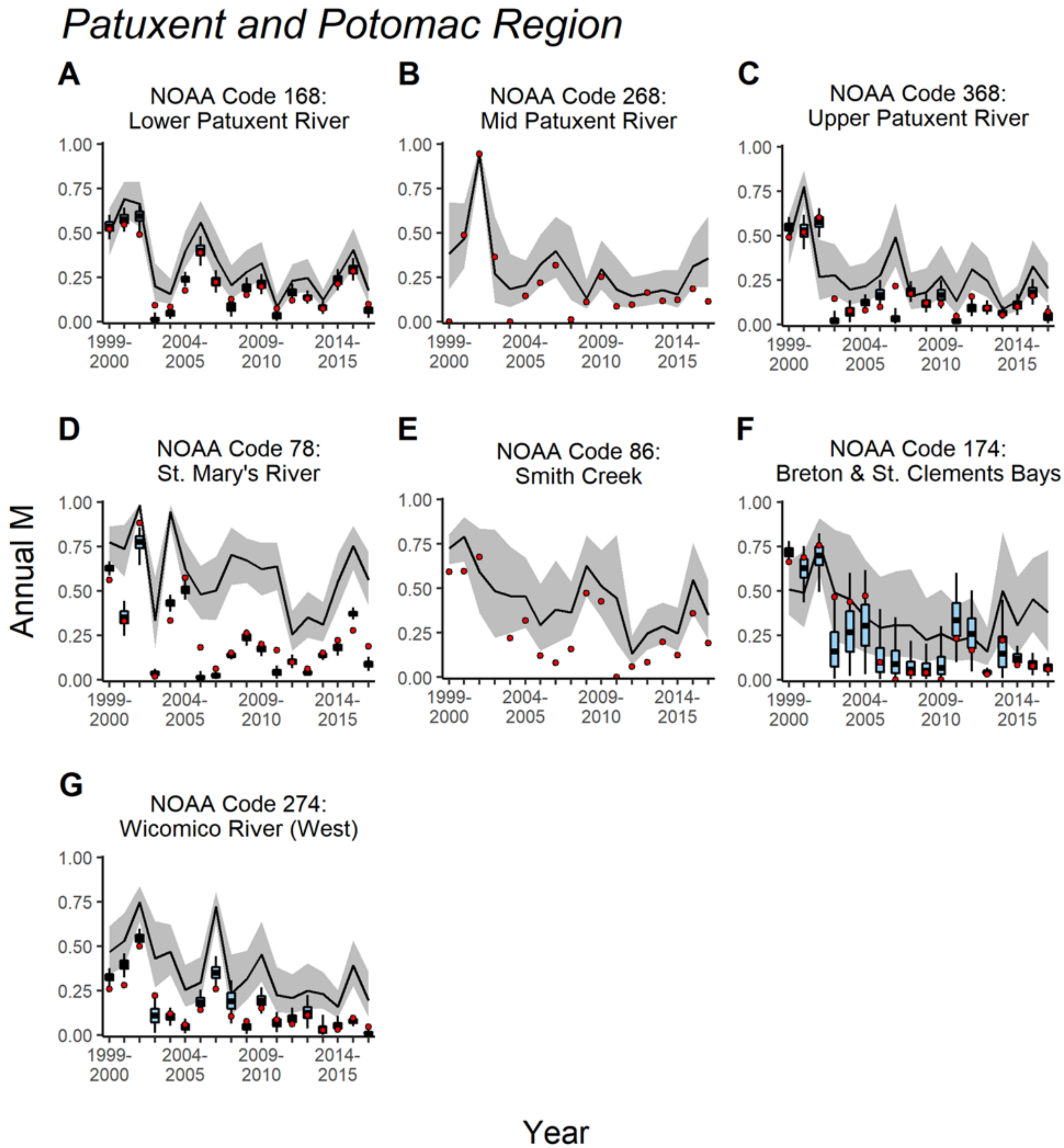

Figure 65. Annual natural mortality (M; fraction per year) by NOAA code for adult oysters in the Patuxent and Potomac region. Symbol descriptions as in Figure 61. Natural mortality from the natural mortality model was not calculated for NOAA codes 268 and 86 because there was not sufficient data.

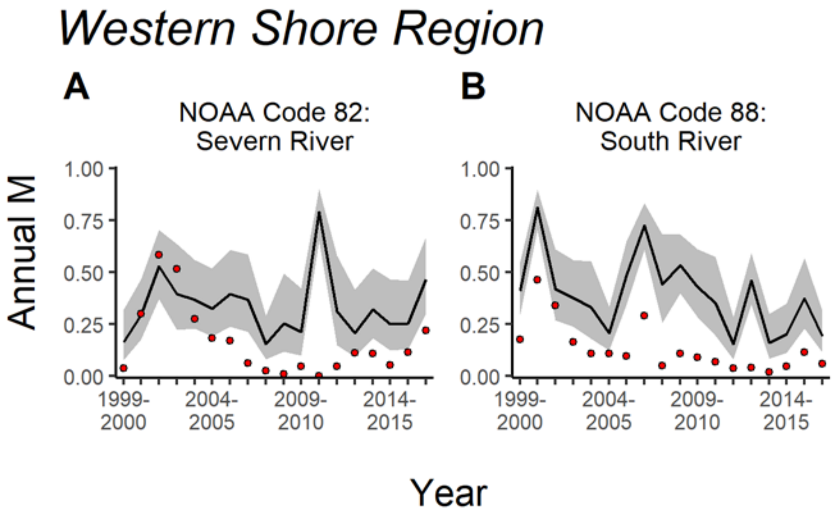

Figure 66. Annual natural mortality (M; fraction per year) by NOAA code for adult oysters in the Western Shore region. Symbol descriptions as in Figure 61. Natural mortality from the natural mortality model was not calculated for NOAA codes 82 and 88 because there was not sufficient data.

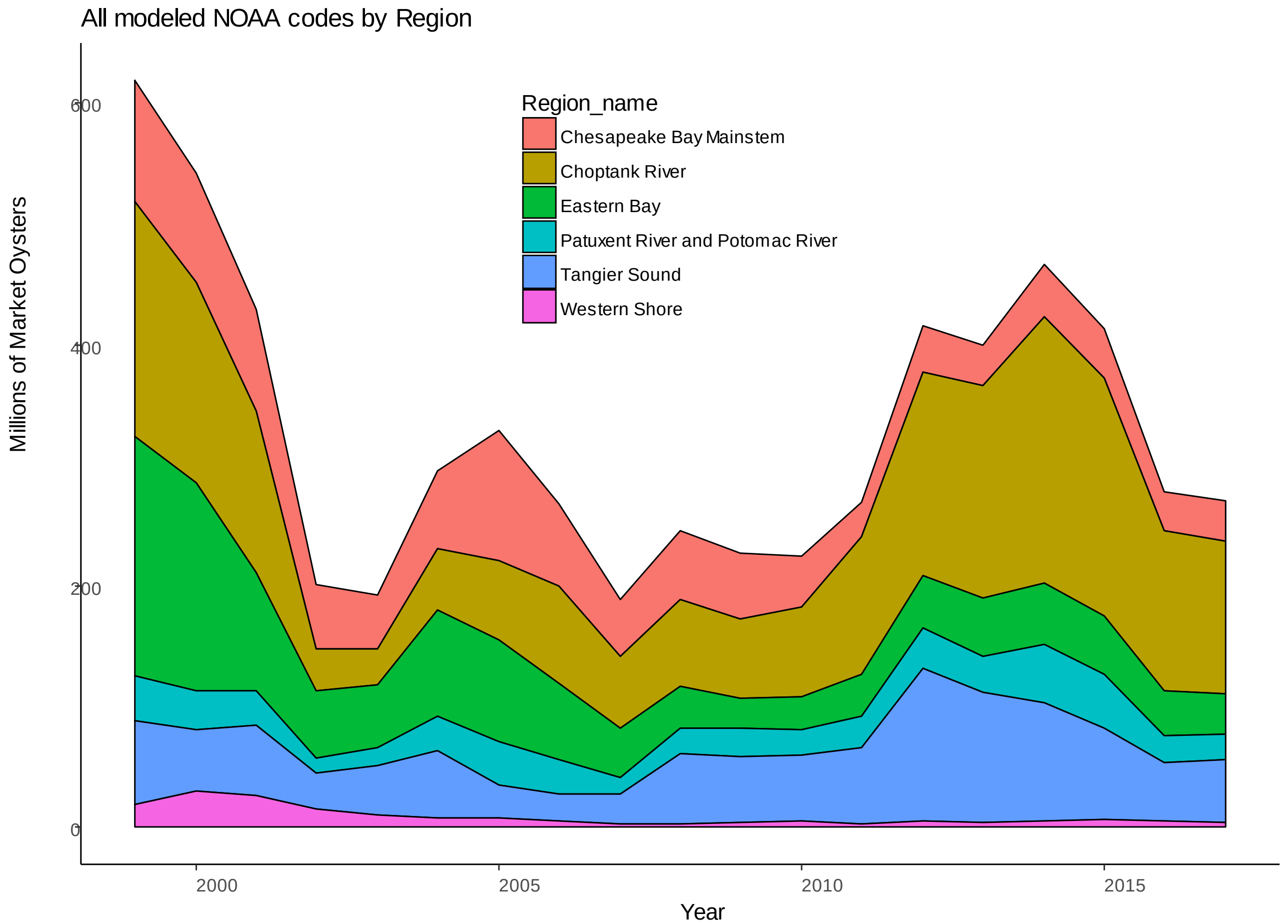

Figure 67. Estimated market oyster abundance among regions in the portion of the Chesapeake Bay under Maryland management during 1999-2017.

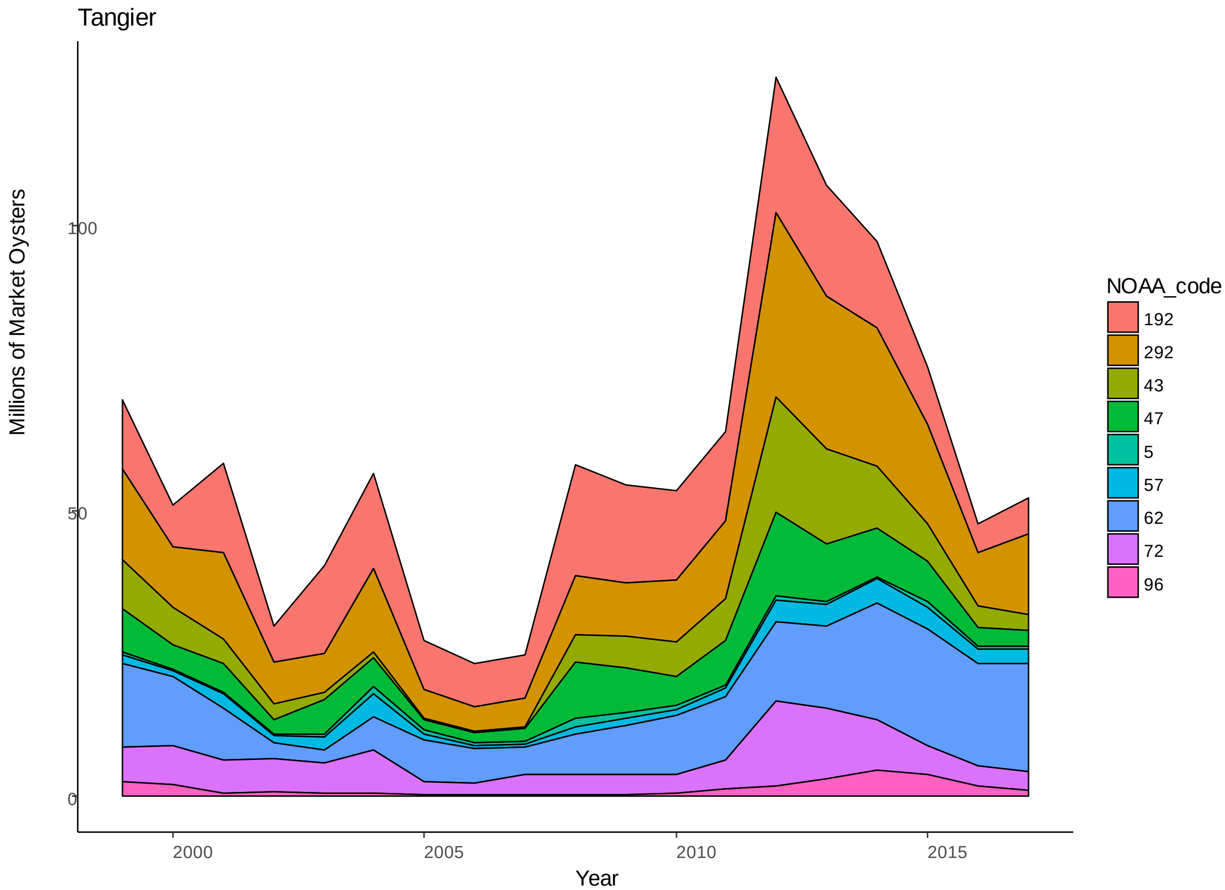

Figure 68. Estimated market oyster abundance among NOAA codes in the Tangier Sound Region under Maryland management during 1999-2017.

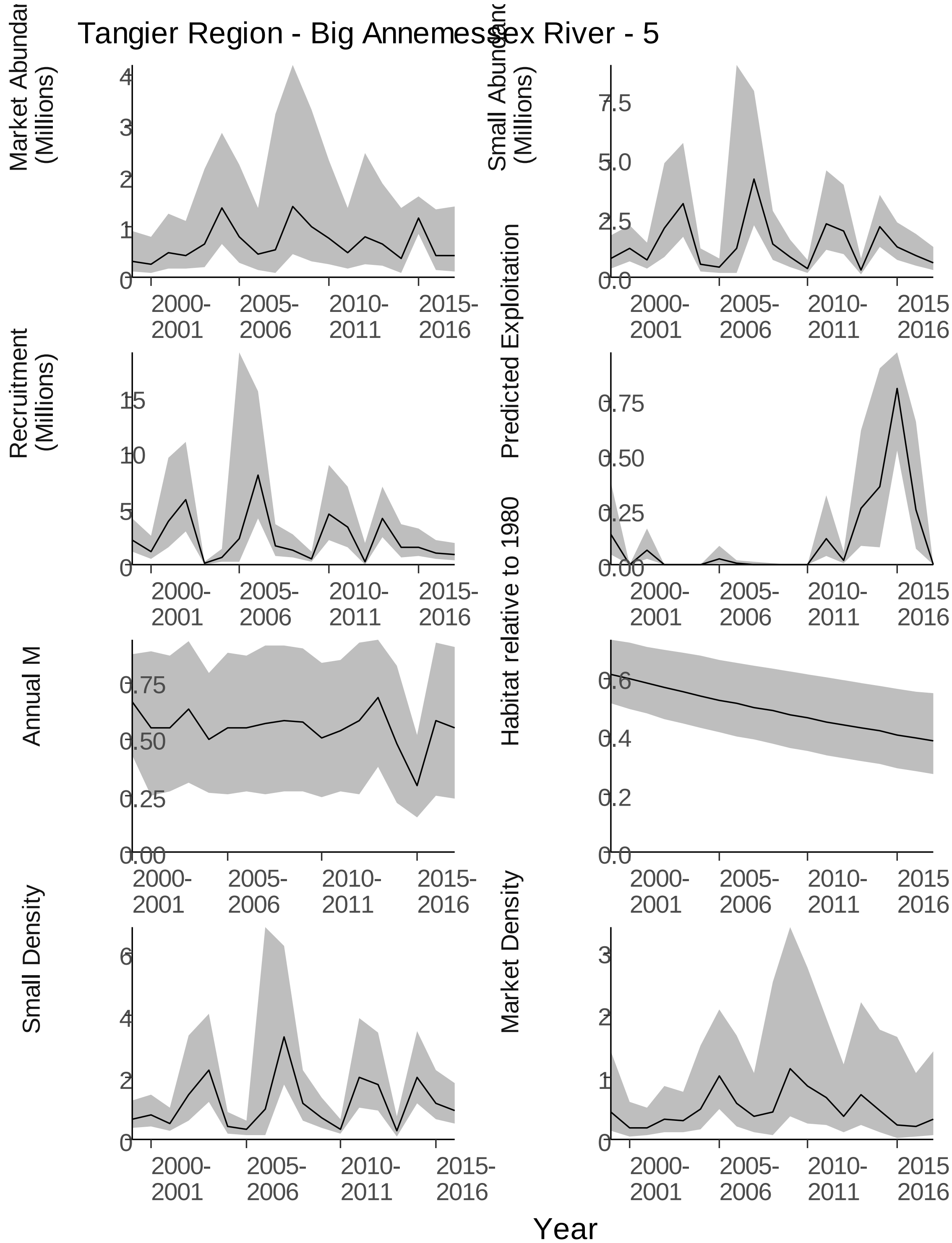

Figure 69. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Big Annemessex River (NOAA code 5).

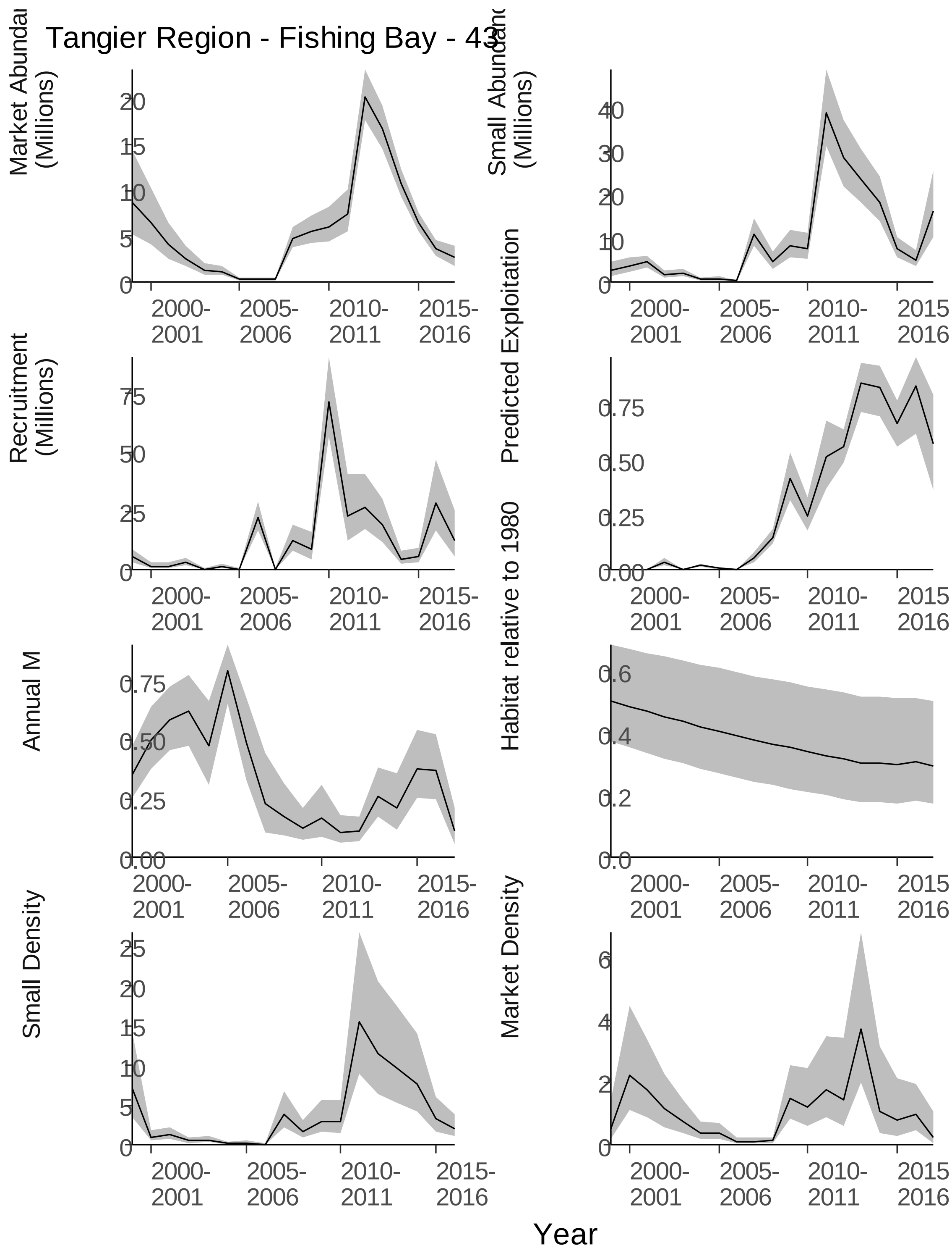

Figure 70. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in Fishing Bay (NOAA code 43).

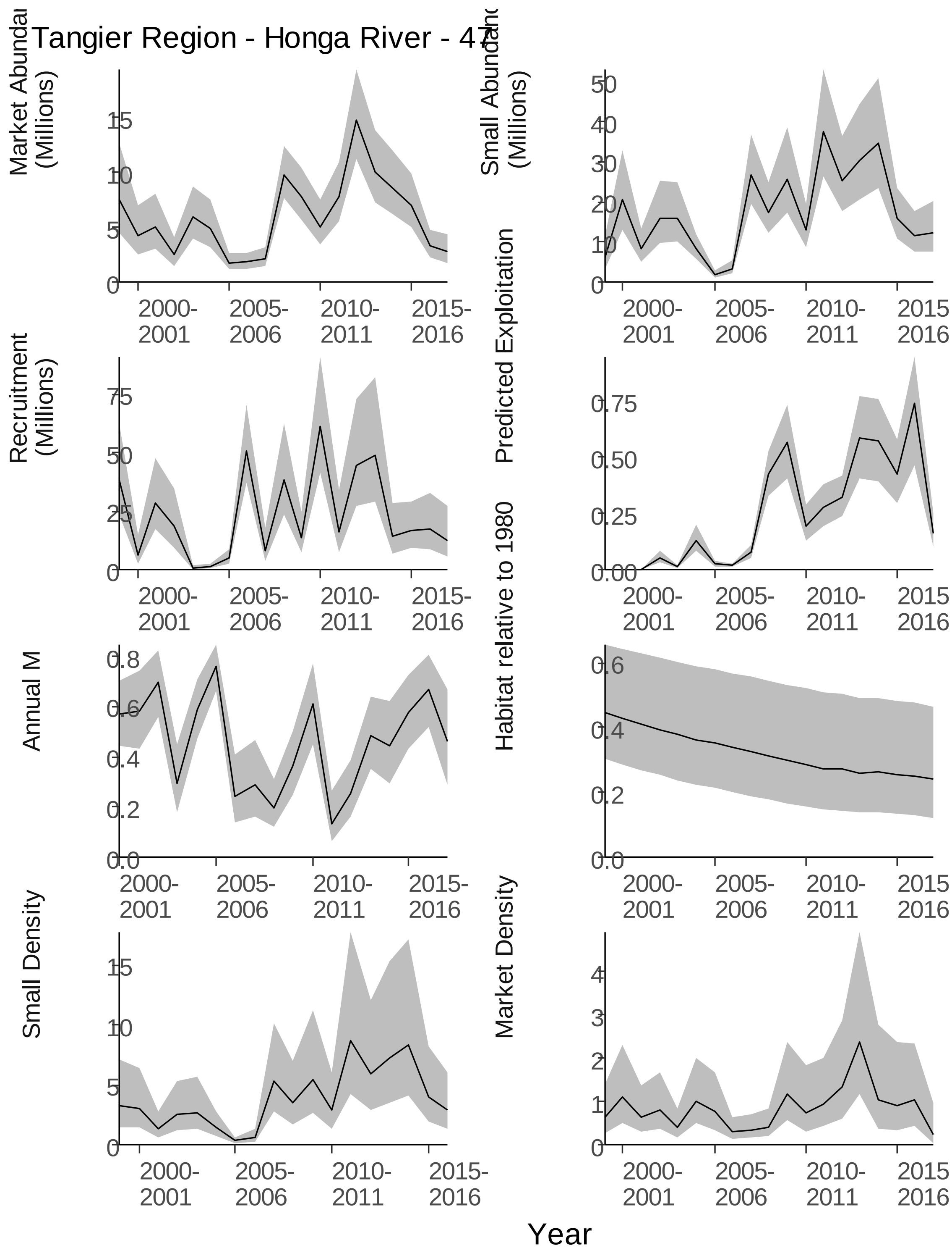

Figure 71. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Honga River (NOAA code 47).

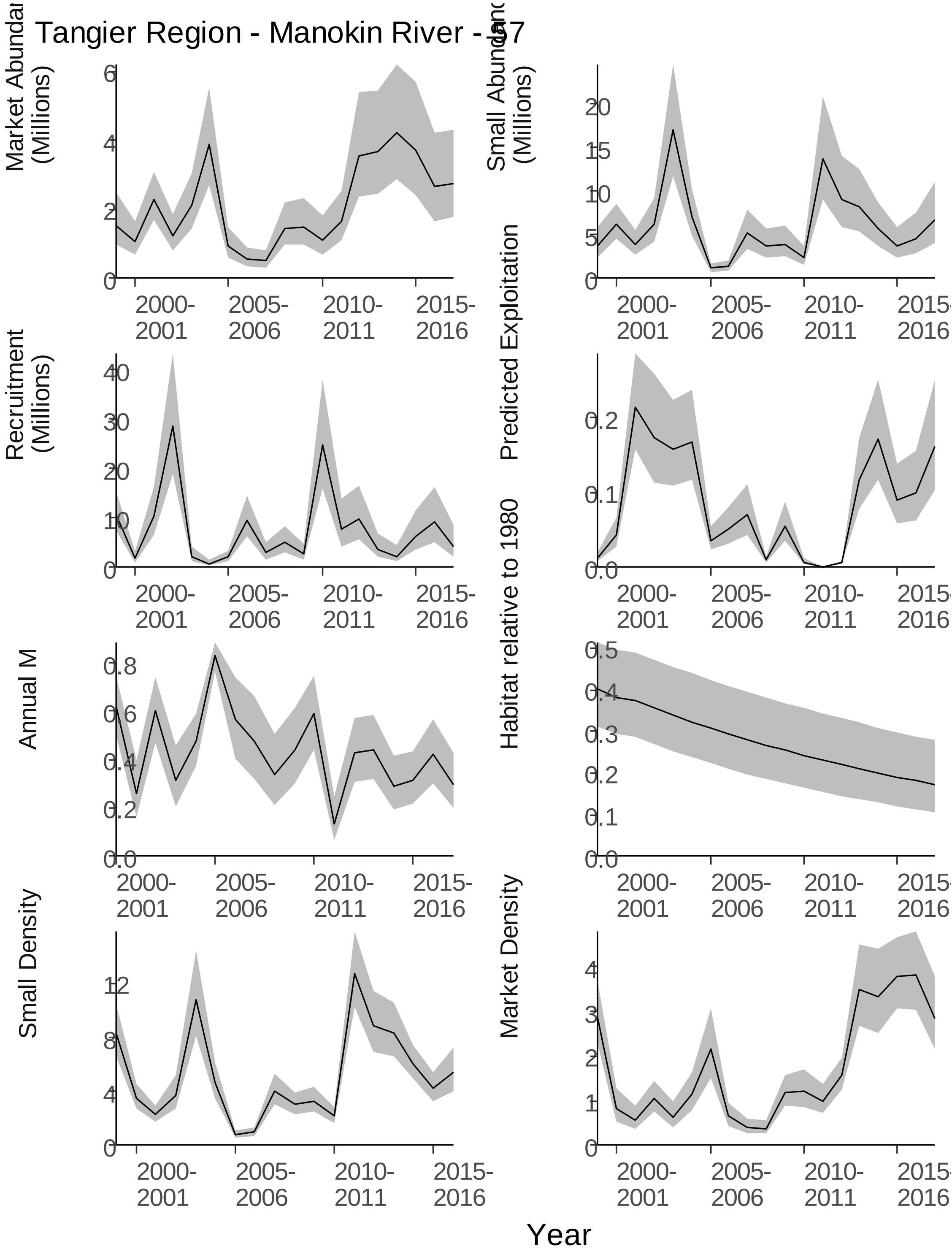

Figure 72. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Manokin River (NOAA code 57).

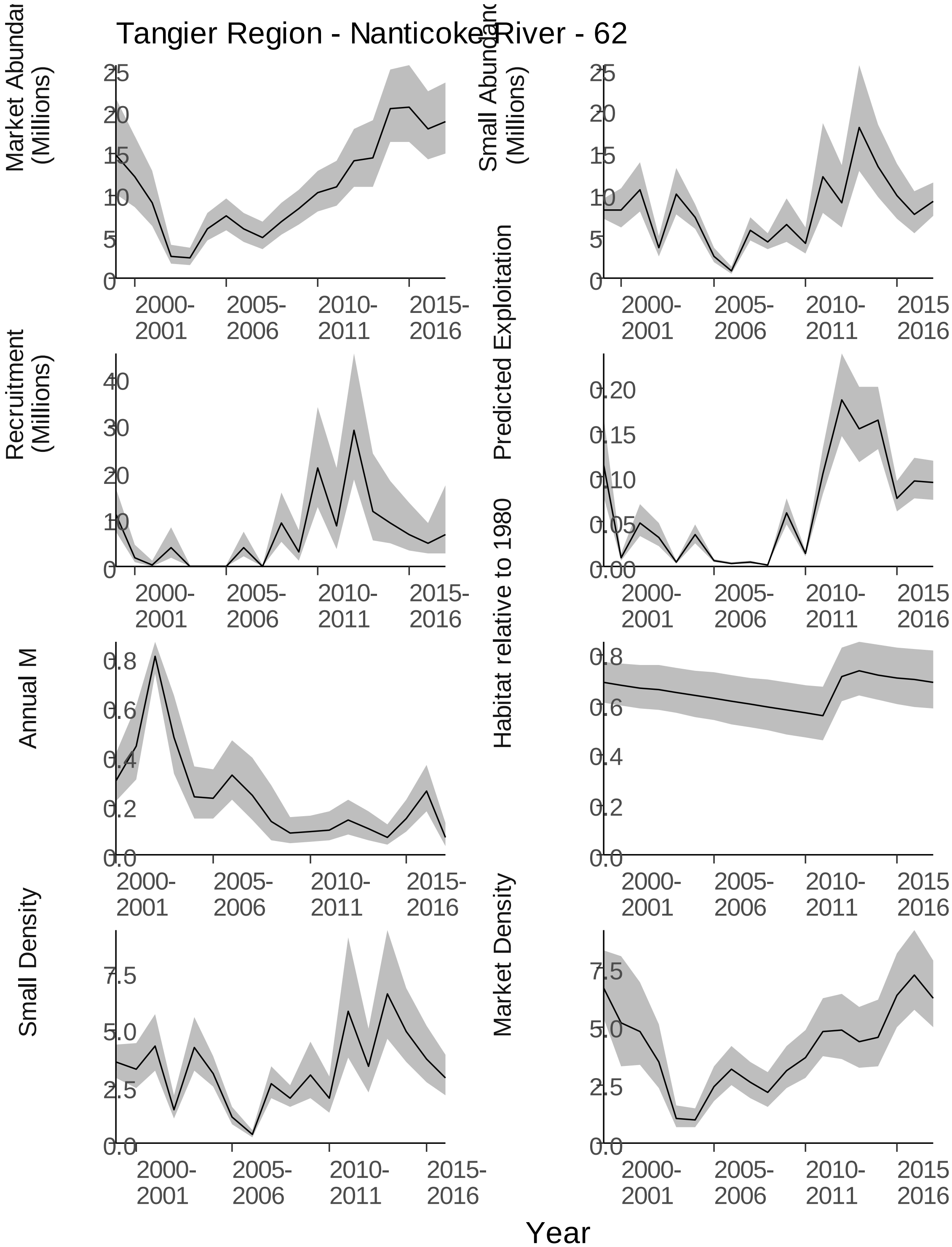

Figure 73. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Nanticoke River (NOAA code 62).

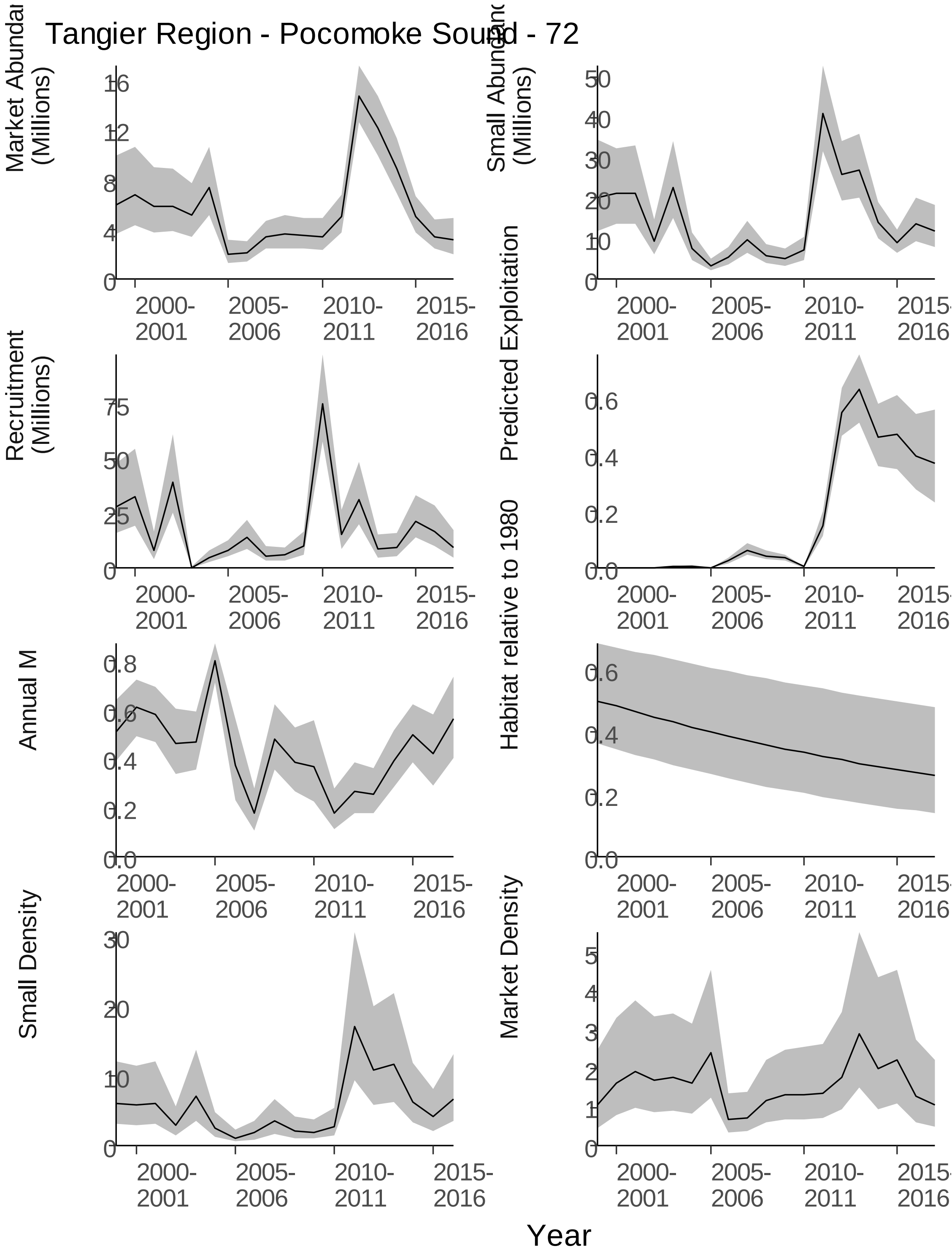

Figure 74. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in Pocomoke Sound (NOAA code 72).

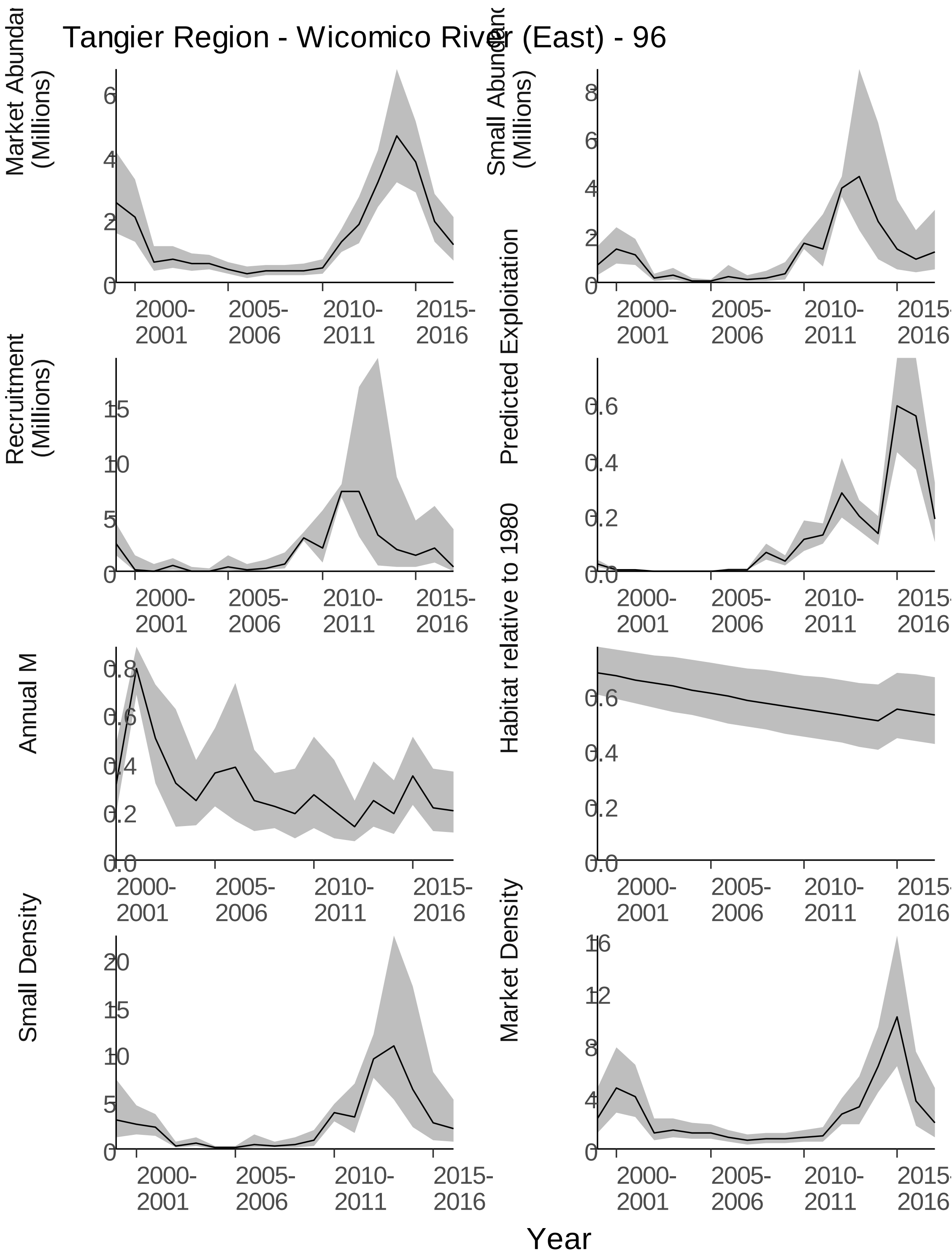

Figure 75. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Wicomico River (NOAA code 96).

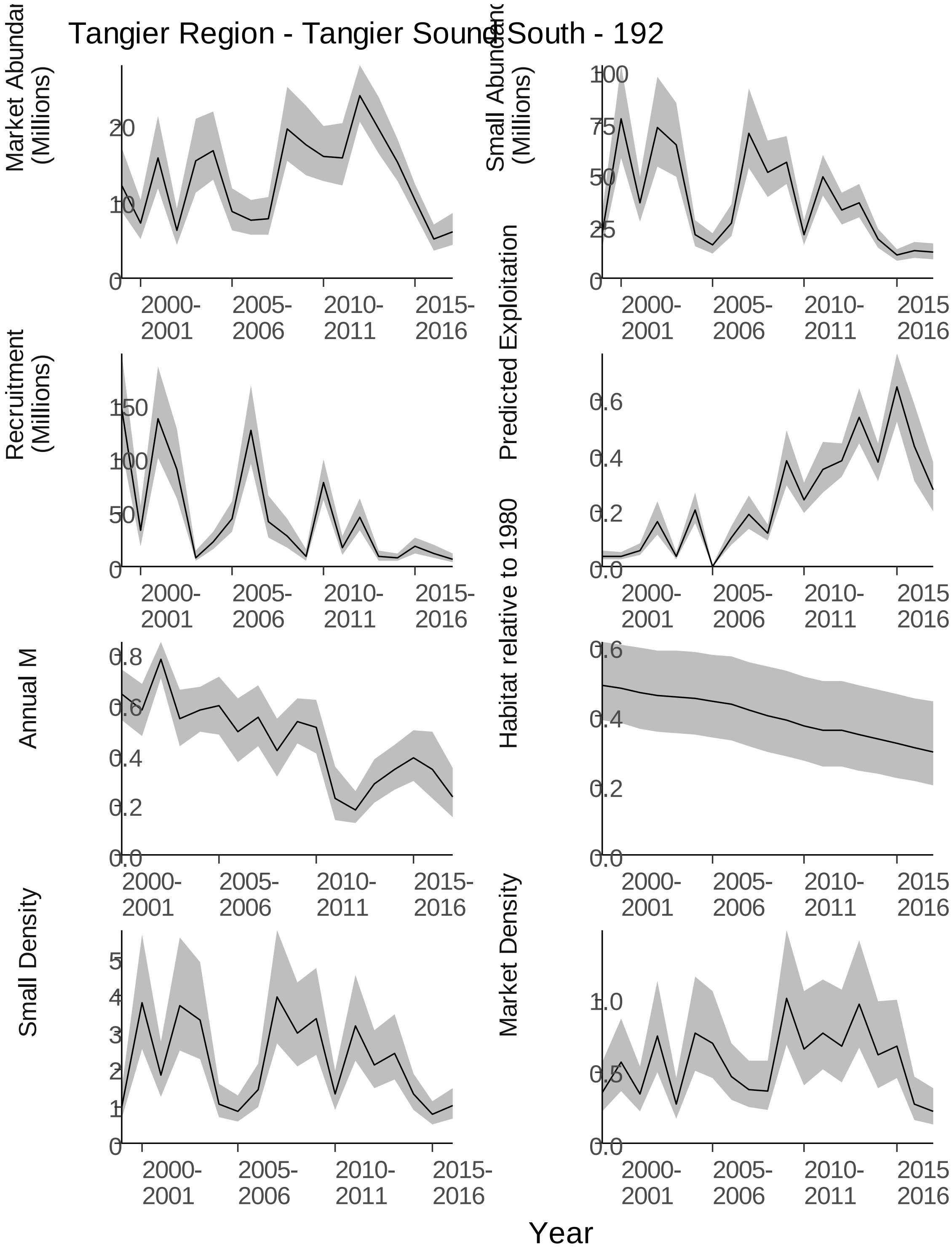

Figure 76. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in lower Tangier Sound (NOAA code 192).

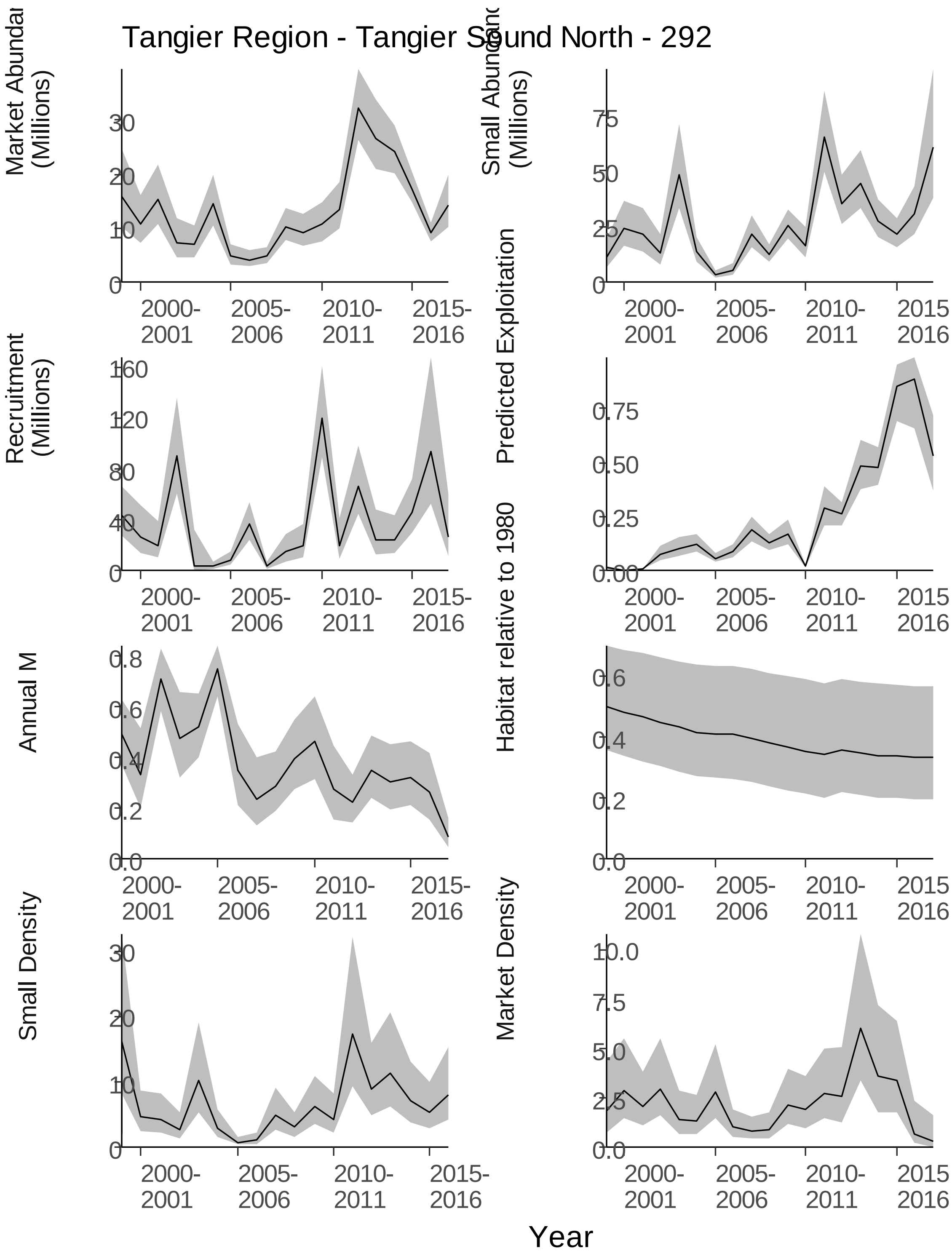

Figure 77. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in upper Tangier Sound (NOAA code 292).

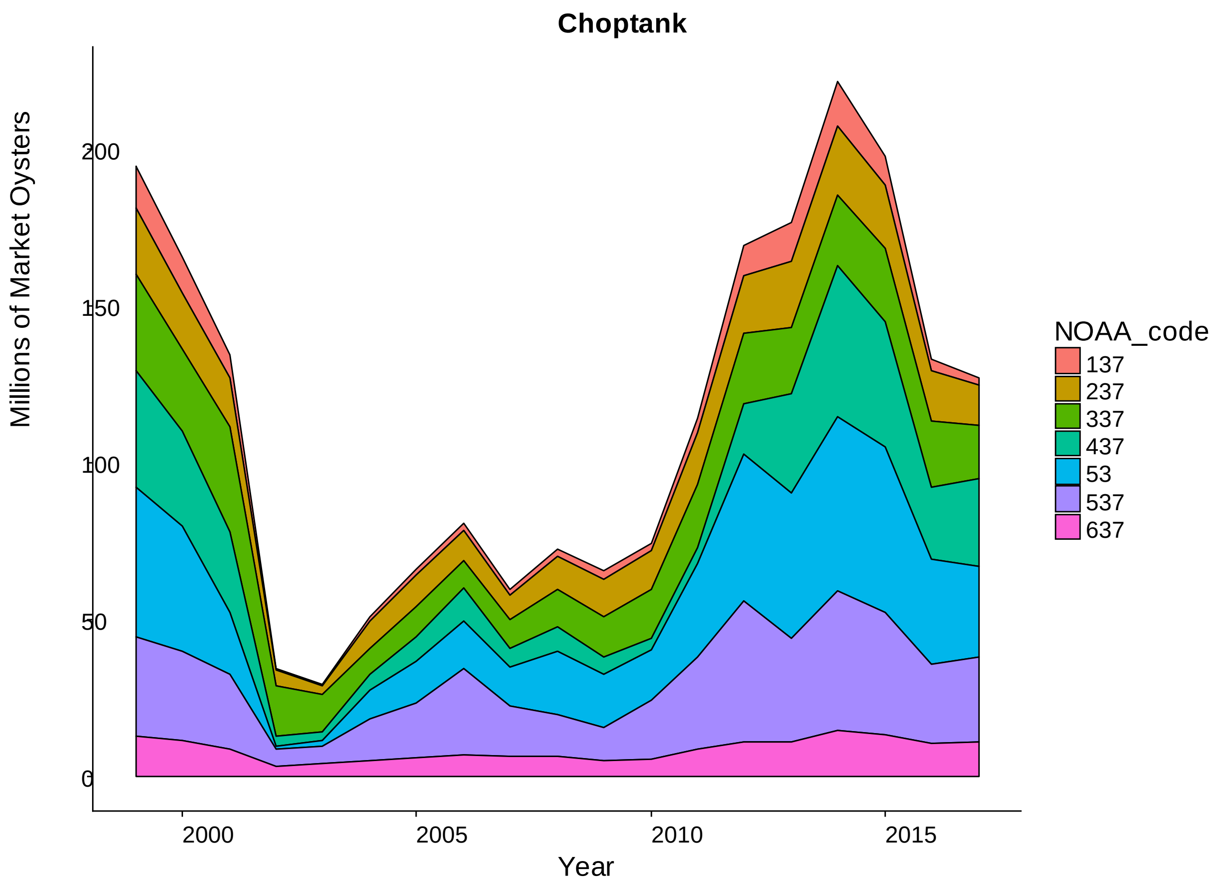

Figure 78. Estimated market oyster abundance among all NOAA codes in the Choptank region under Maryland management during 1999-2017.

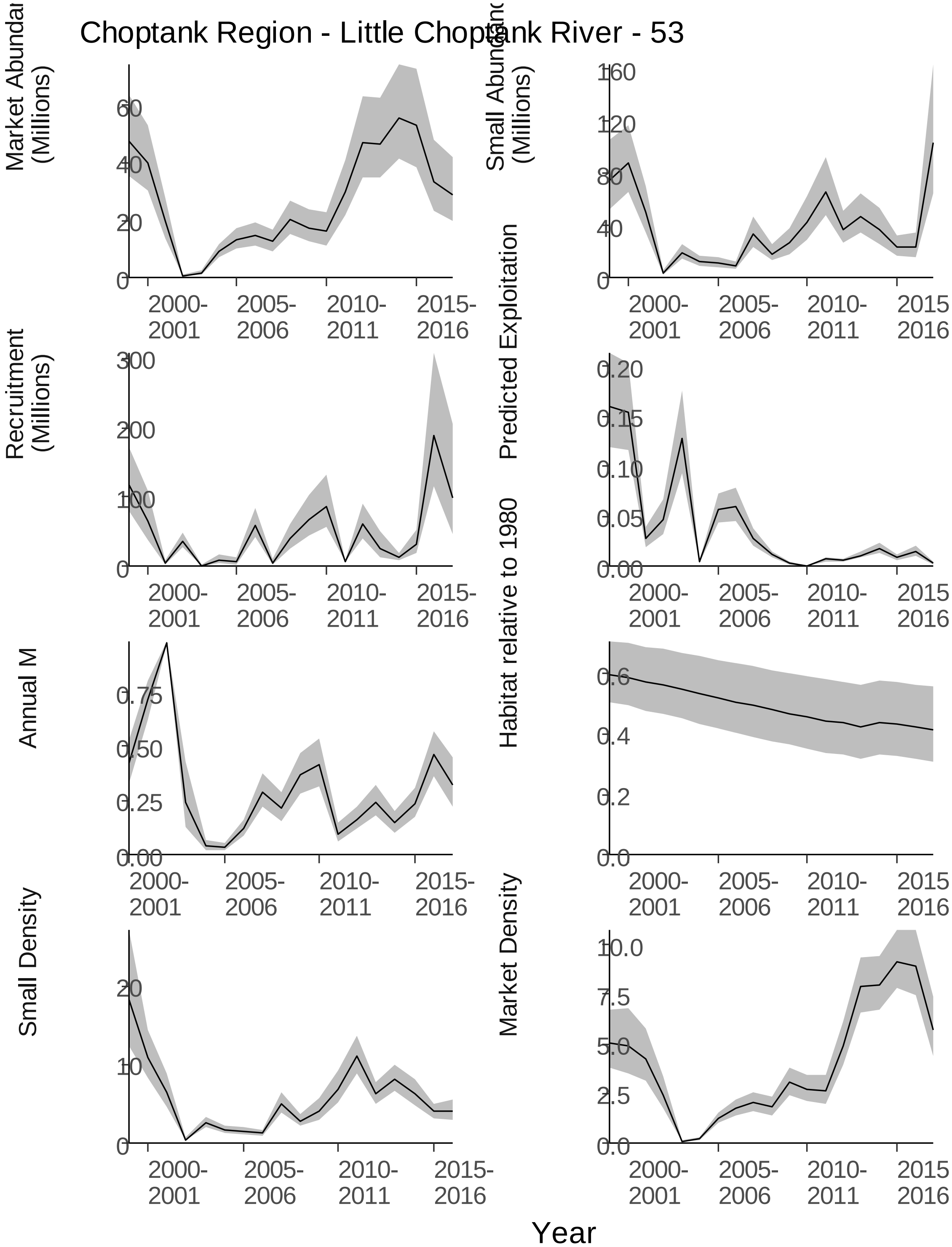

Figure 79. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Little Choptank River (NOAA code 53).

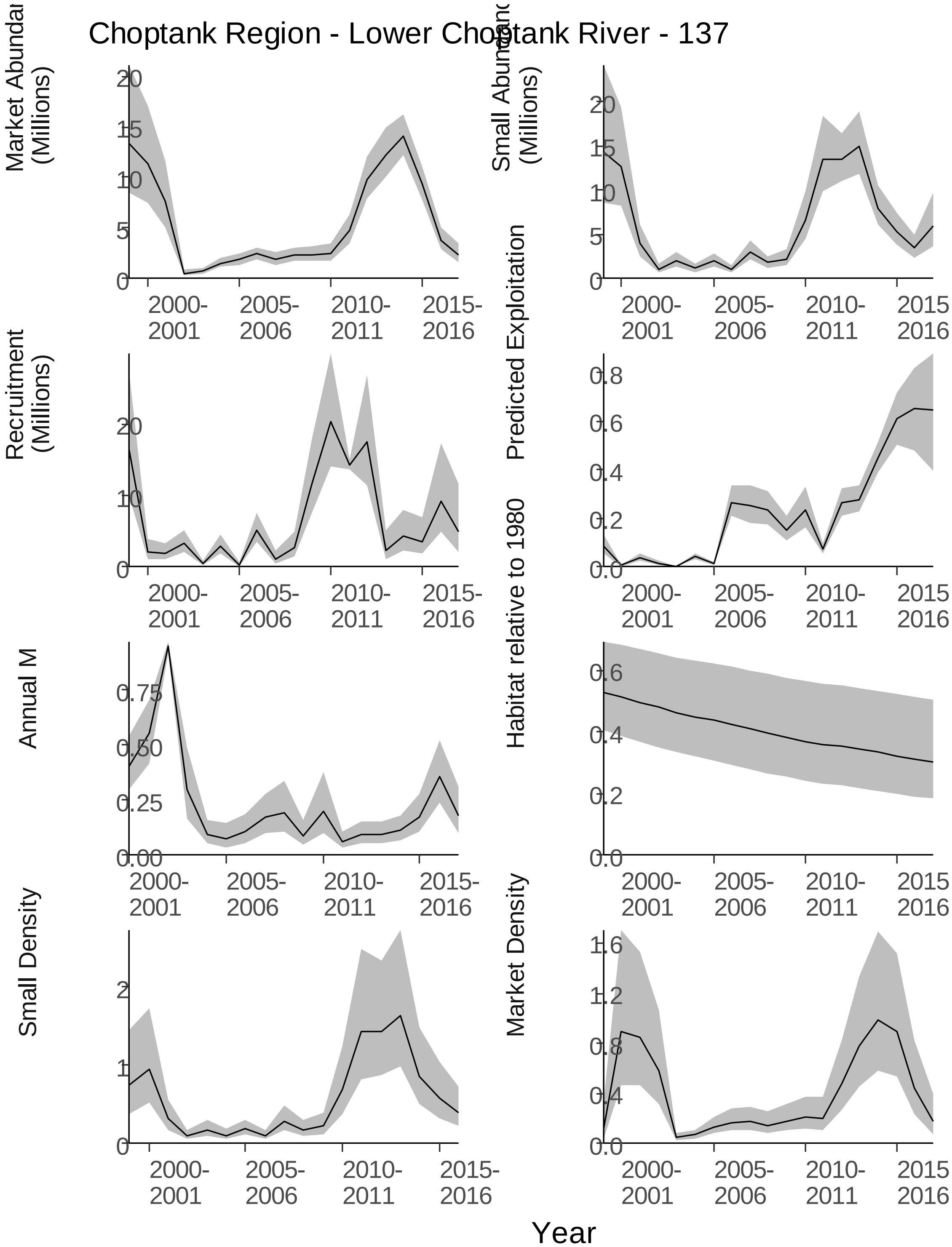

Figure 80. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Lower Choptank River (NOAA code 137).

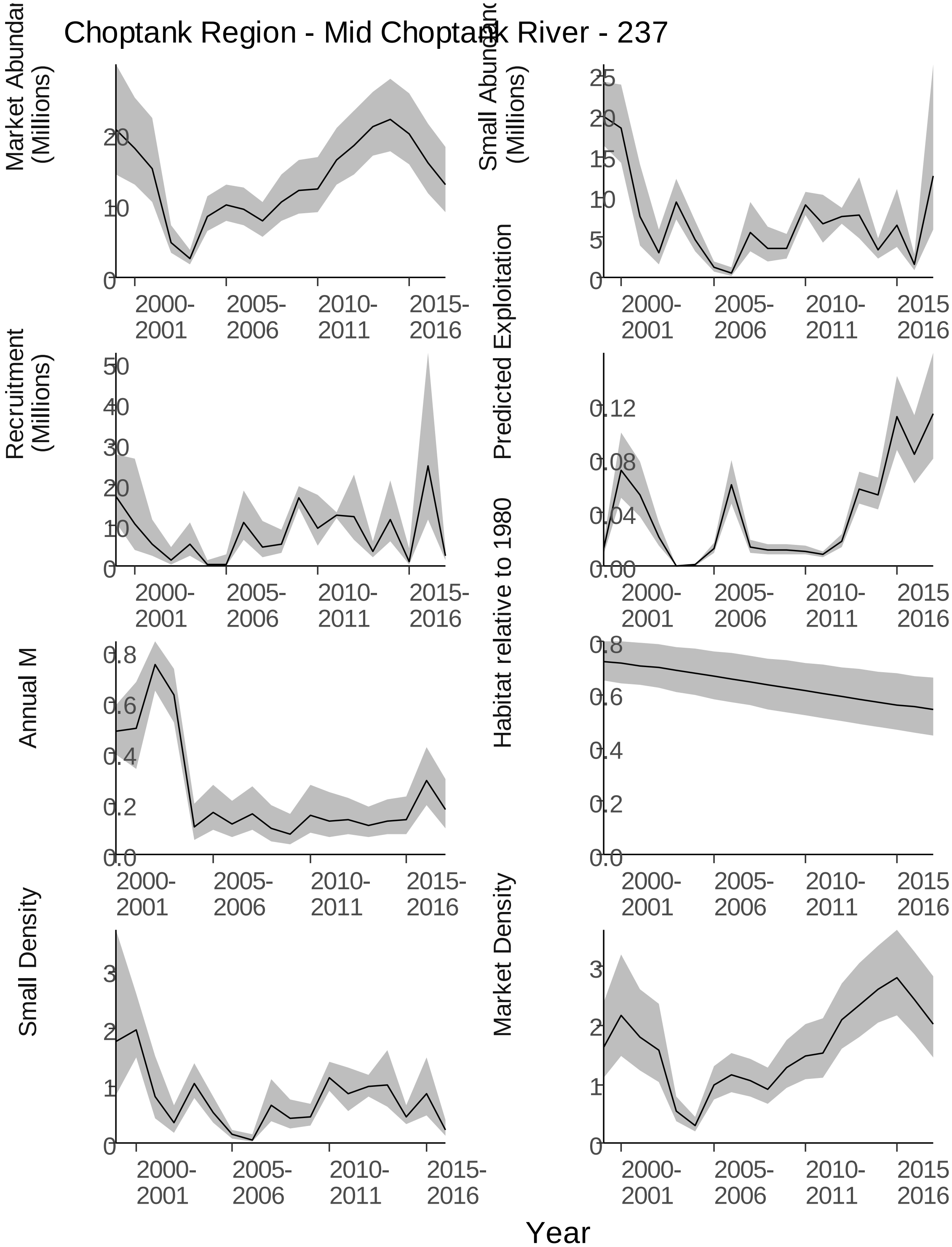

Figure 81. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Middle Choptank River (NOAA code 237).

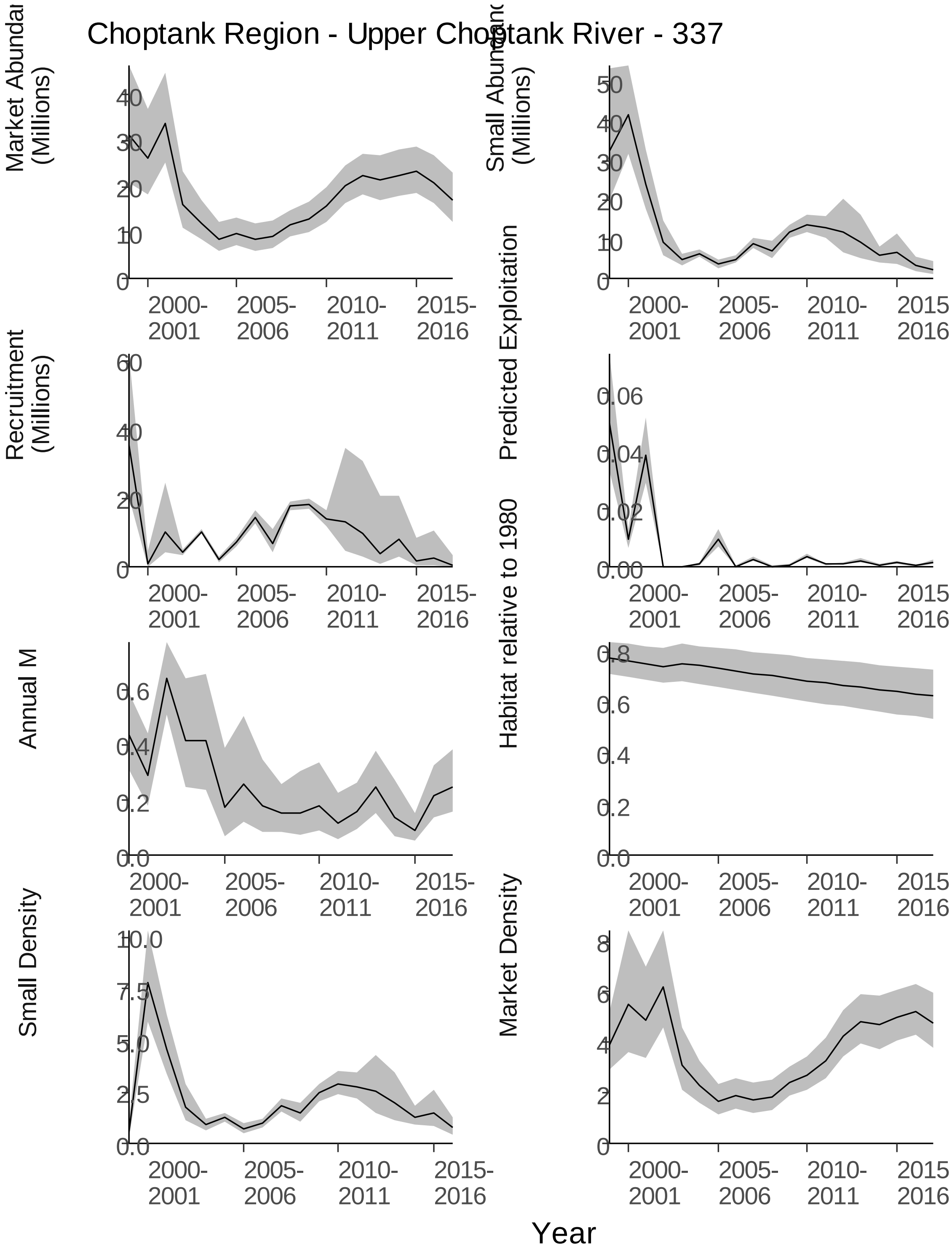

Figure 82. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Upper Choptank River (NOAA code 337).

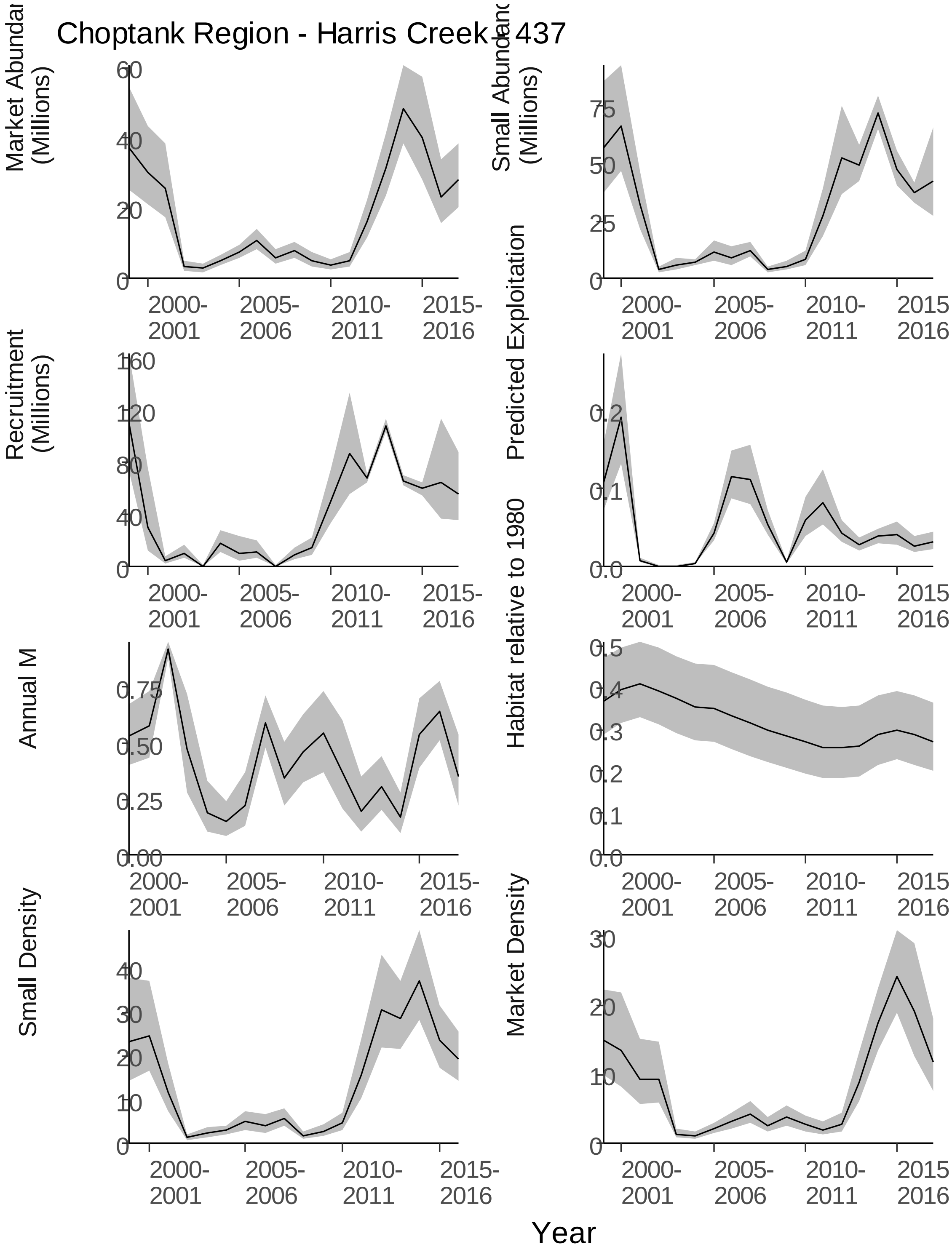

Figure 83. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in Harris Creek (NOAA code 437).

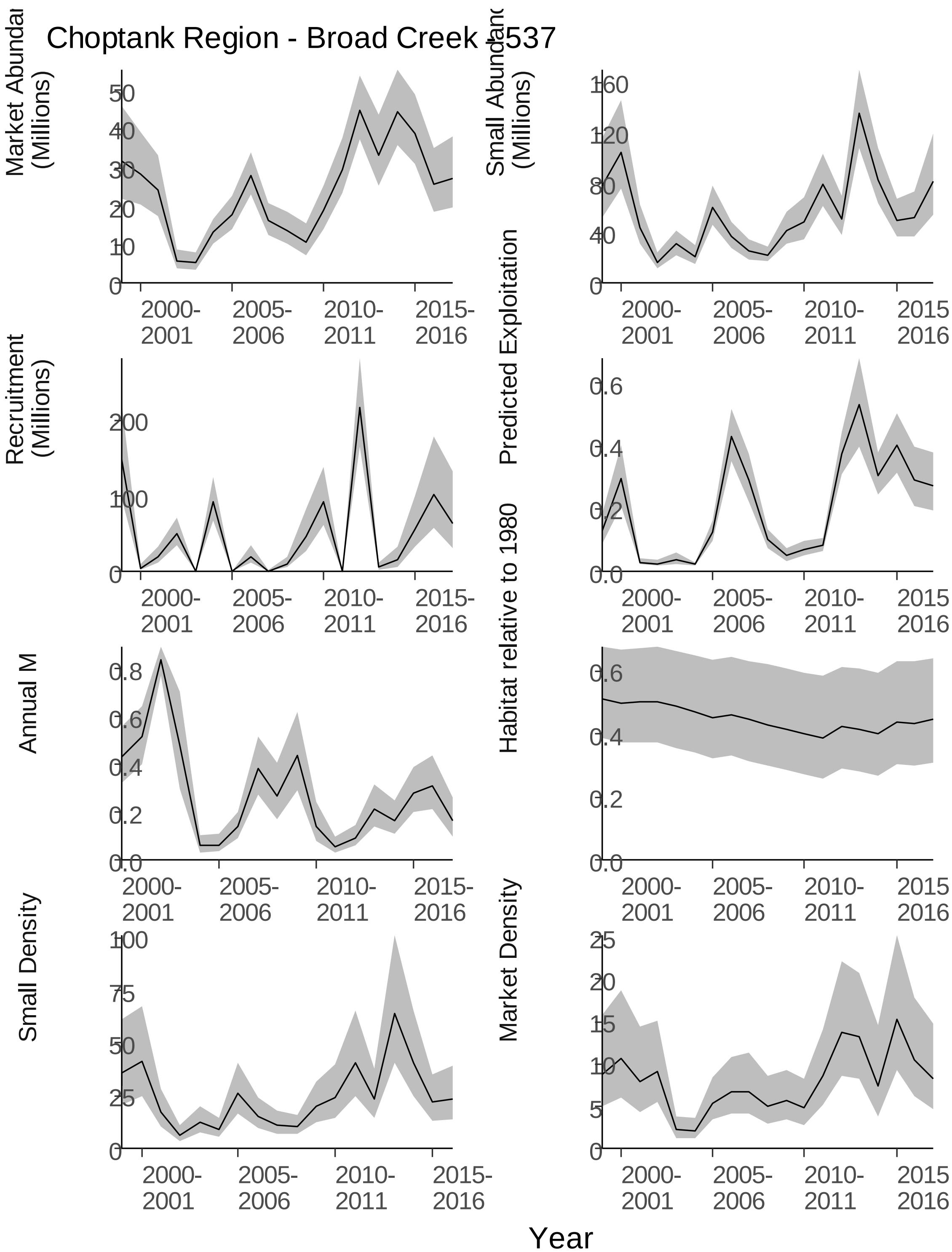

Figure 84. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in Broad Creek (NOAA code 537).

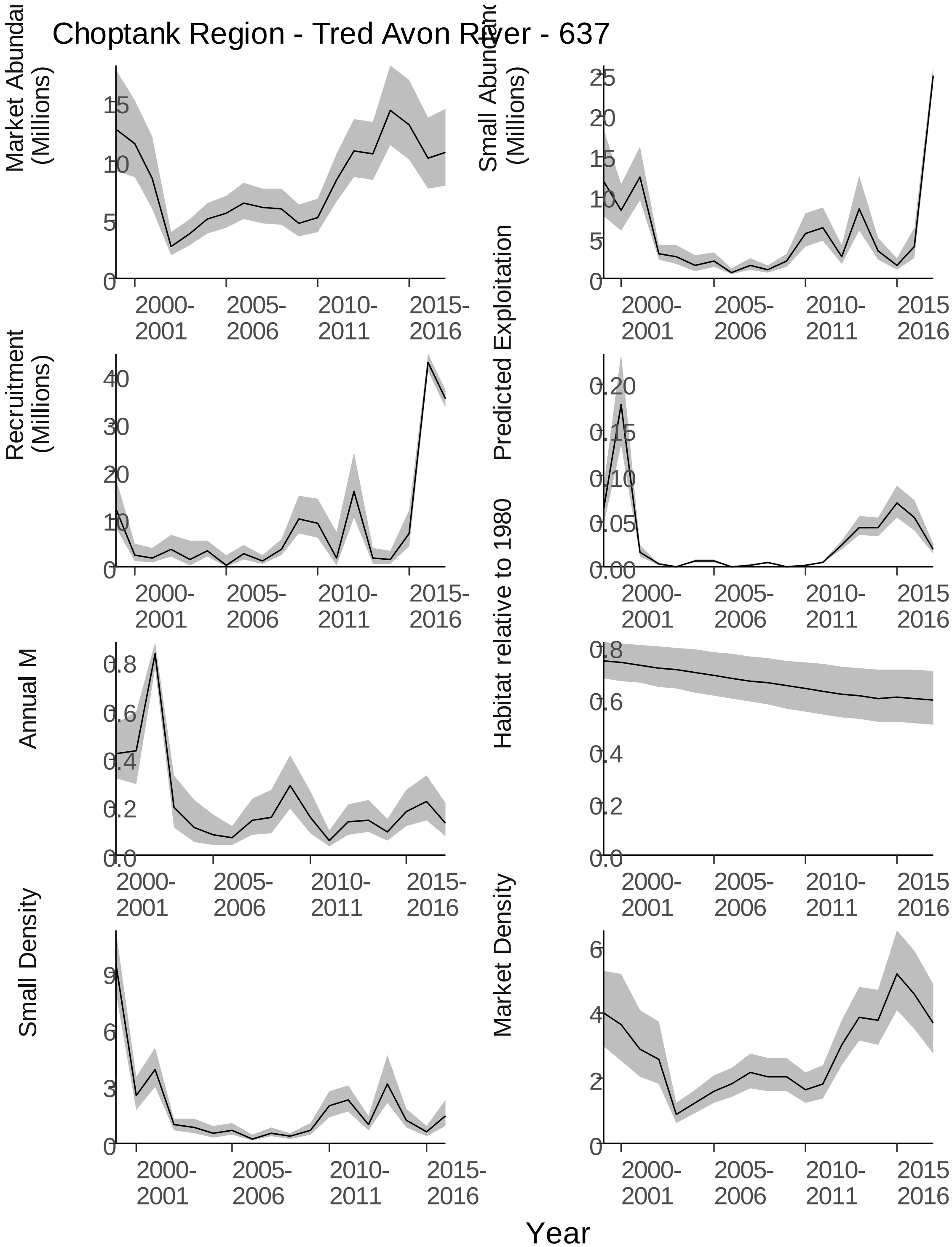

Figure 85. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Tred Avon River (NOAA code 637).

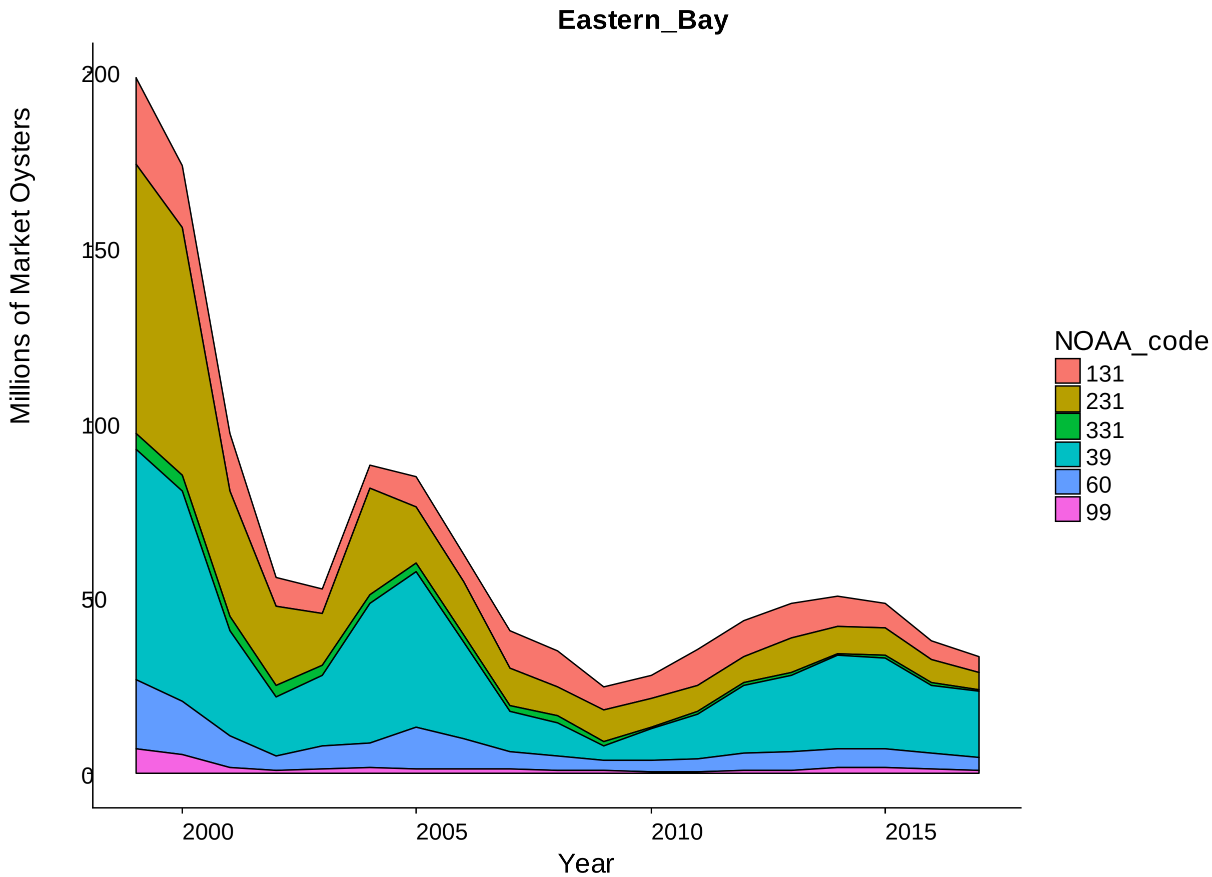

Figure 86. Estimated market oyster abundance among NOAA codes in the Eastern Bay Region under Maryland management during 1999-2017.

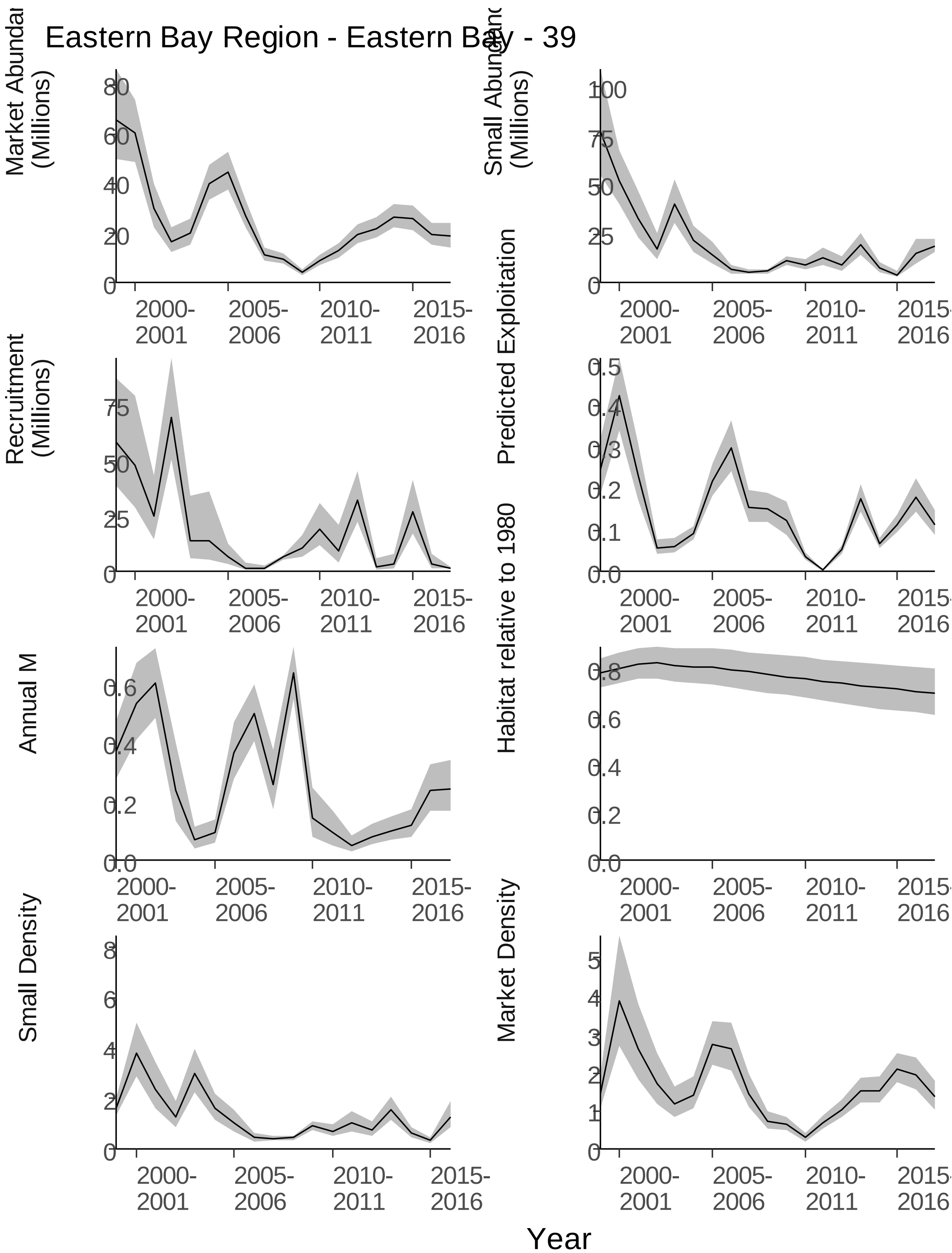

Figure 87. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in Eastern Bay (NOAA code 39).

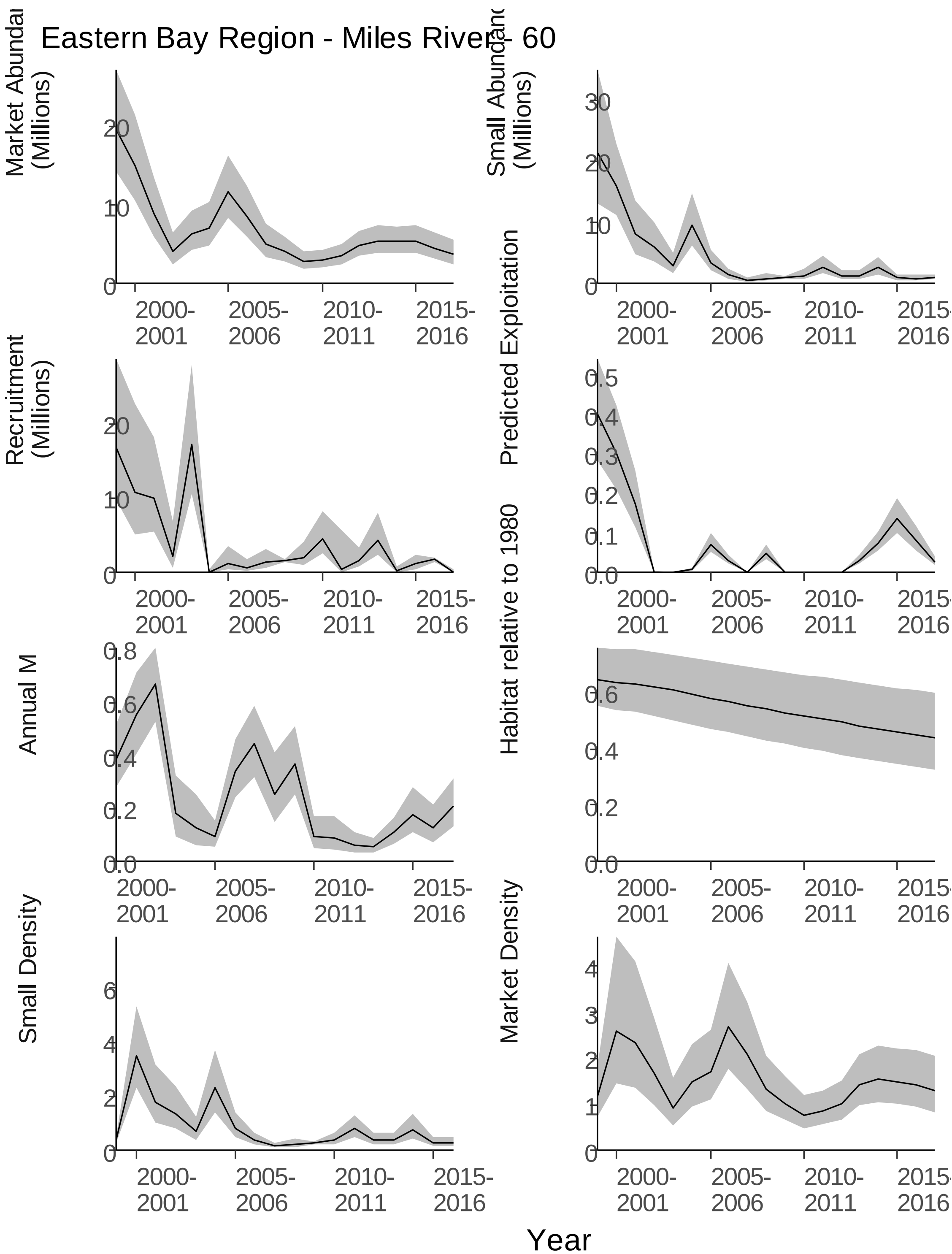

Figure 88. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Miles River (NOAA code 60).

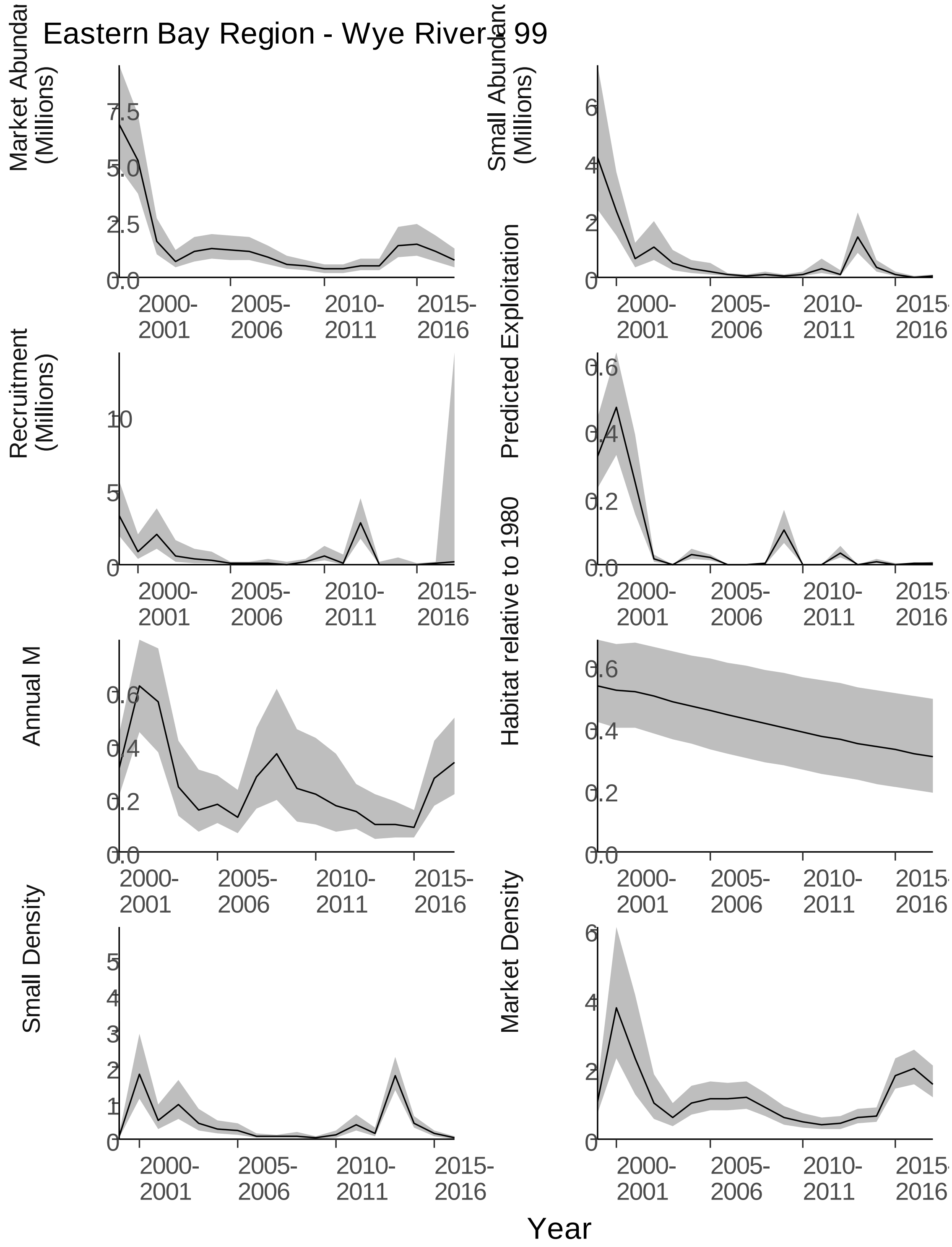

Figure 89. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Wye River (NOAA code 99).

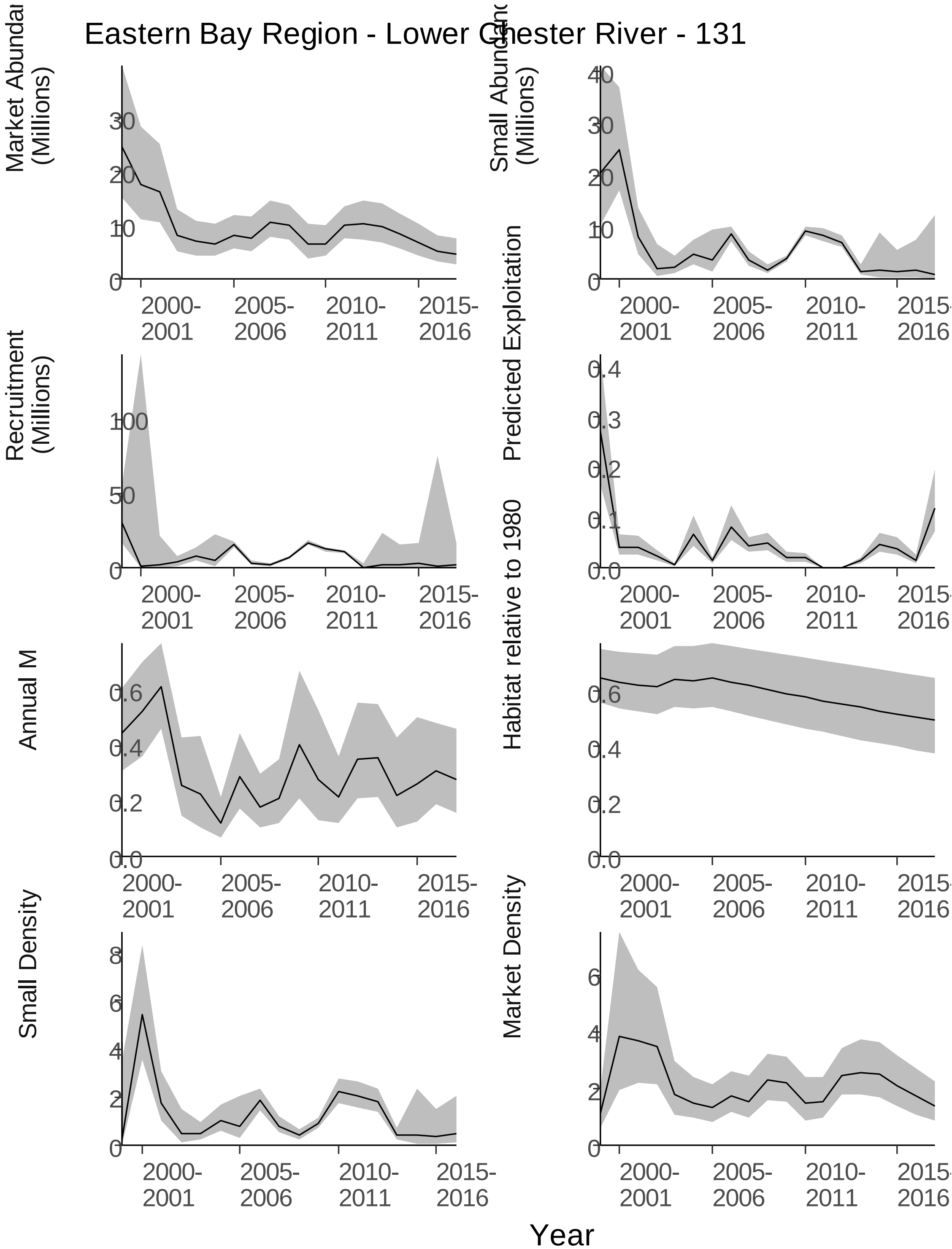

Figure 90. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the lower Chester River (NOAA code 131).

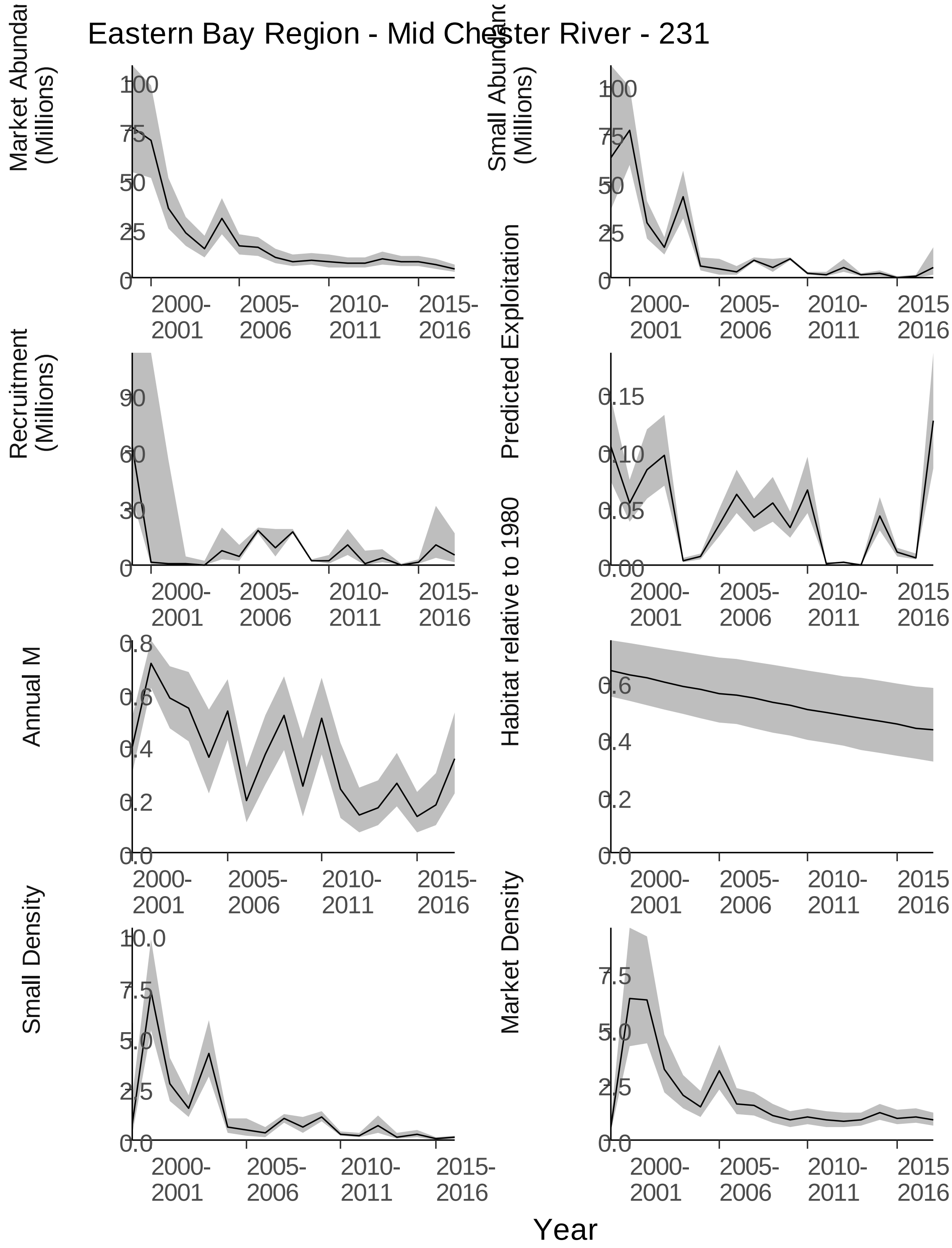

Figure 91. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the middle Chester River (NOAA code 231).

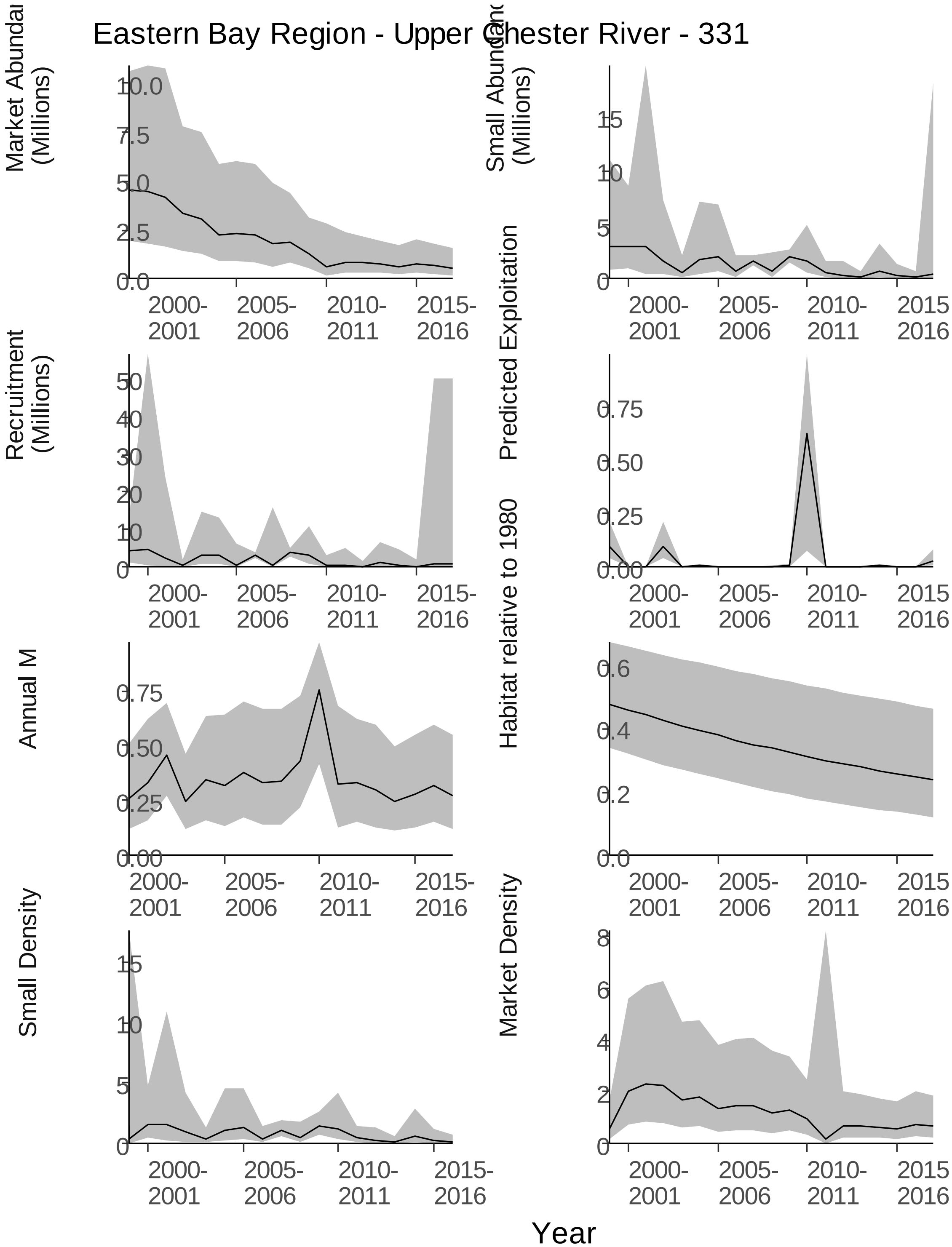

Figure 92. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the upper Chester River (NOAA code 331).

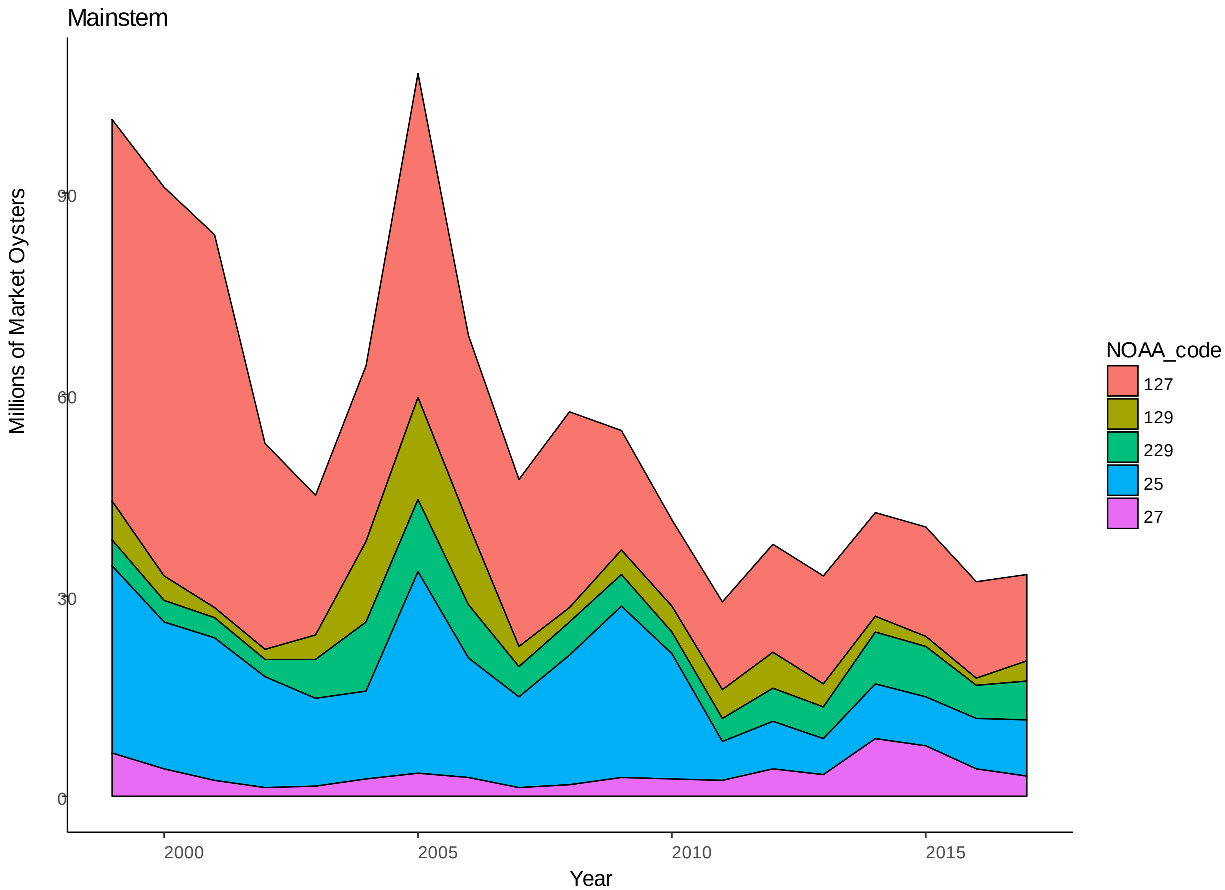

Figure 93. Estimated market oyster abundance among NOAA codes in the Chesapeake Bay Mainstem Region under Maryland management during 1999-2017.

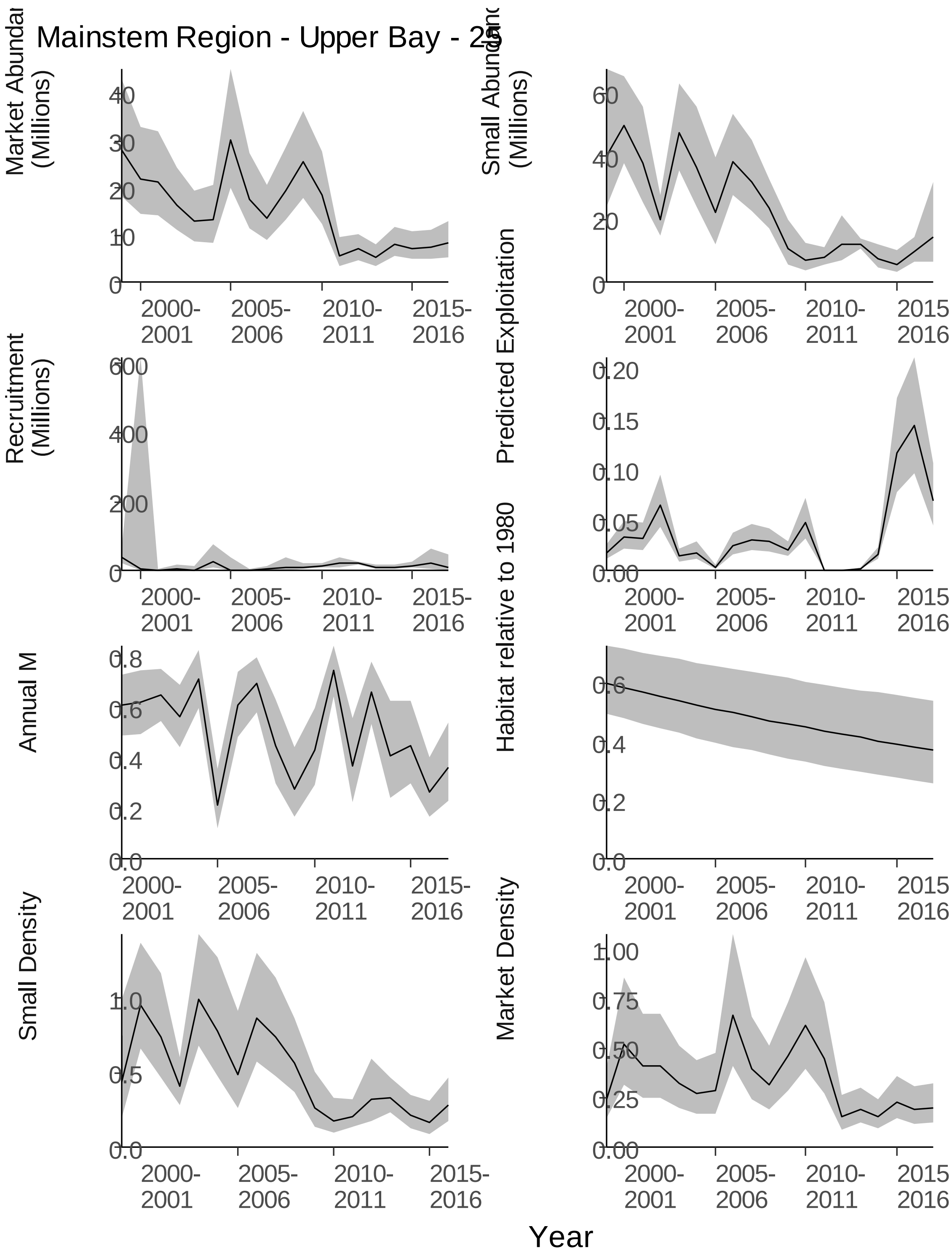

Figure 94. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Upper Bay (NOAA code 25).

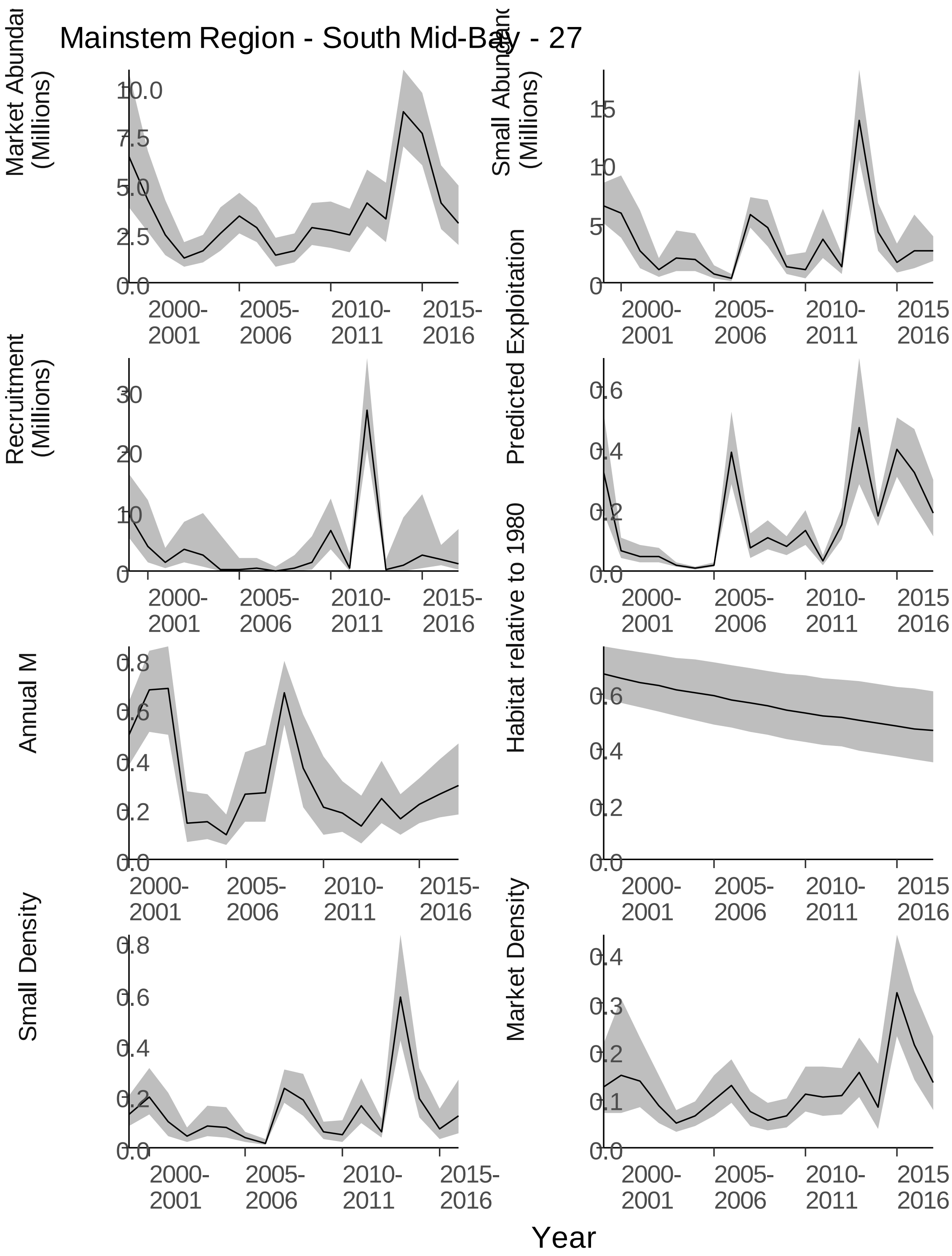

Figure 95. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the South Mid-Bay (NOAA code 27).

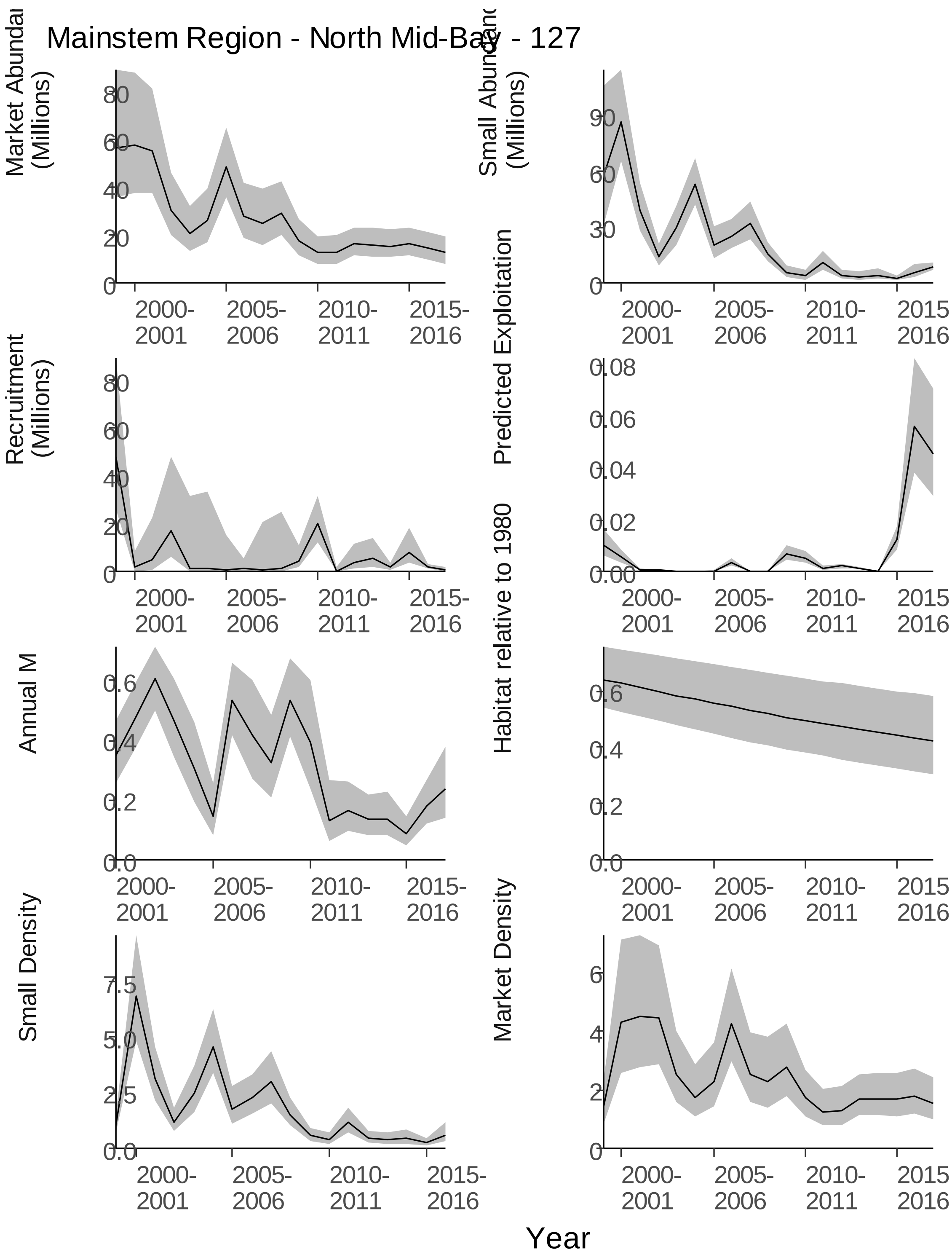

Figure 96. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the North Mid-Bay (NOAA code 127).

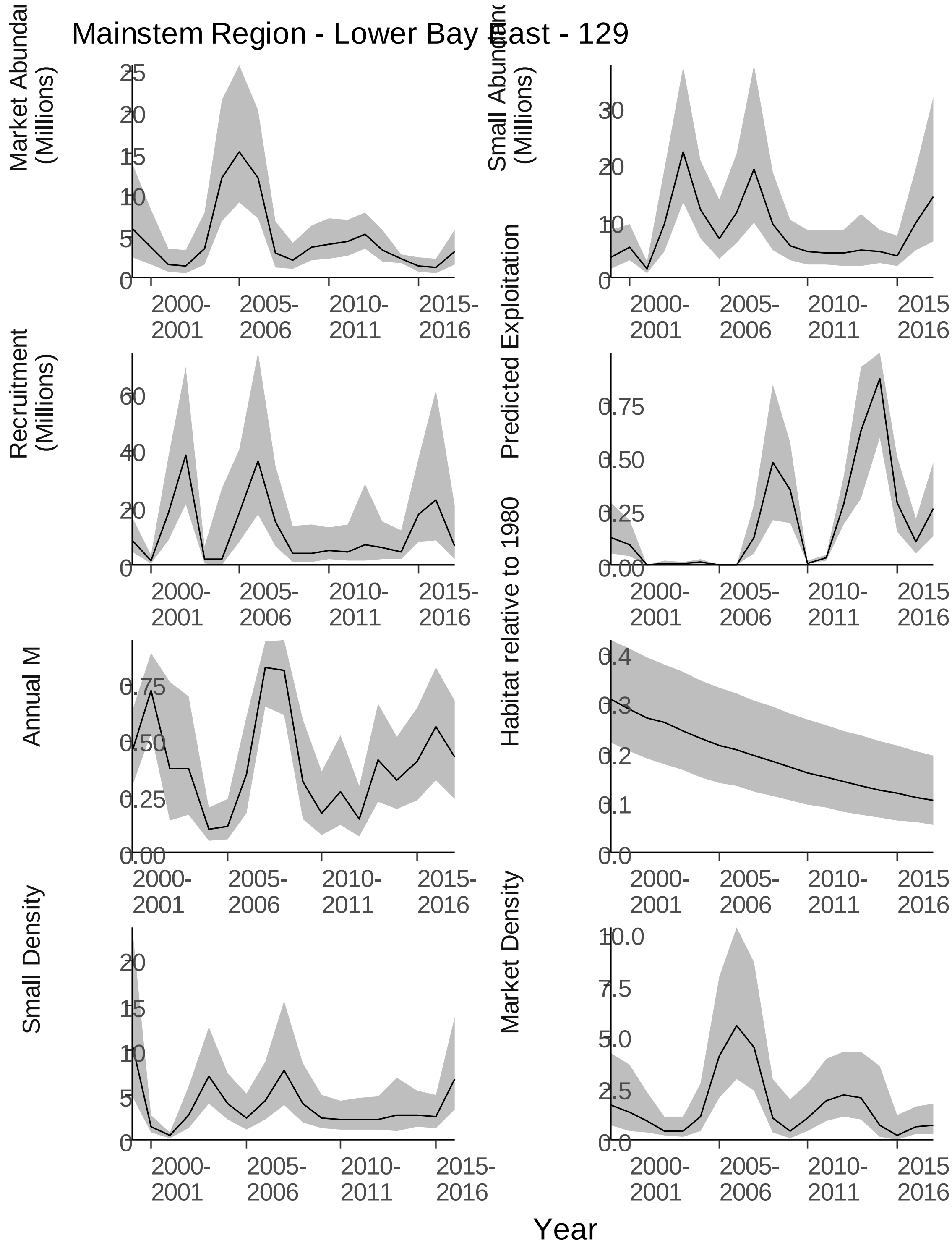

Figure 97. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Lower Bay East (NOAA code 129).

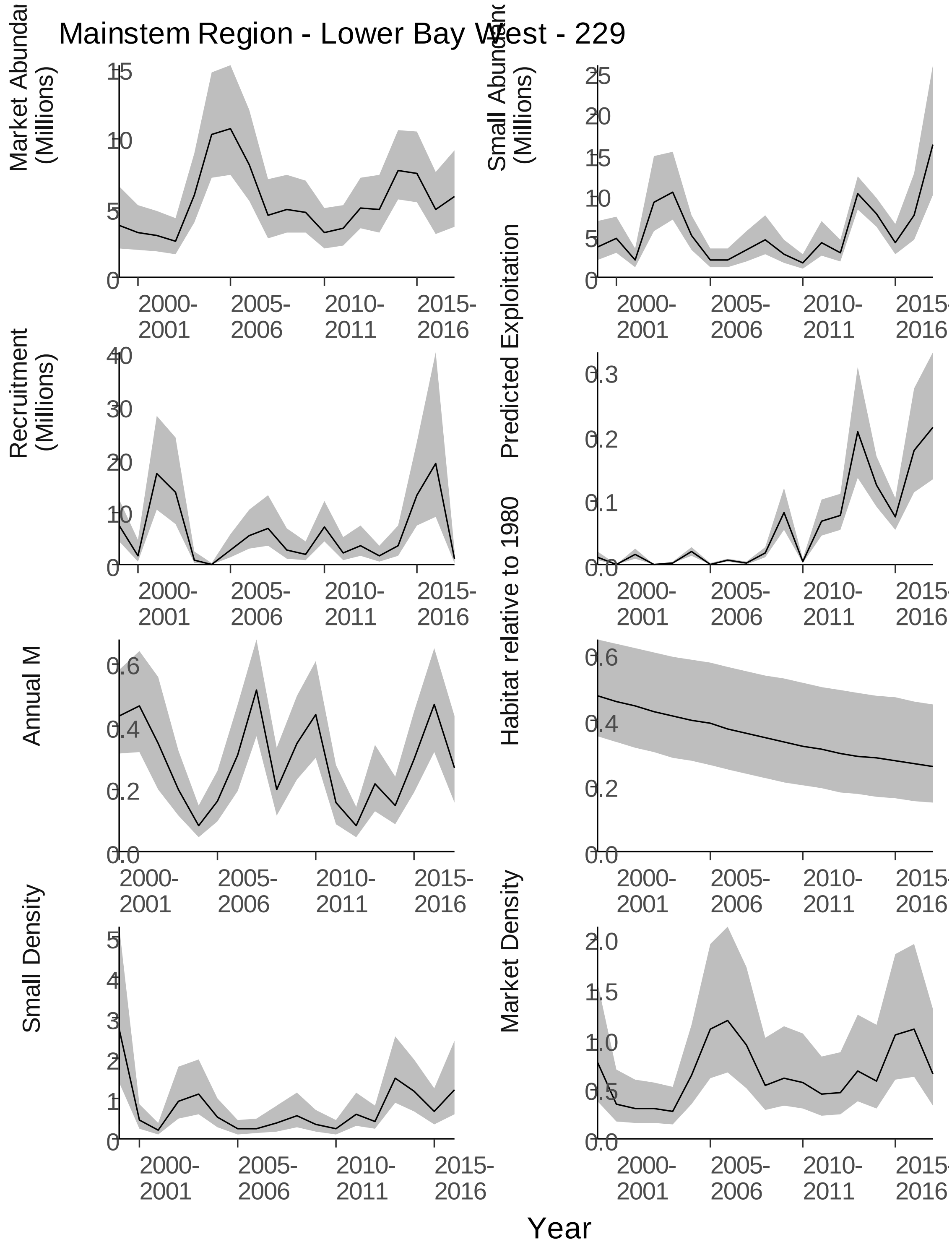

Figure 98. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Lower Bay West (NOAA code 229).

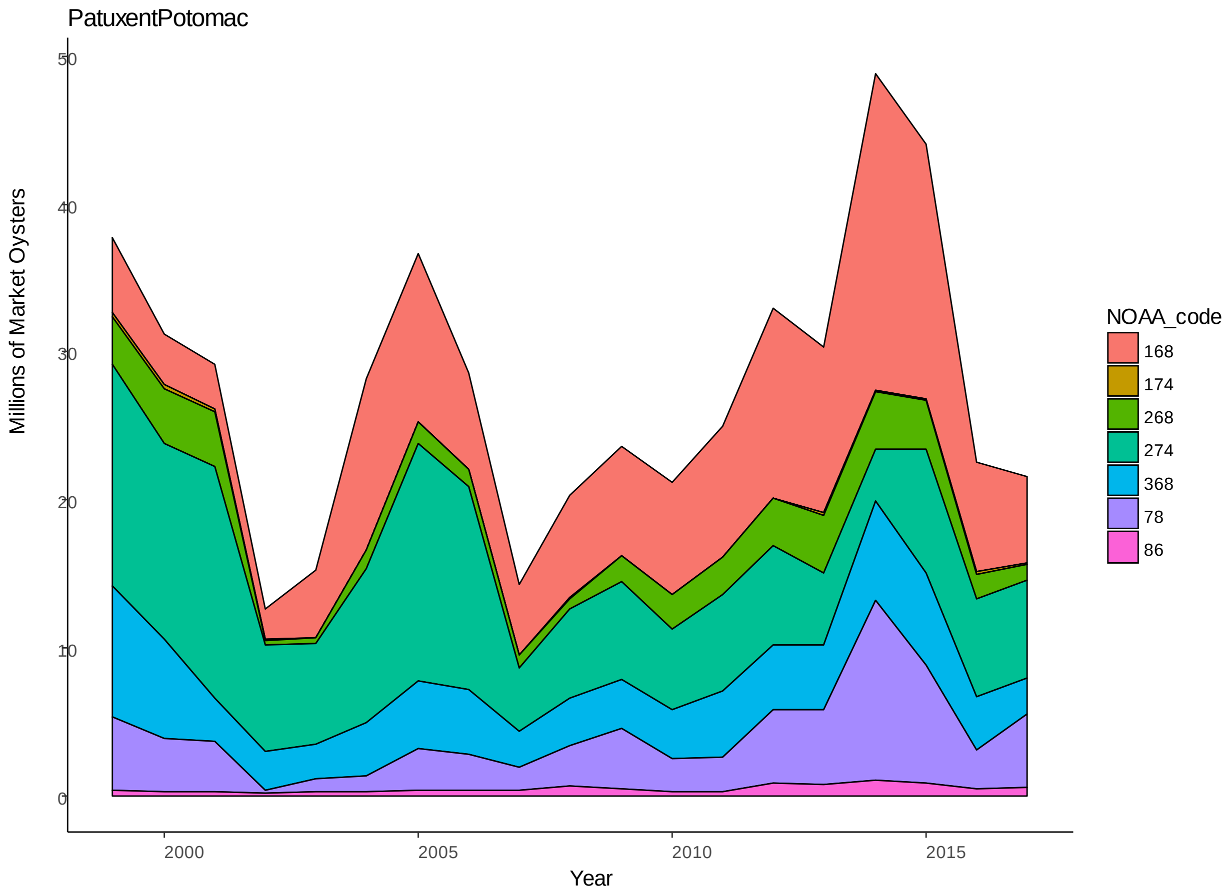

Figure 99. Estimated market oyster abundance among NOAA codes in the Patuxent and Potomac River Region under Maryland management during 1999-2017.

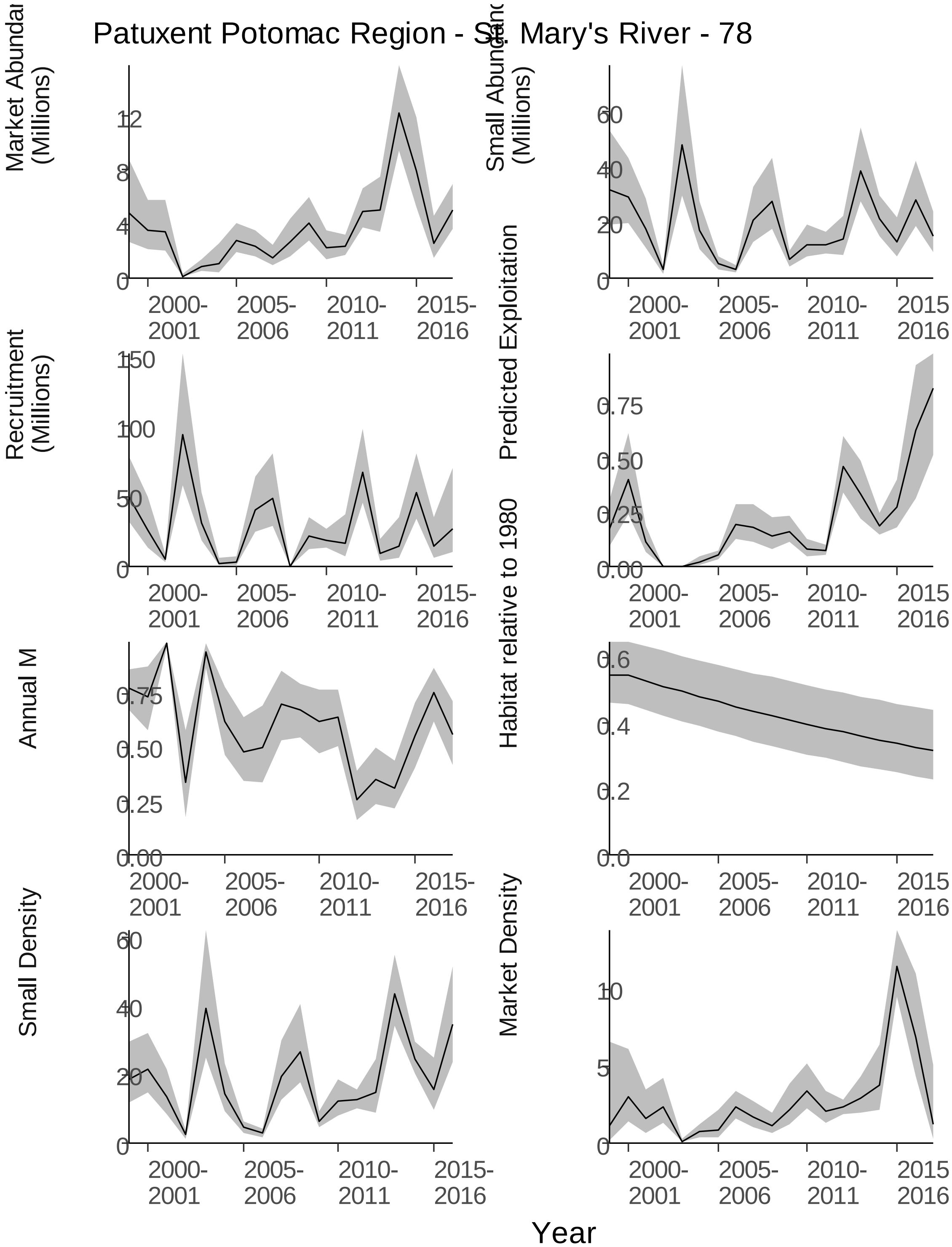

Figure 100. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the St. Mary's River (NOAA code 78).

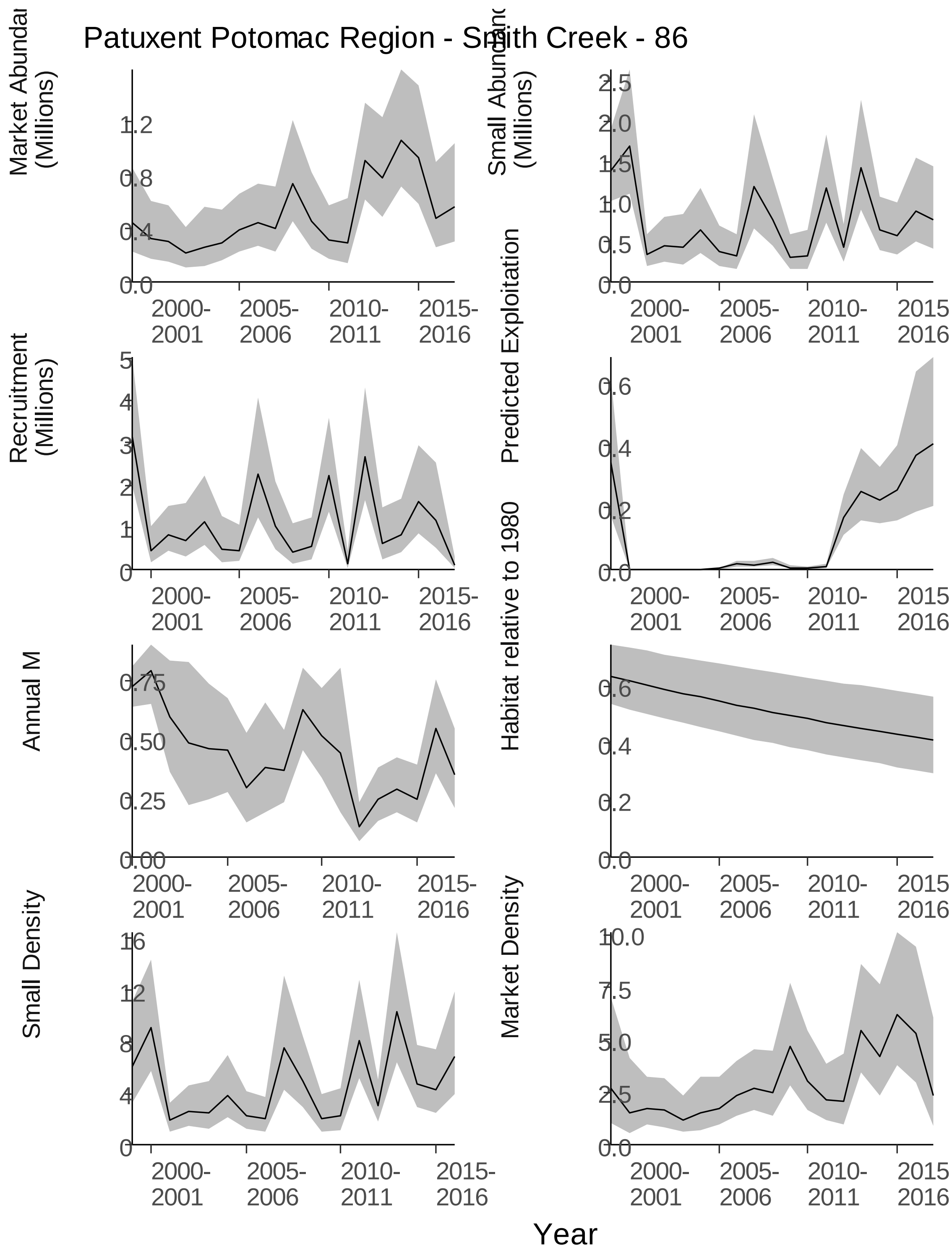

Figure 101. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in Smith Creek (NOAA code 86).

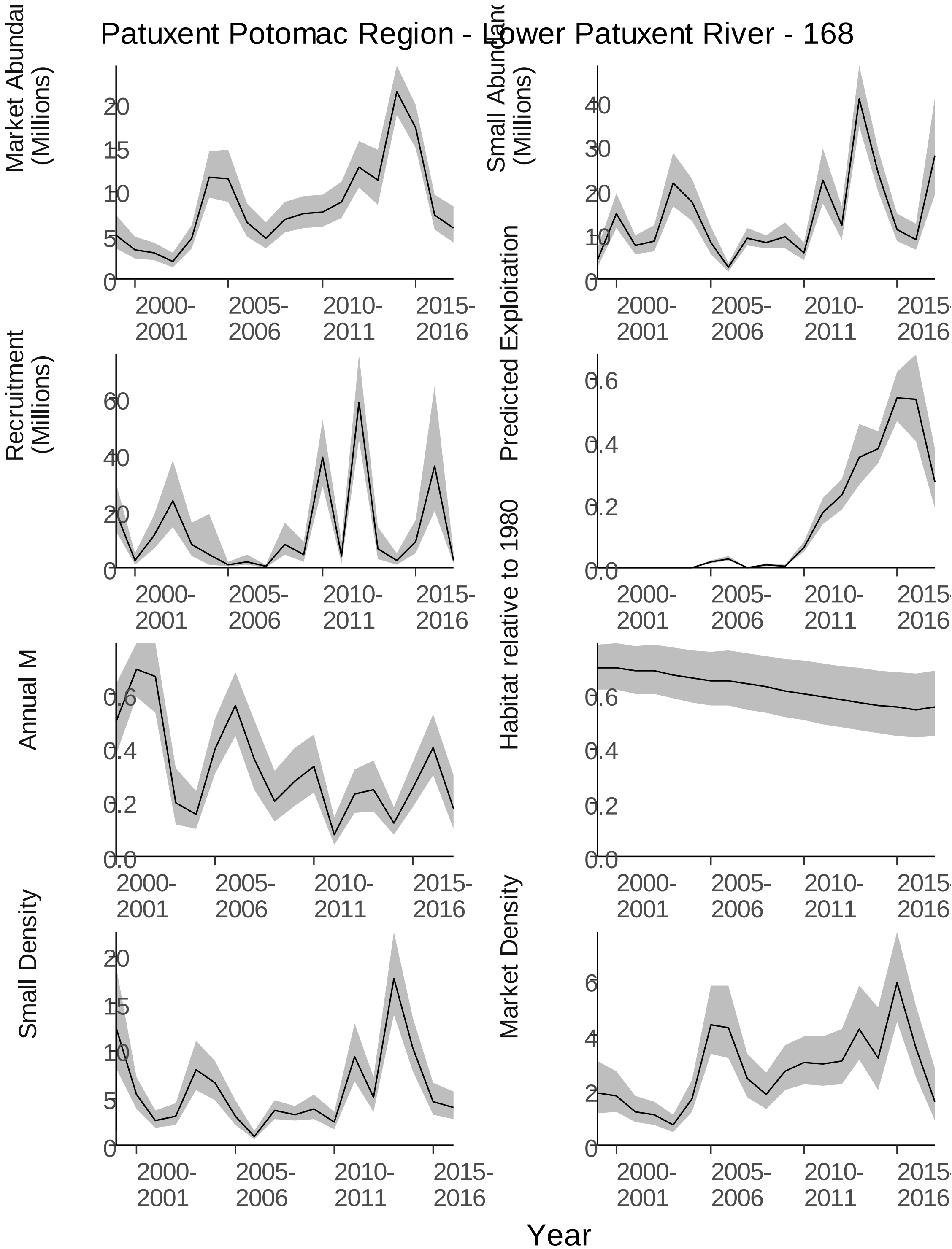

Figure 102. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the lower Patuxent River (NOAA code 168).

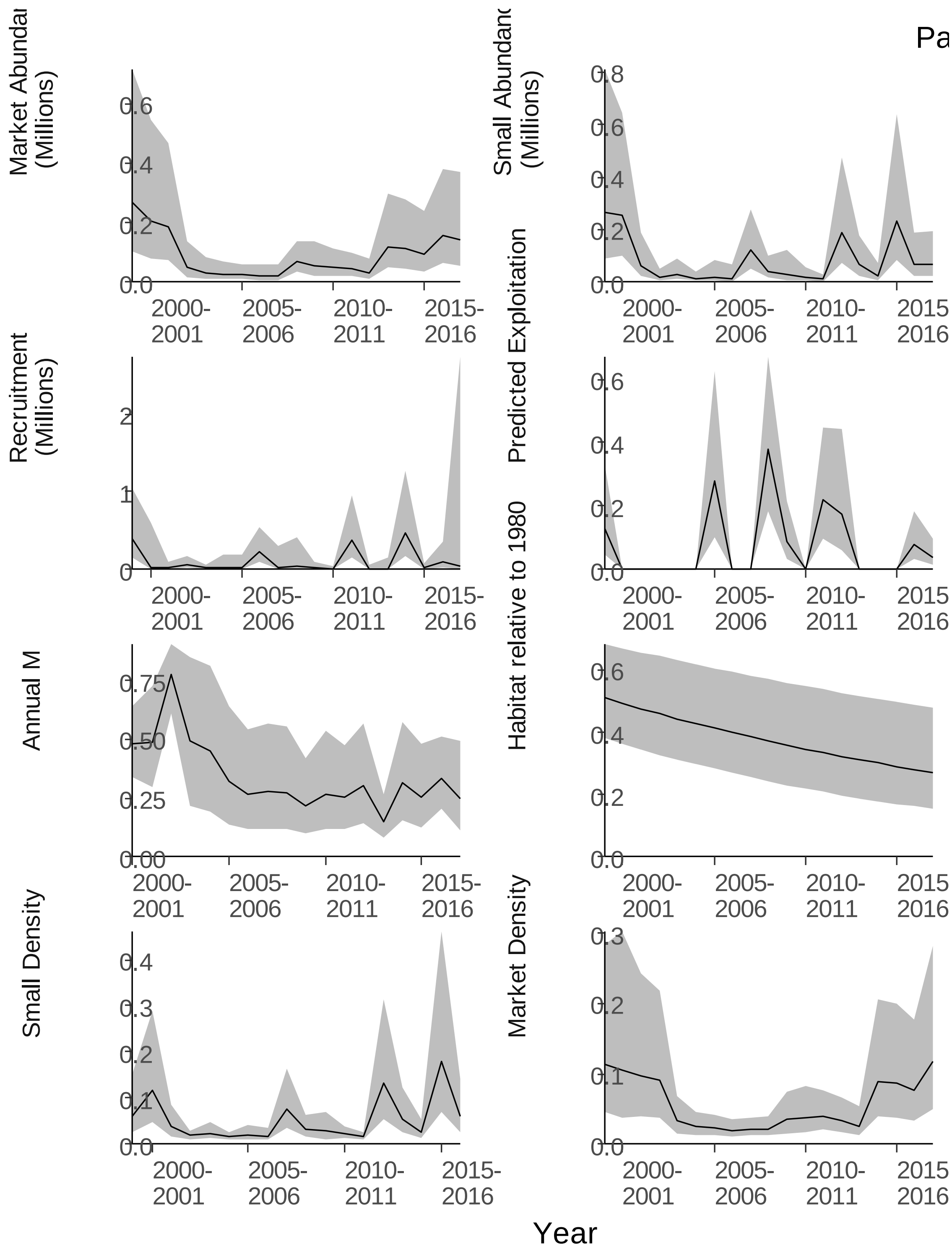

Figure 103. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in Breton and St. Clements Bay (NOAA code 174).

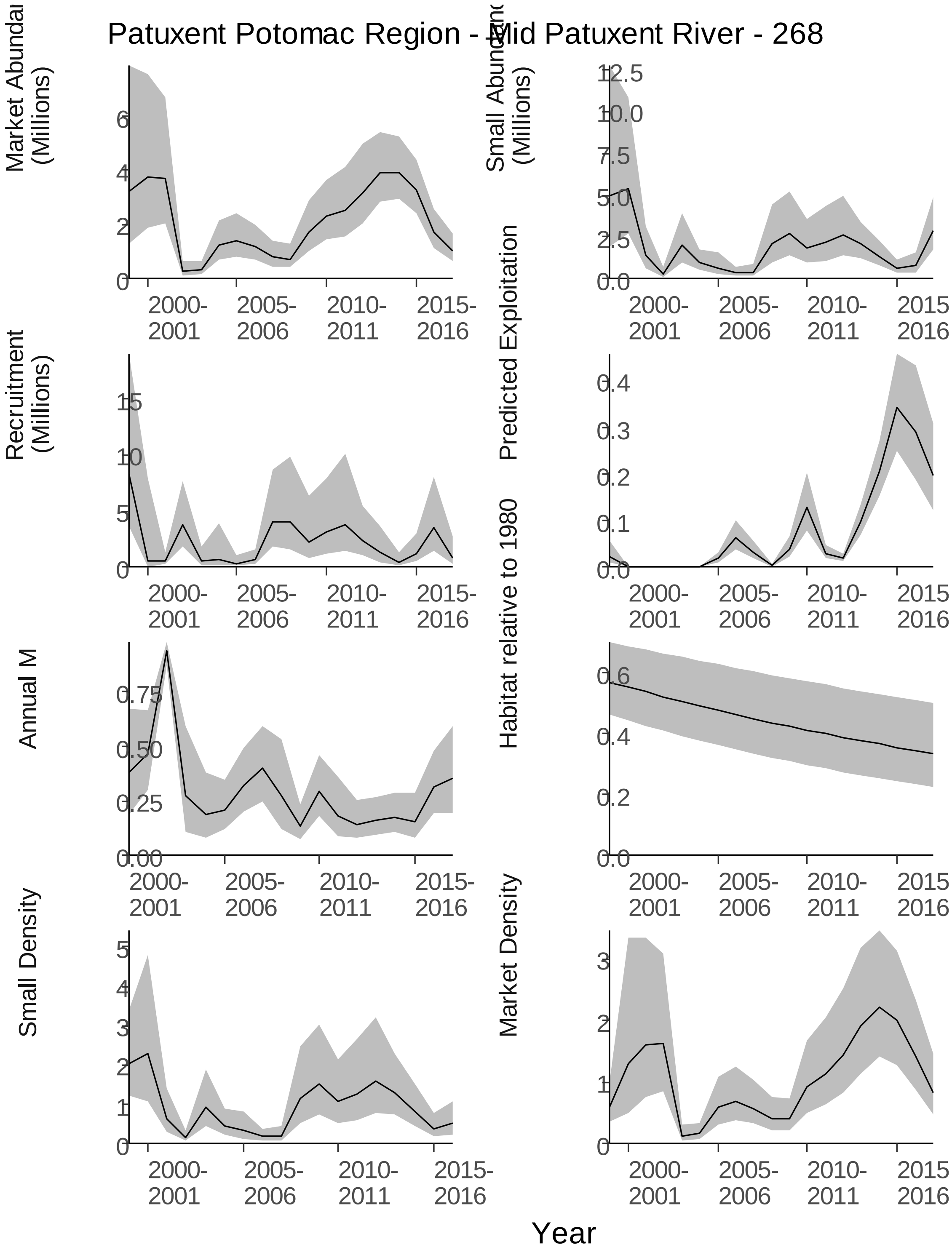

Figure 104. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the middle Patuxent River (NOAA code 268).

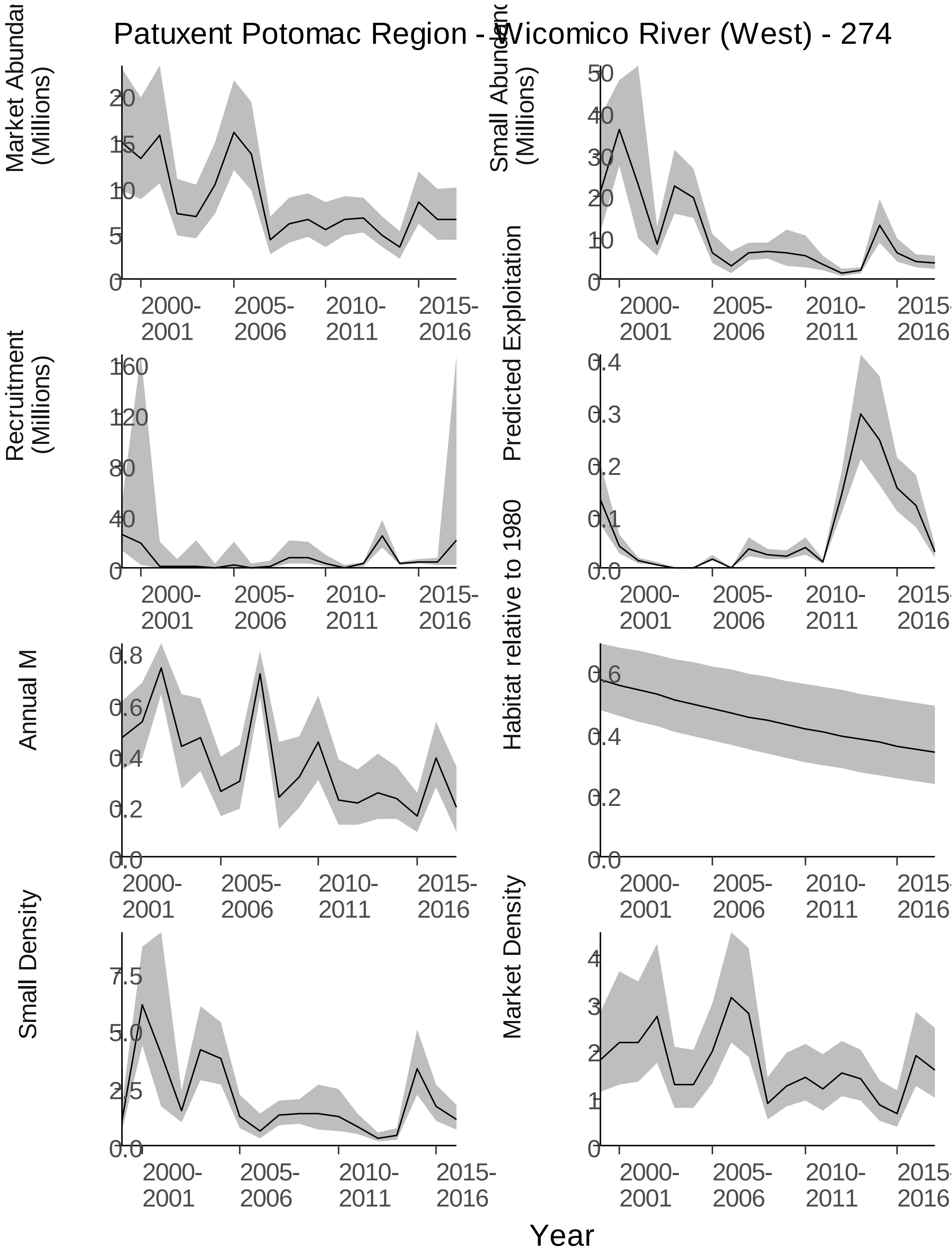

Figure 105. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Wicomico River (NOAA code 274).

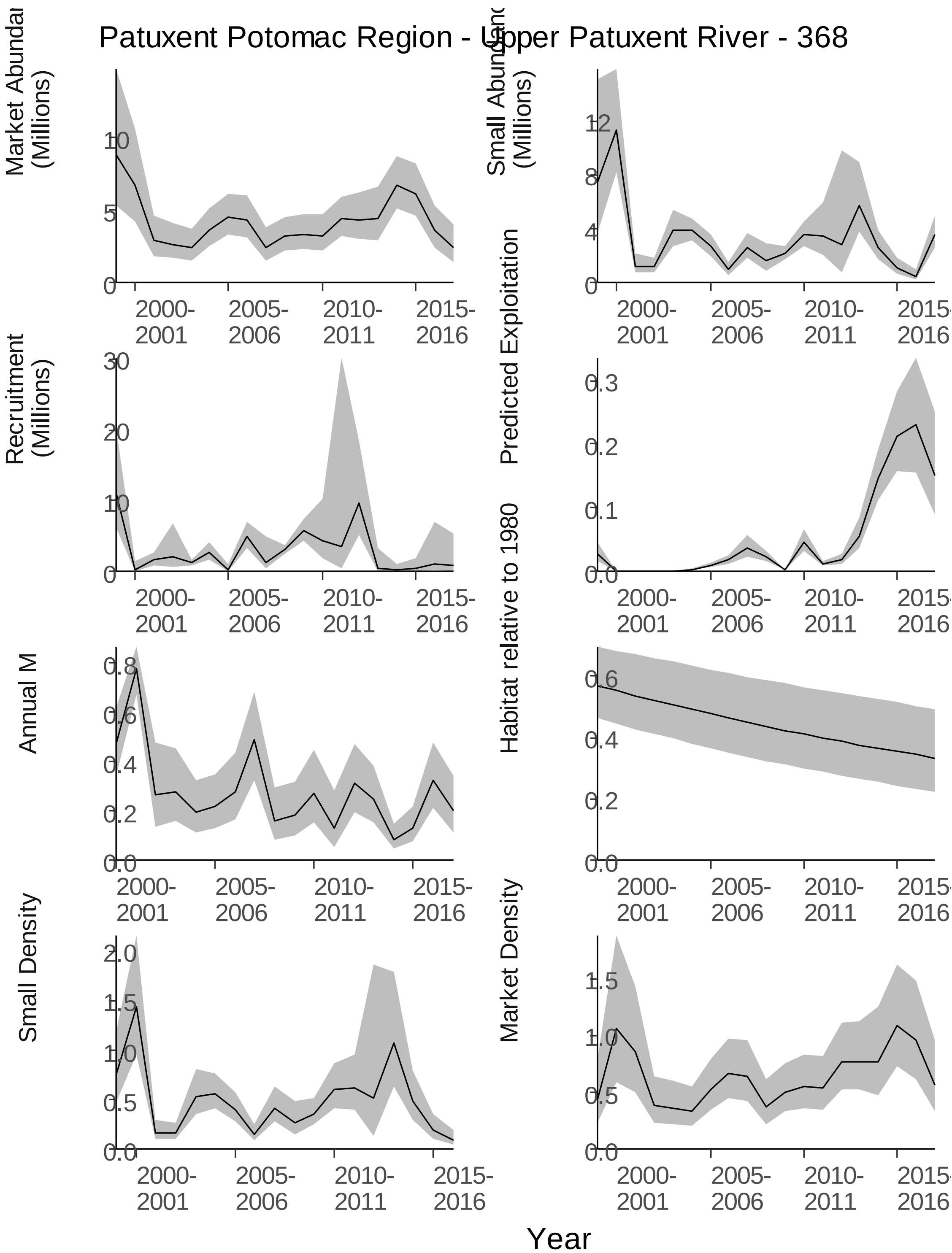

Figure 106. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the upper Patuxent River (NOAA code 368).

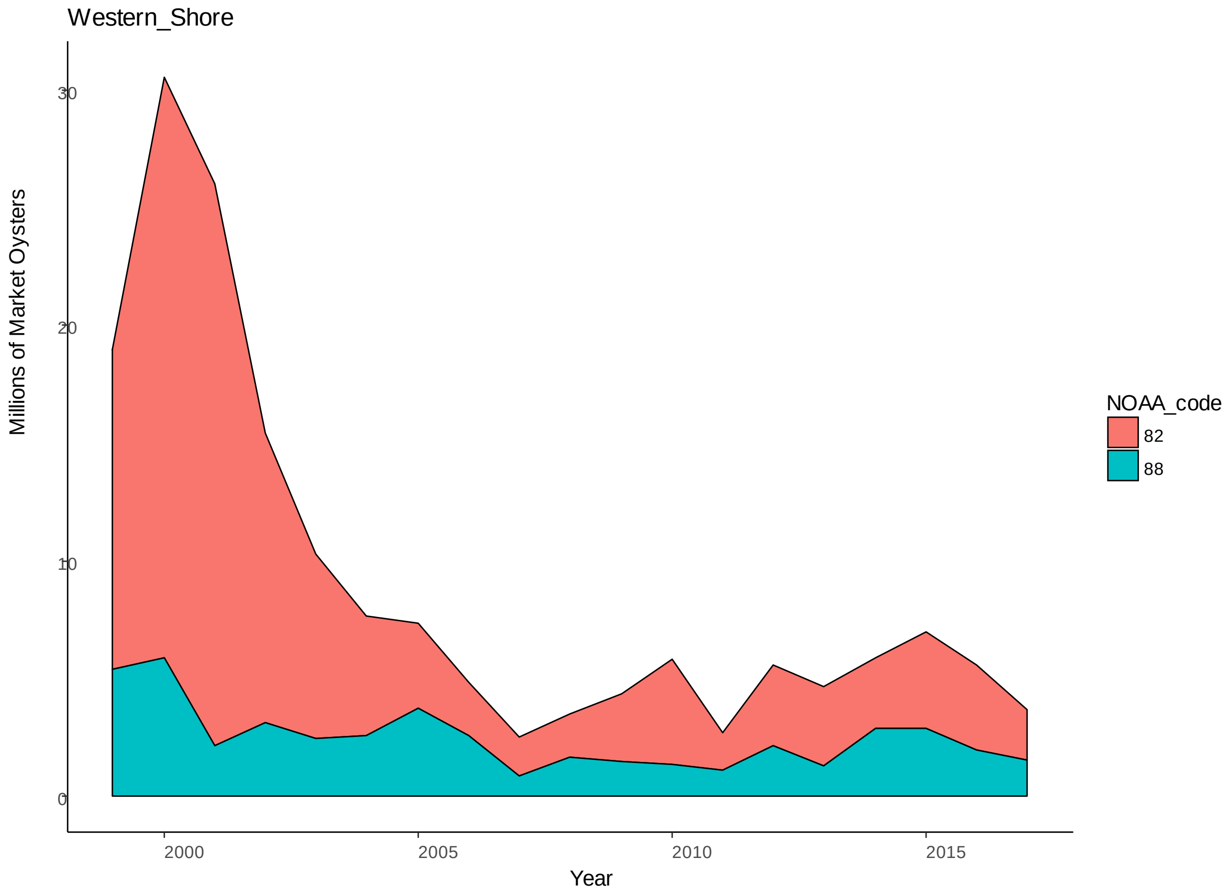

Figure 107. Estimated market oyster abundance among NOAA codes in the Western Shore Region under Maryland management during 1999-2017.

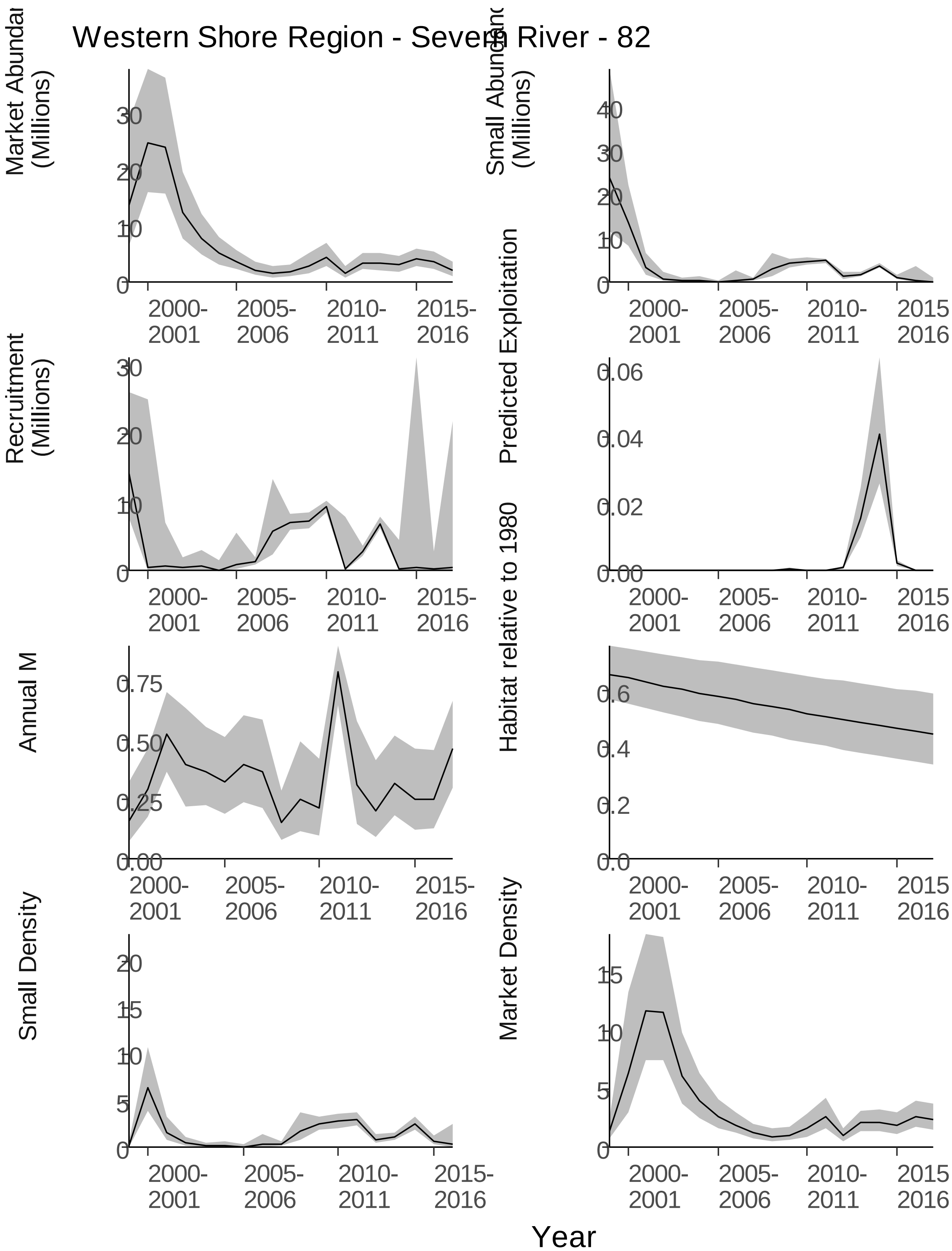

Figure 108. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the Severn River (NOAA code 82).

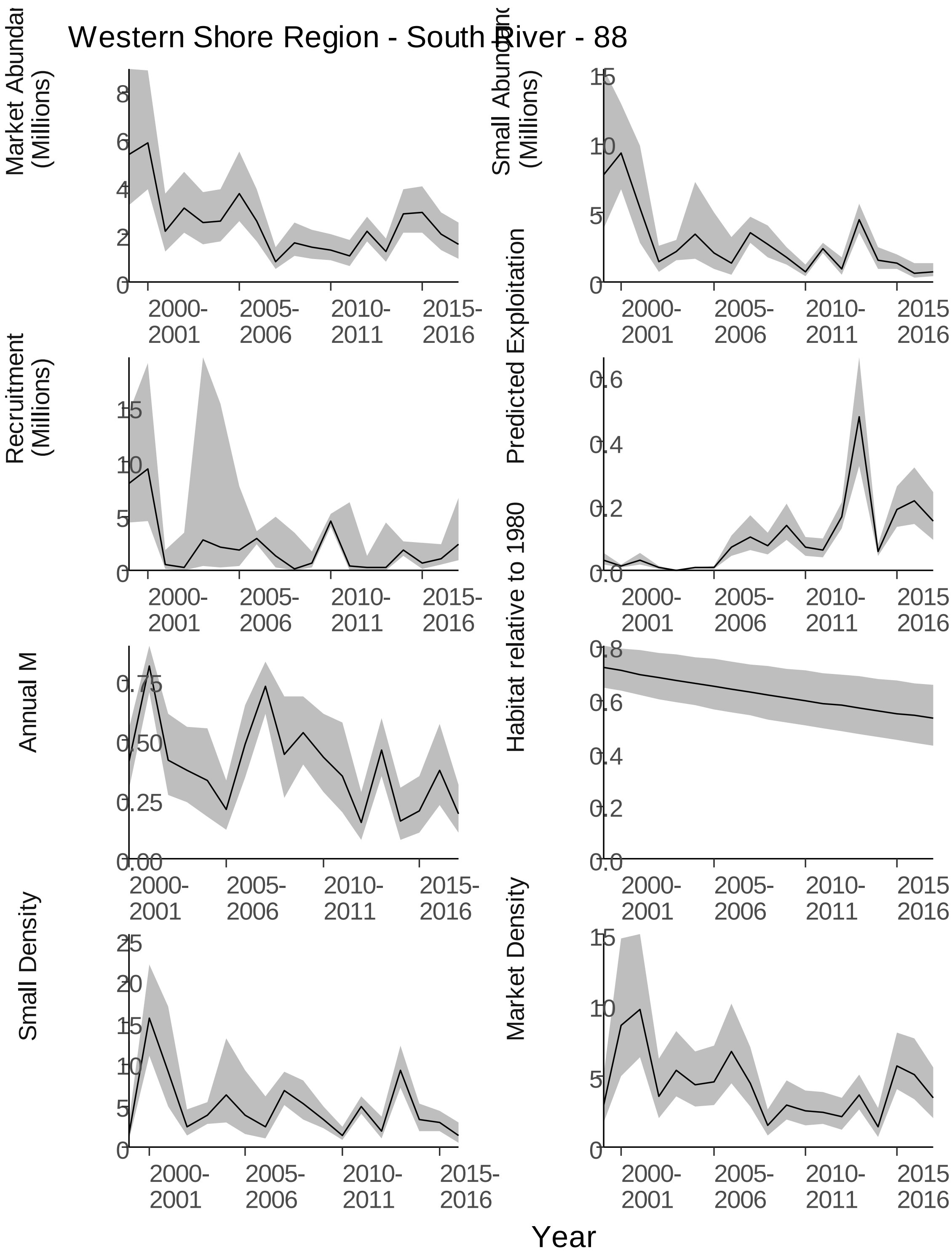

Figure 109. Estimated abundance of market, small and spat oysters, exploitation and natural mortality rates (proportion yr^{-1}), change in habitat relative to 1980 and density (number m^{-2}) of small and market oysters during 1999-2017 in the South River (NOAA code 88).

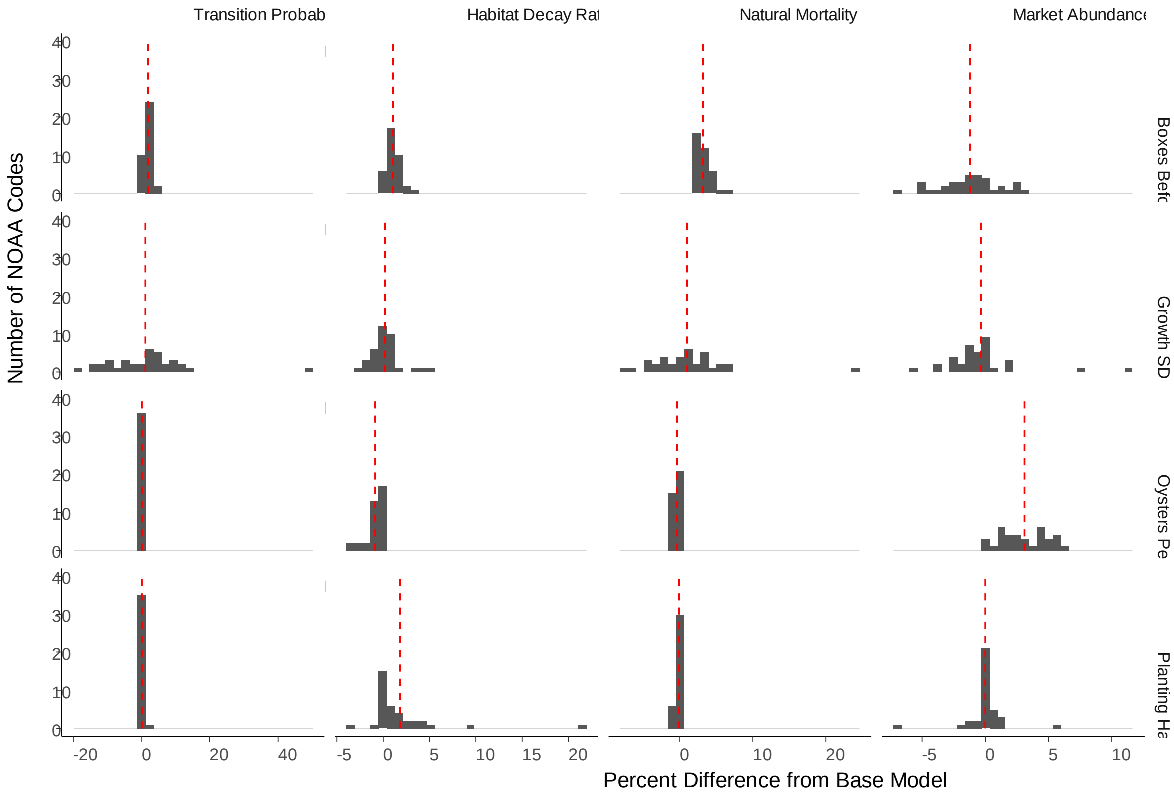

Figure 110. Results of sensitivity analyses for the mean of the prior for the difference between box and small-market catchability (top row), the standard deviation (SD) of the growth prior (second row), the number of oysters per bushel (third panel) and the fraction of habitat created when planting (bottom row). Bars indicate frequency histogram of relative errors between the base model and sensitivity analysis for all NOAA codes. The mean relative error (over NOAA codes) is indicated in red for each parameter.

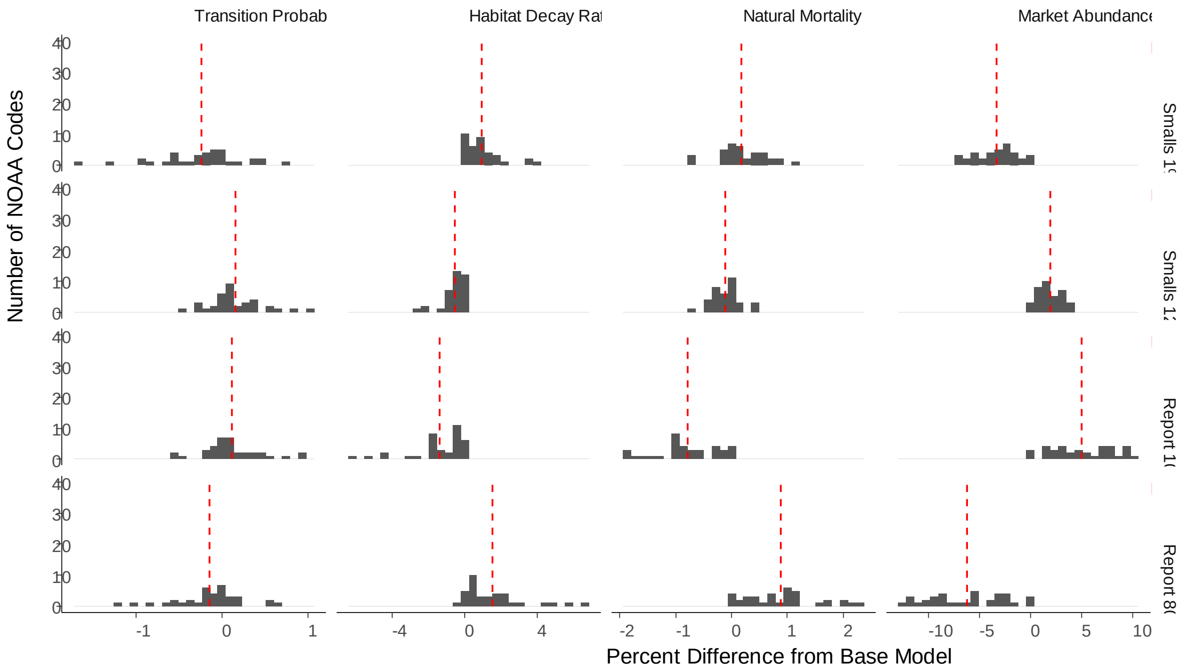

Figure 111. Results of sensitivity analyses for 1% smalls per bushel (top row), 12% smalls per bushel (second row), 100% reporting rate (third panel) and 80% reporting rate (bottom row). Bars indicate frequency histogram of relative errors between the base model and sensitivity analysis for all NOAA codes. The mean relative error (over NOAA codes) is indicated in red for each parameter.

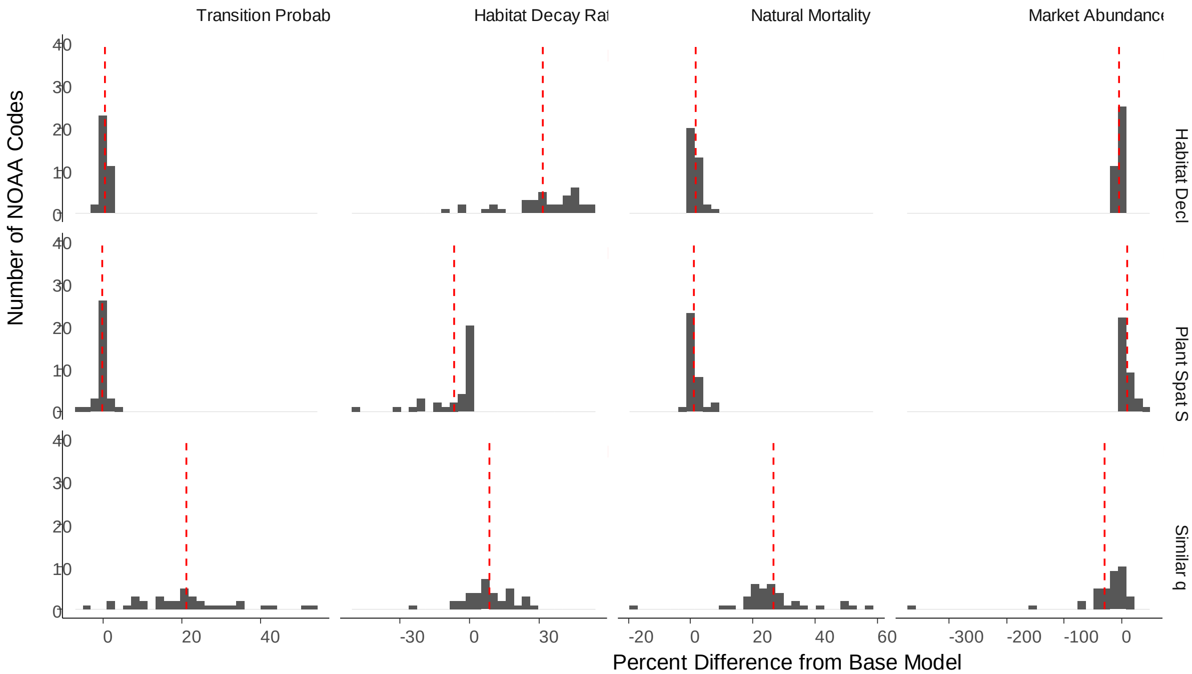

Figure 112. Results of sensitivity analyses for the standard deviation (SD)of the prior for habitat decline (top row), the survival of planted spat (SD) of the growth prior (second row) and forcing the model to estimate approximately the same catchability (q) for the three fall dredge survey categories (bottom row). Bars indicate frequency histogram of relative errors between the base model and sensitivity analysis for all NOAA Codes. The mean relative error (over NOAA Codes) is indicated in red for each parameter.

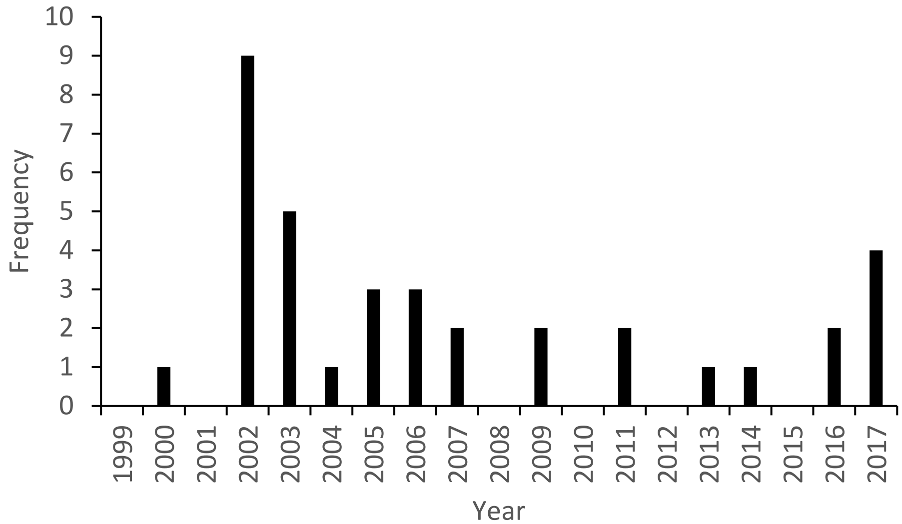

Figure 113. Frequency histogram of year of the estimated minimum abundance (threshold reference point) of market-sized oysters.

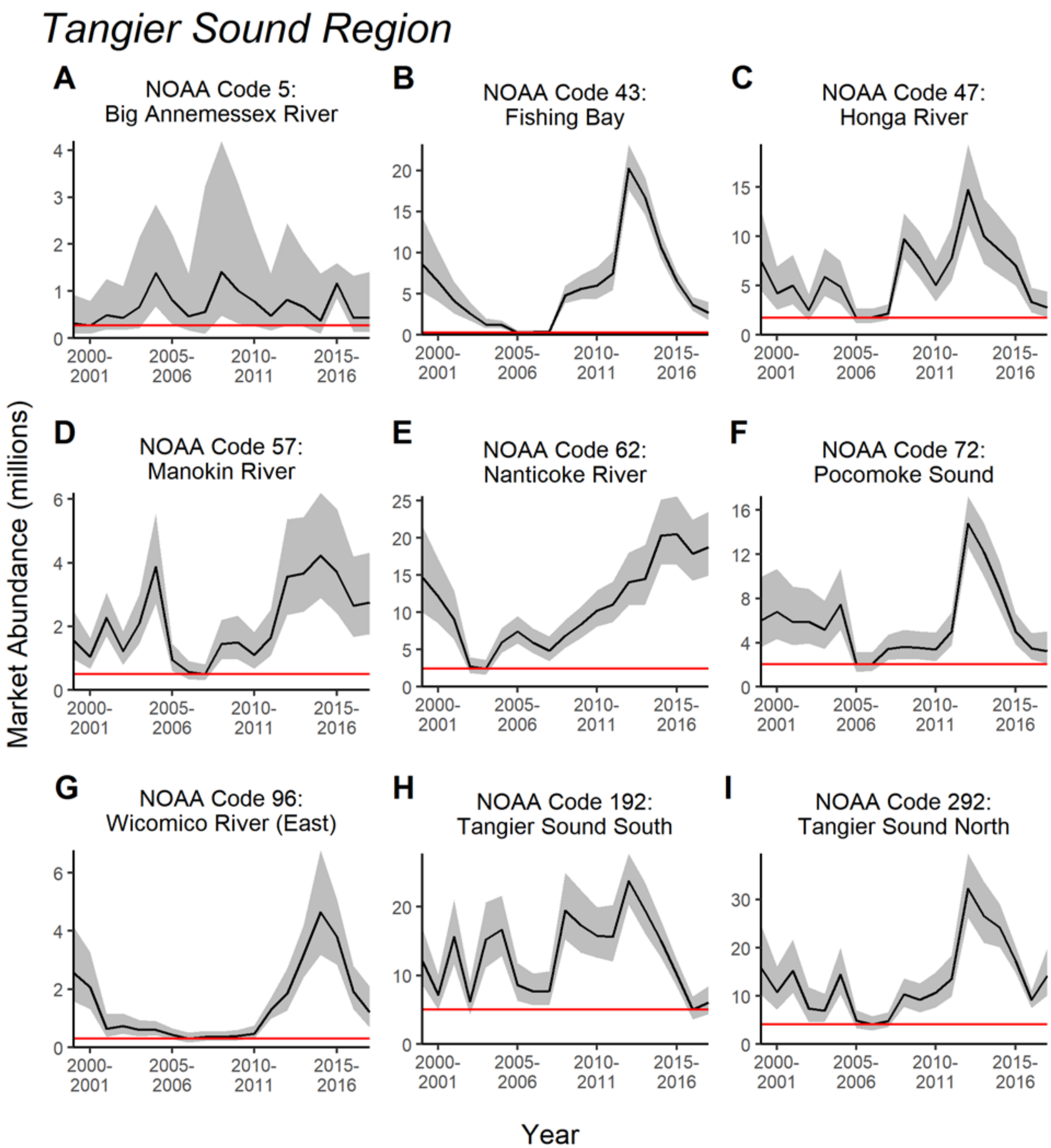

Figure 114. Estimated abundance of market-size oysters (black line) with approximate 95% confidence intervals (gray shaded region) relative to the minimum abundance (lower limit; red horizontal line) reference point for NOAA codes in the Tangier Sound region.

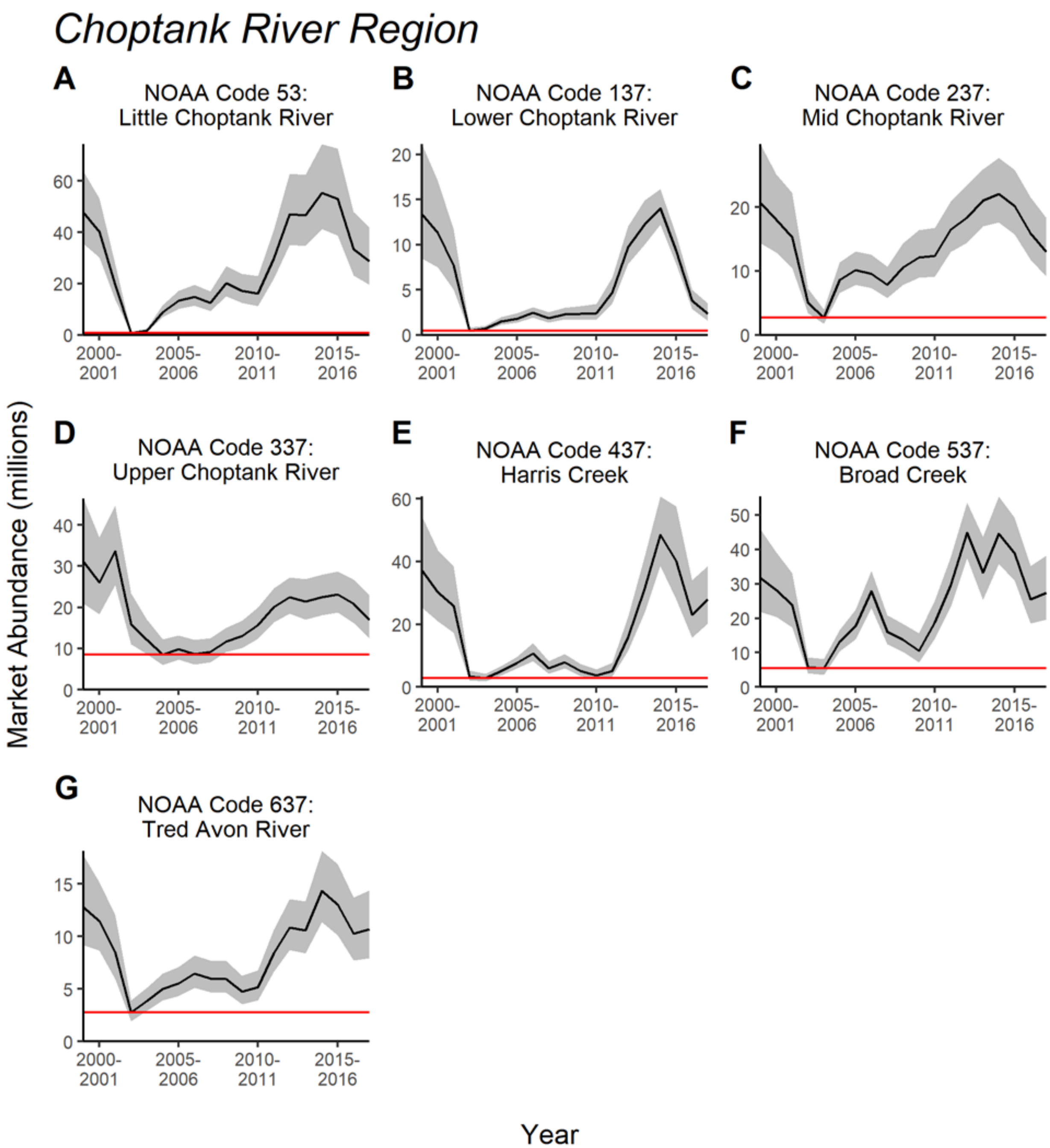

Figure 115. Estimated abundance of market-size oysters (black line) with approximate 95% confidence intervals (gray shaded region) relative to the minimum abundance (lower limit; red horizontal line) reference point for NOAA codes in the Choptank River region.

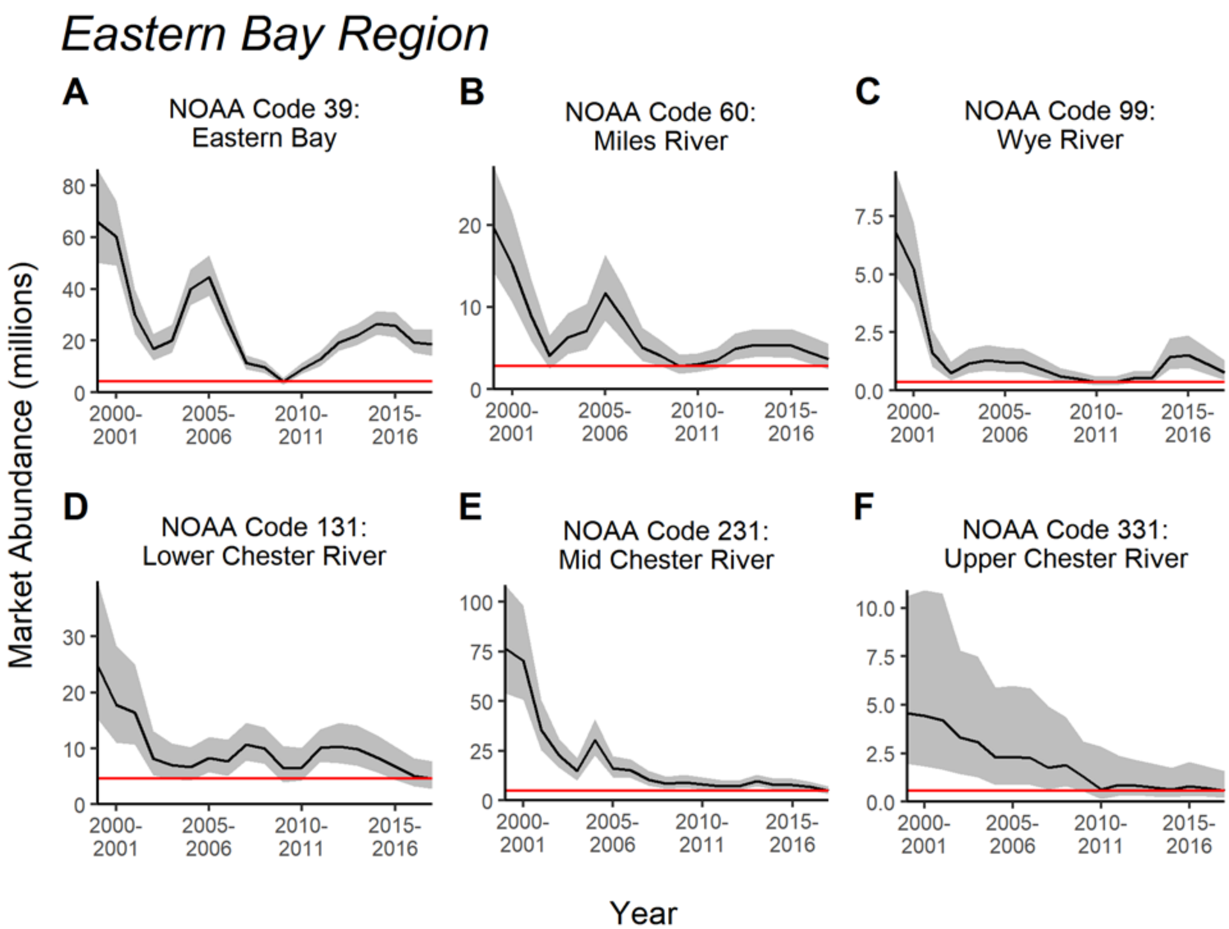

Figure 116. Estimated abundance of market-size oysters (black line) with approximate 95% confidence intervals (gray shaded region) relative to the minimum abundance (lower limit; red horizontal line) reference point for NOAA codes in the Eastern Bay region.

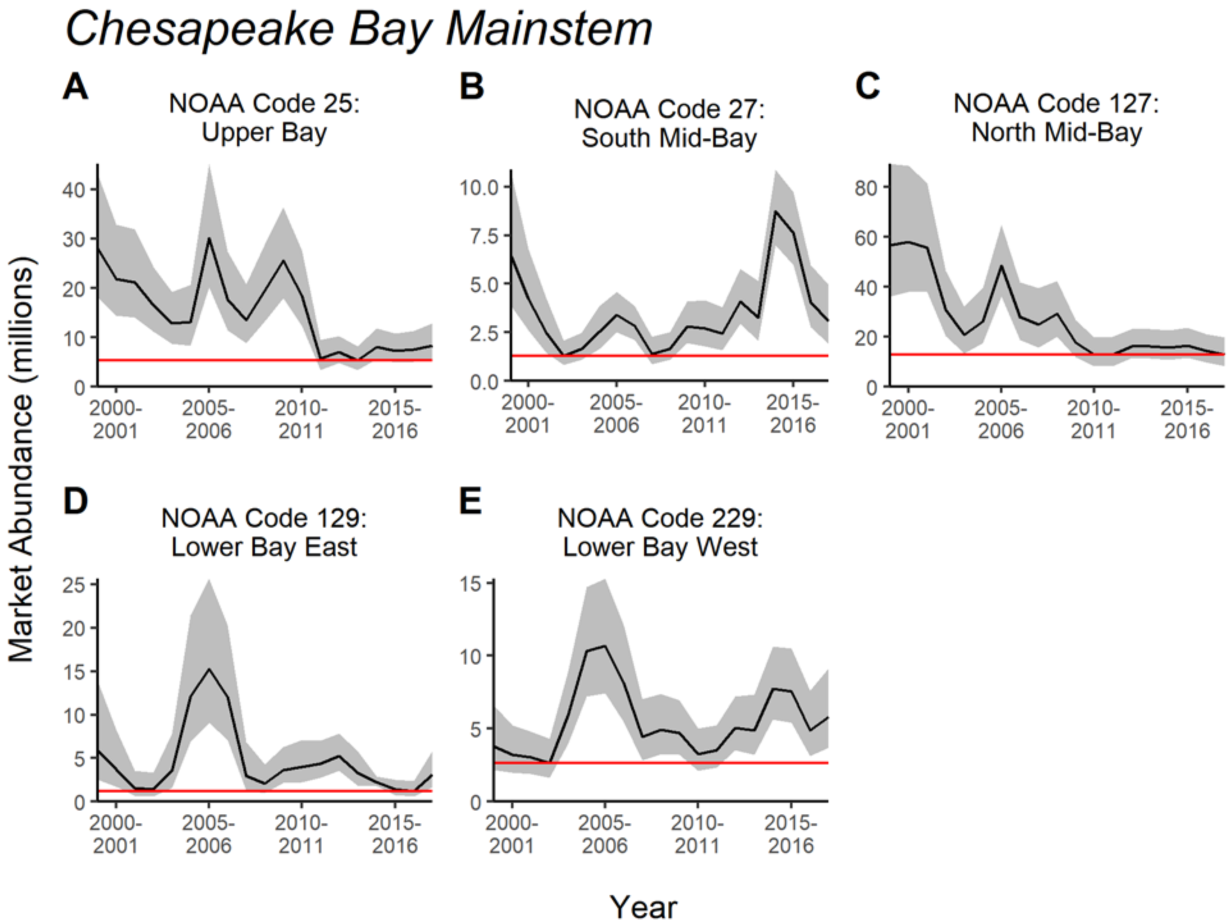

Figure 117. Estimated abundance of market-size oysters (black line) with approximate 95% confidence intervals (gray shaded region) relative to the minimum abundance (lower limit; red horizontal line) reference point for NOAA codes in the Chesapeake Bay Mainstem region.

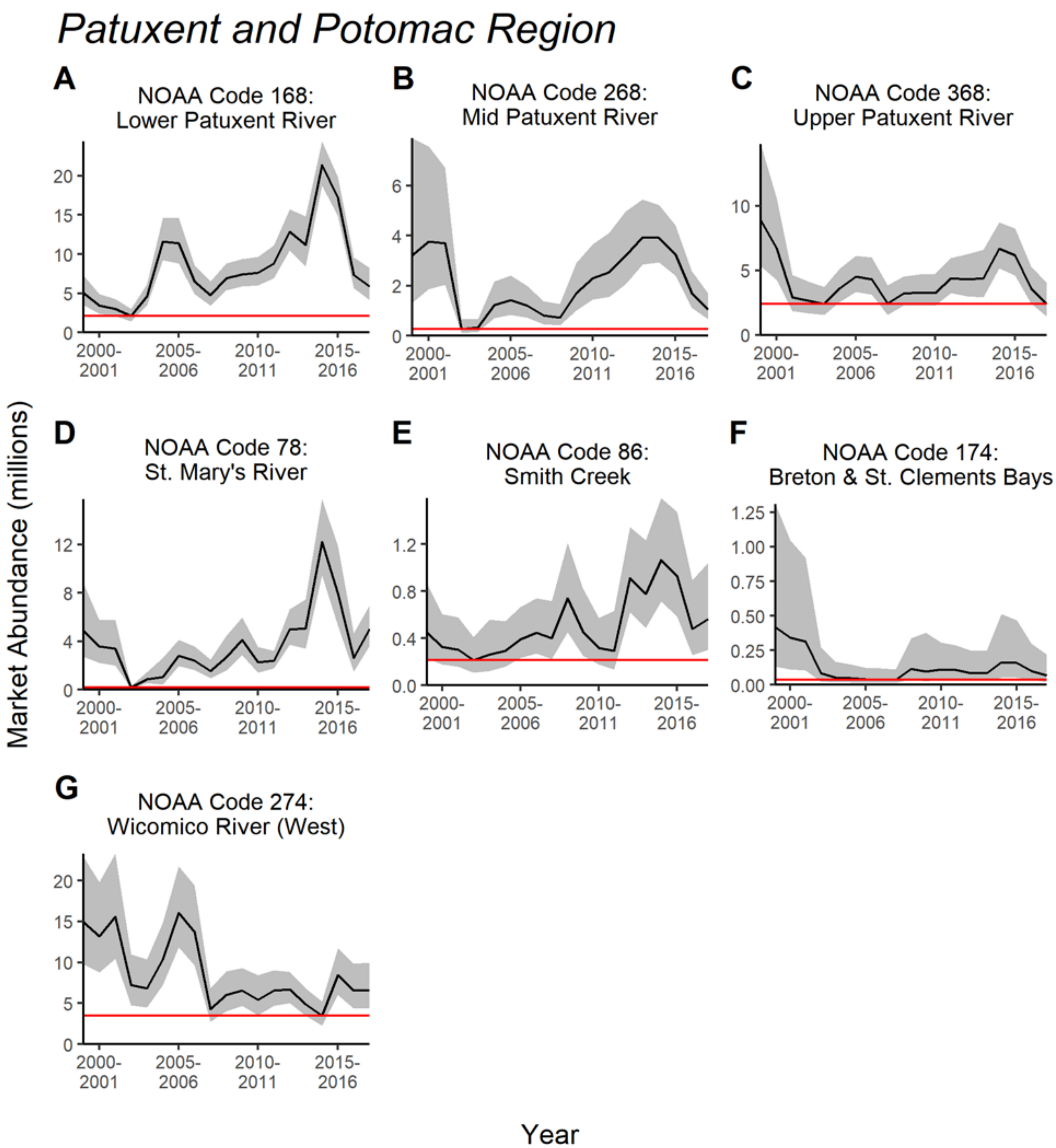

Figure 118. Estimated abundance of market-size oysters (black line) with approximate 95% confidence intervals (gray shaded region) relative to the minimum abundance (lower limit; red horizontal line) reference point for NOAA codes in the Patuxent and Potomac Rivers region.

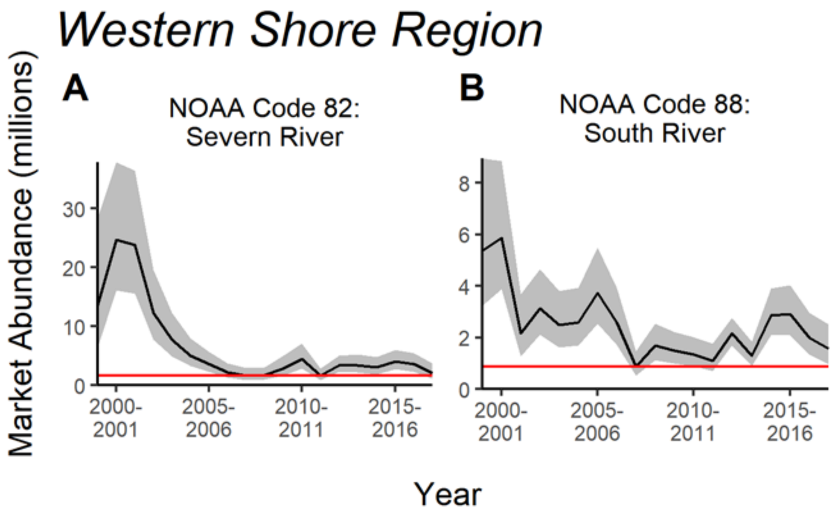

Figure 119. Estimated abundance of market-size oysters (black line) with approximate 95% confidence intervals (gray shaded region) relative to the minimum abundance (lower limit; red horizontal line) reference point for NOAA codes in the Western Shore region.

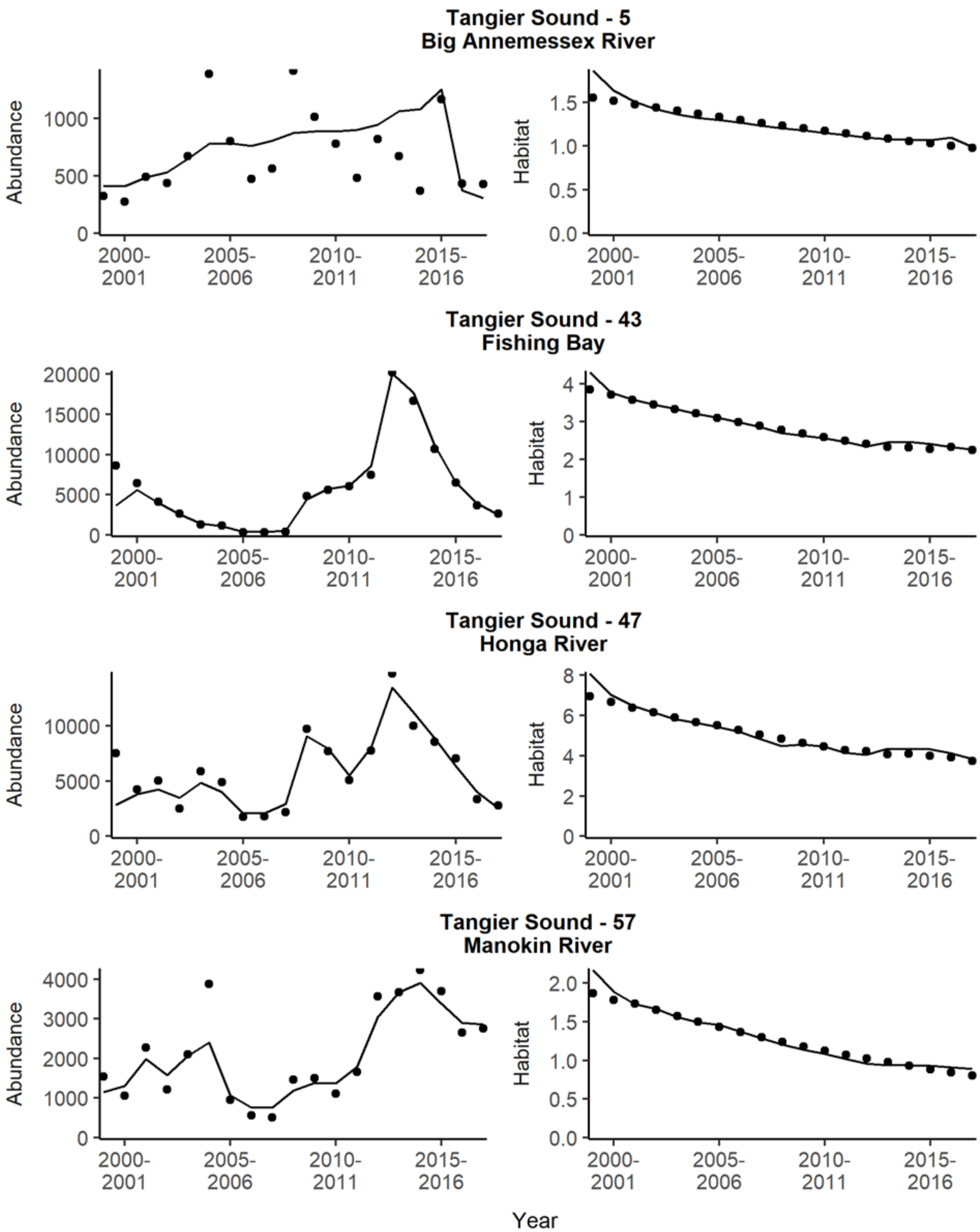

Figure 120. Fits of the reference point model to estimates of market-sized abundance and area of habitat (from the assessment model) by region for each NOAA code. The points indicate stage-structured assessment model estimates and the lines indicate reference point model estimates.

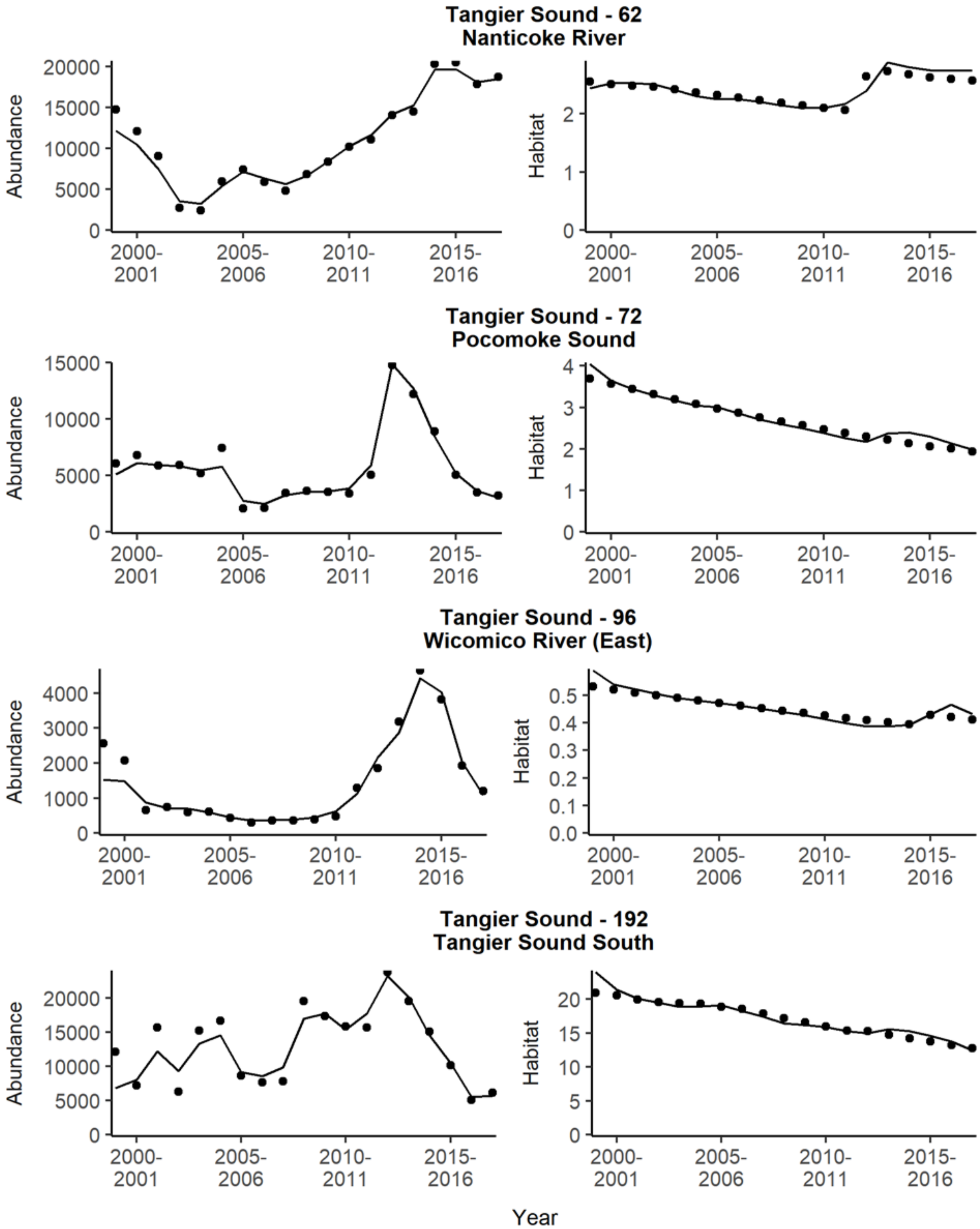

Figure 120 continued.

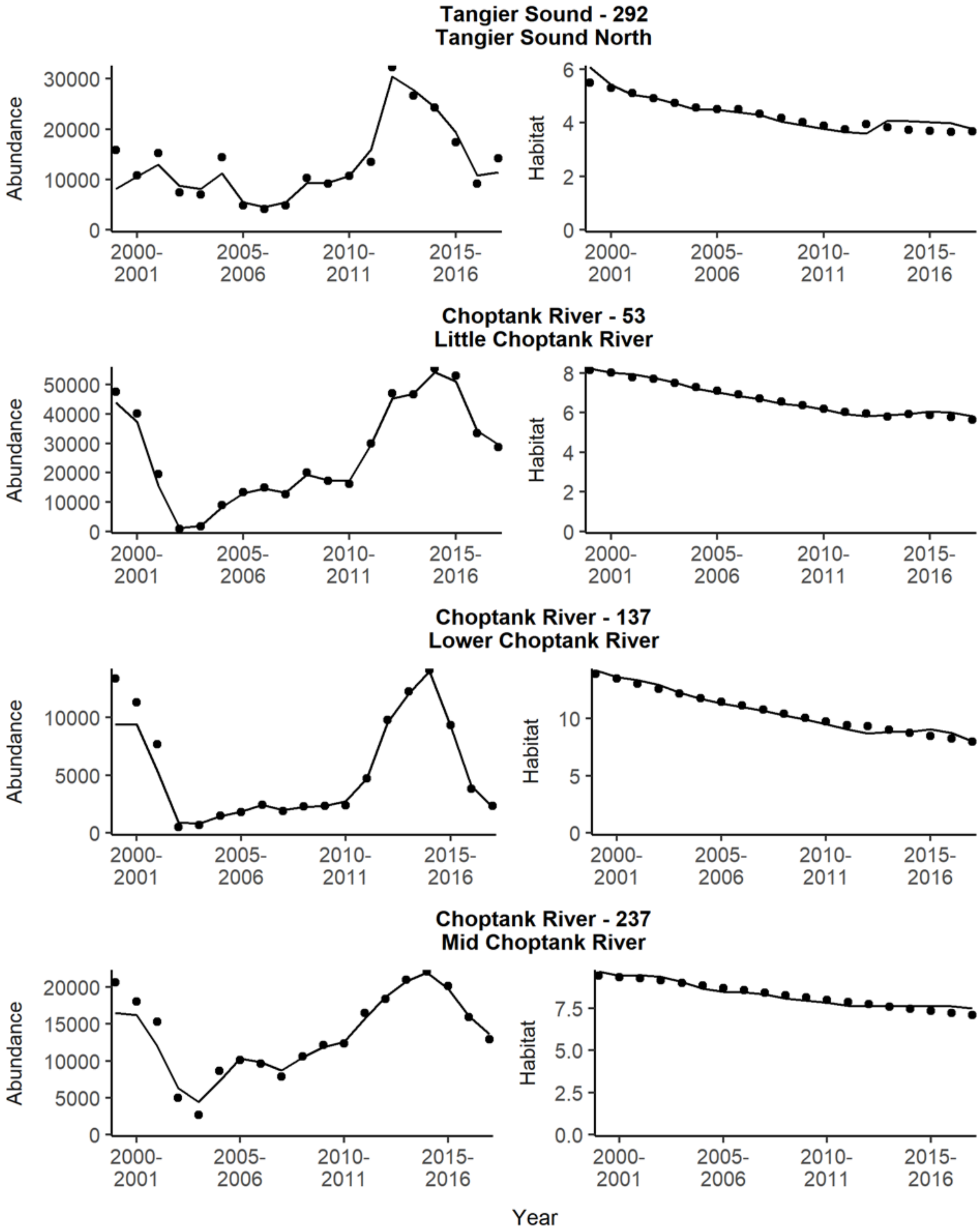

Figure 120 continued.

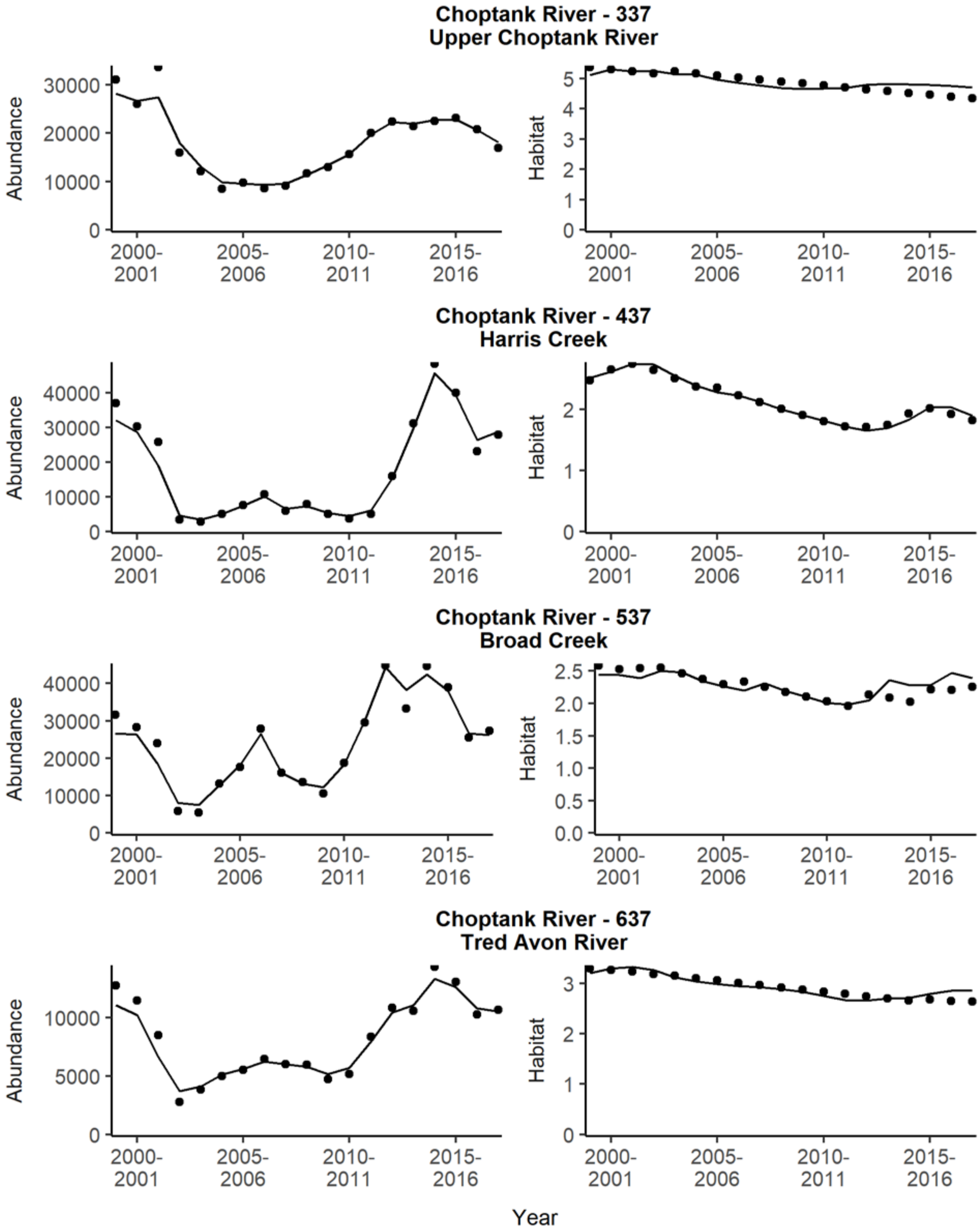

Figure 120 continued.

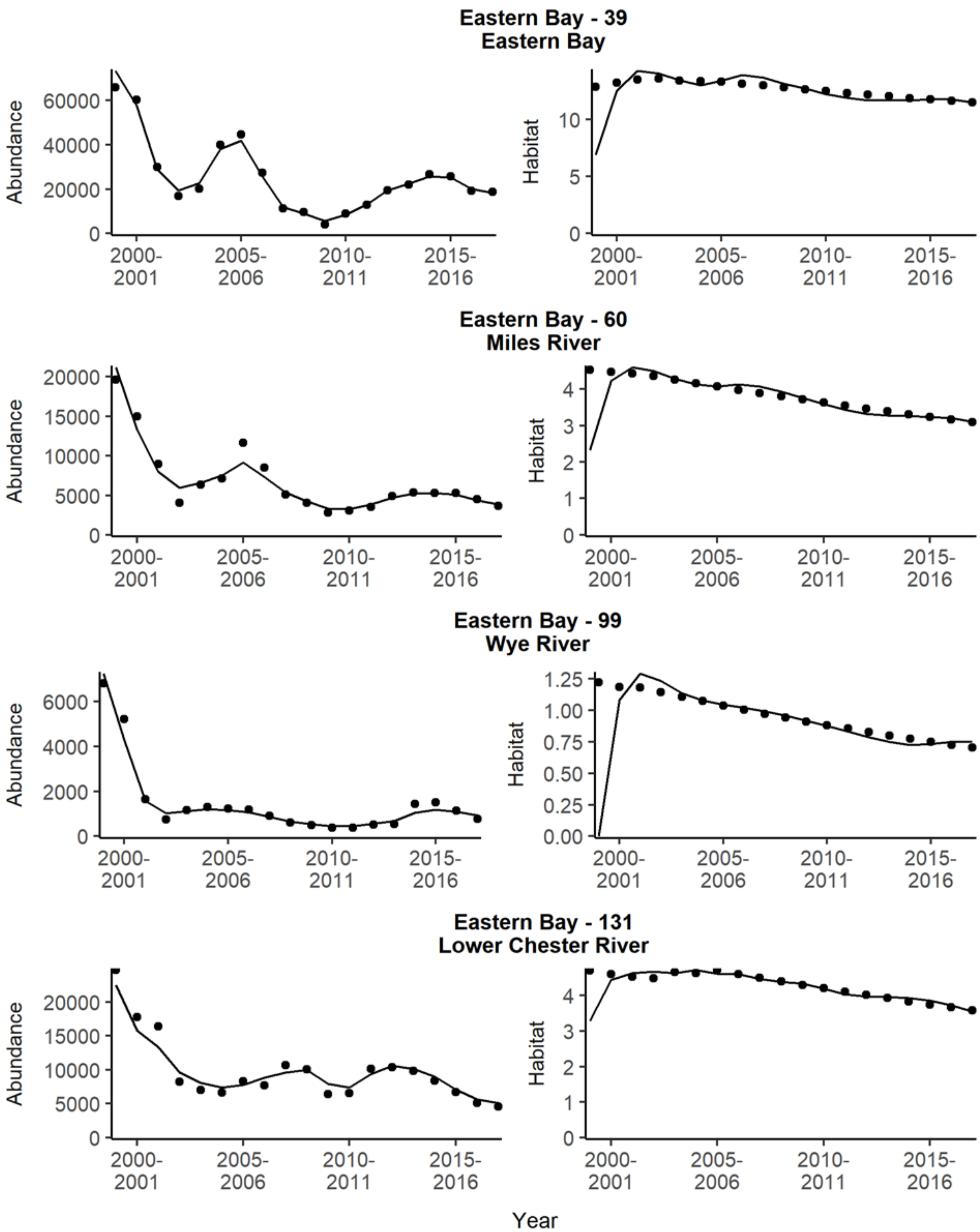

Figure 120 continued.

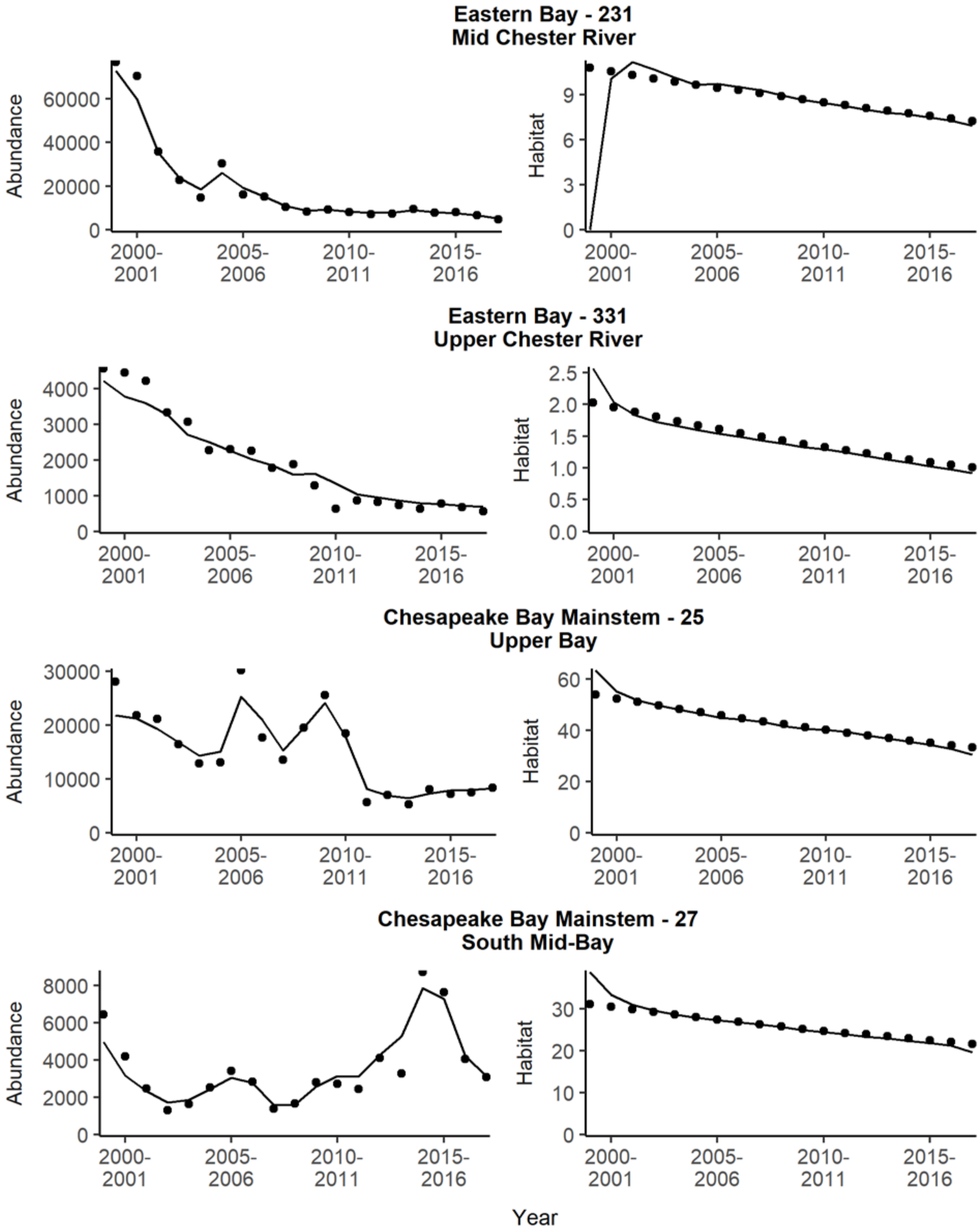

Figure 120 continued.

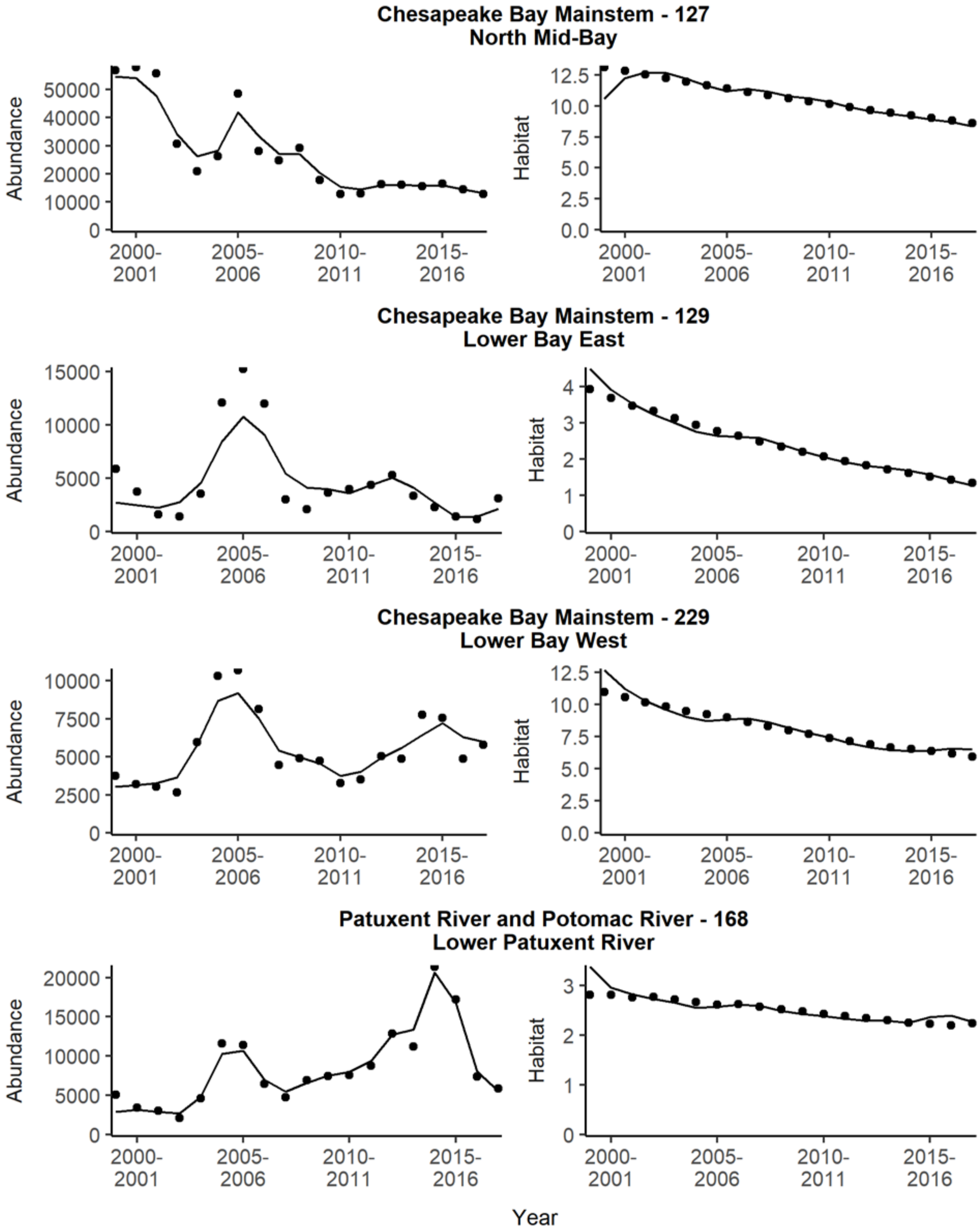

Figure 120 continued.

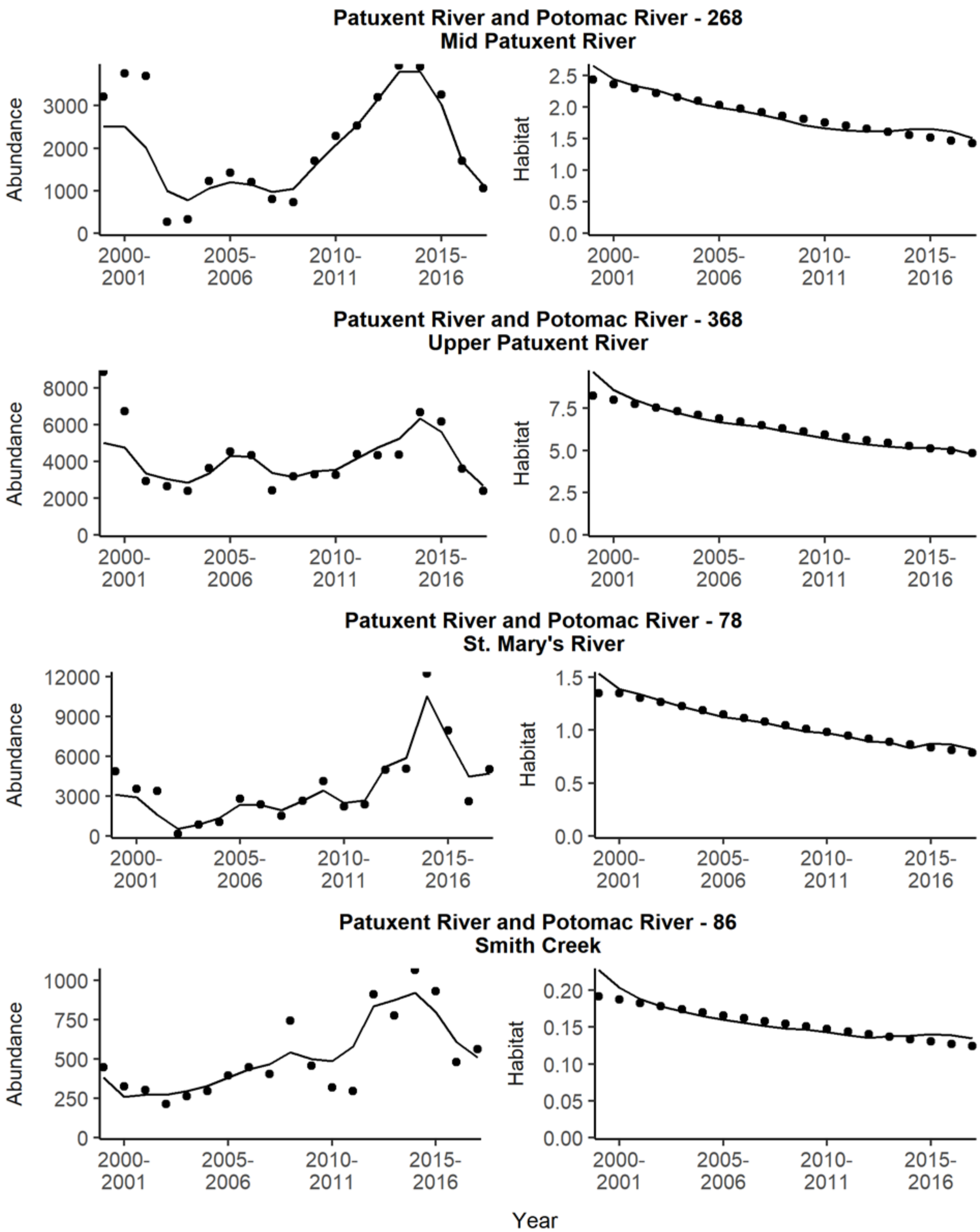

Figure 120 continued.

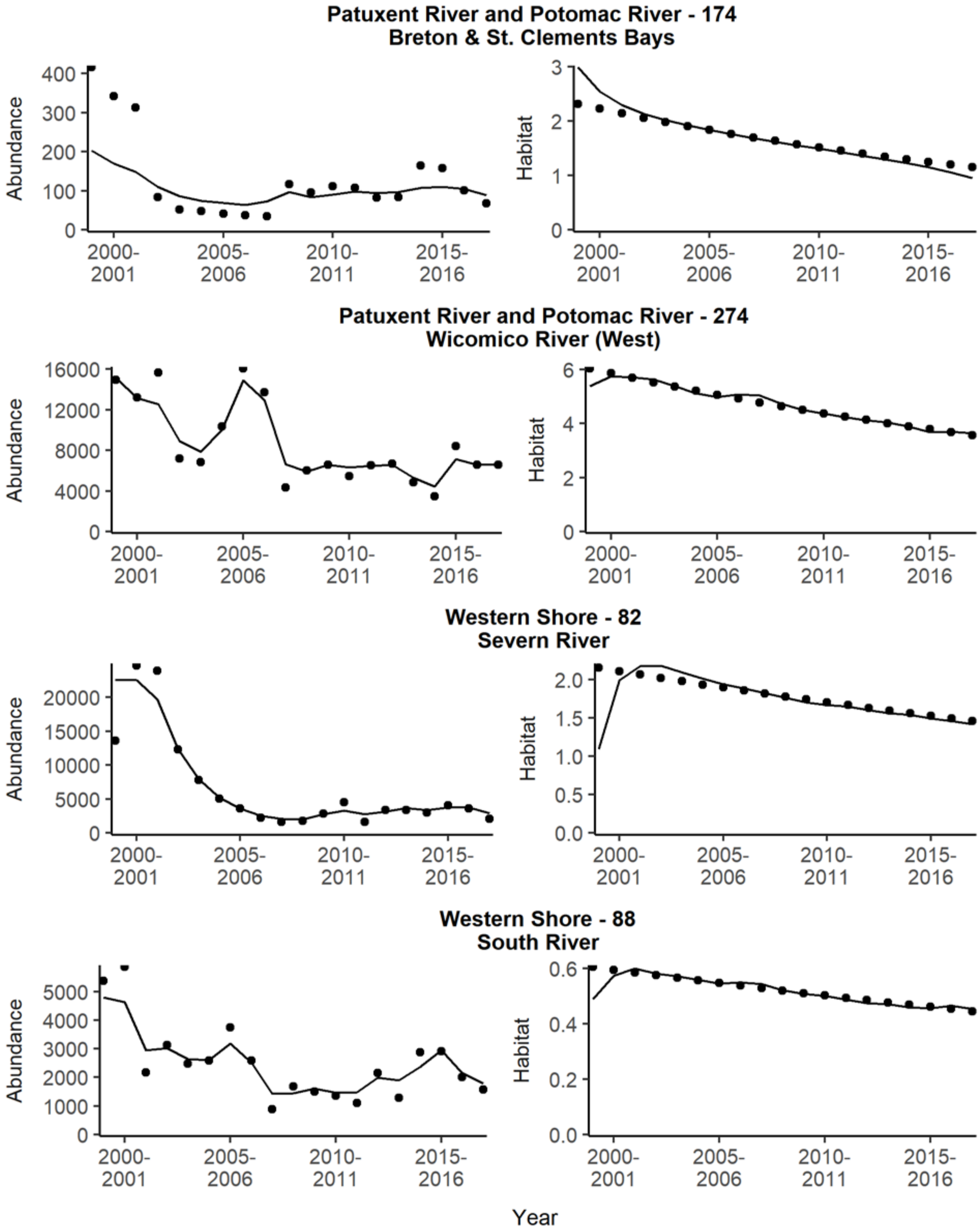

Figure 120 continued.

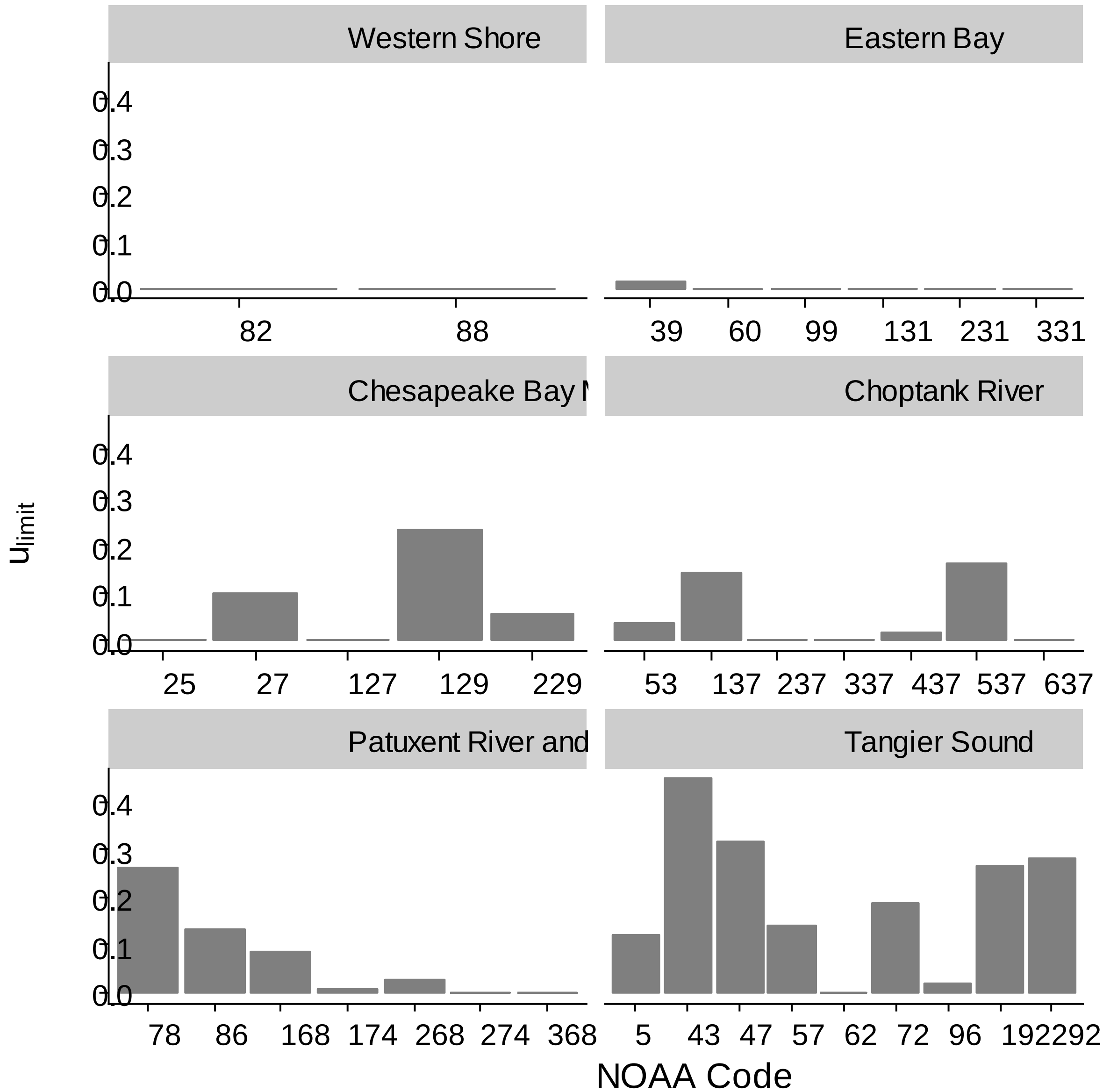

Figure 121. Limit exploitation rate reference point (bars) from the linked population-shell dynamics model by NOAA code. Estimates are grouped by region (panels) and panels are arranged geographically with upper panels representing the northern NOAA codes and the right-most panels representing the eastern most NOAA codes.

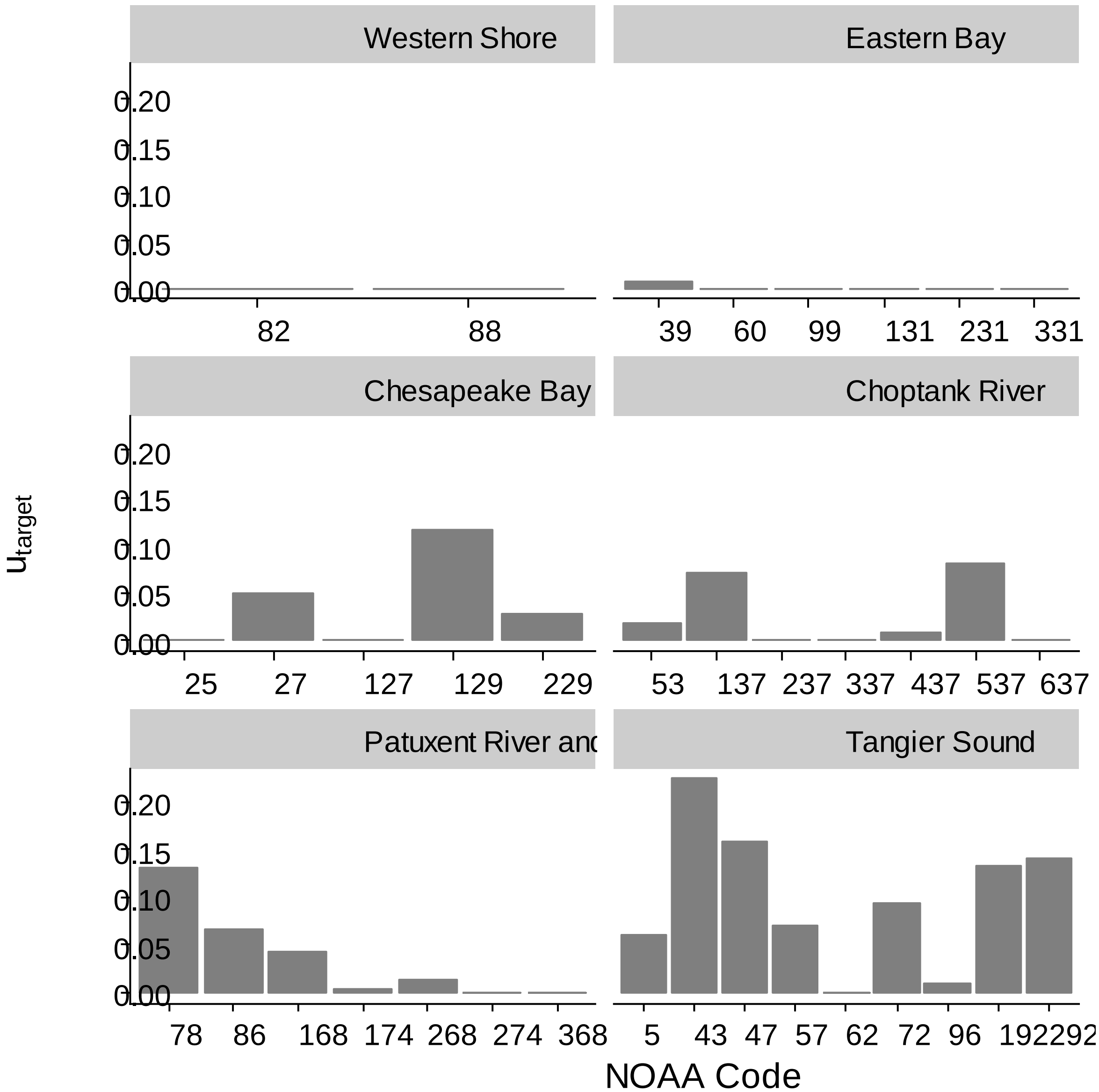

Figure 122. Target exploitation rate reference point (bars) from the linked population-shell dynamics model by NOAA code. Estimates are grouped by region and panel arrangements are the same as figure 121.

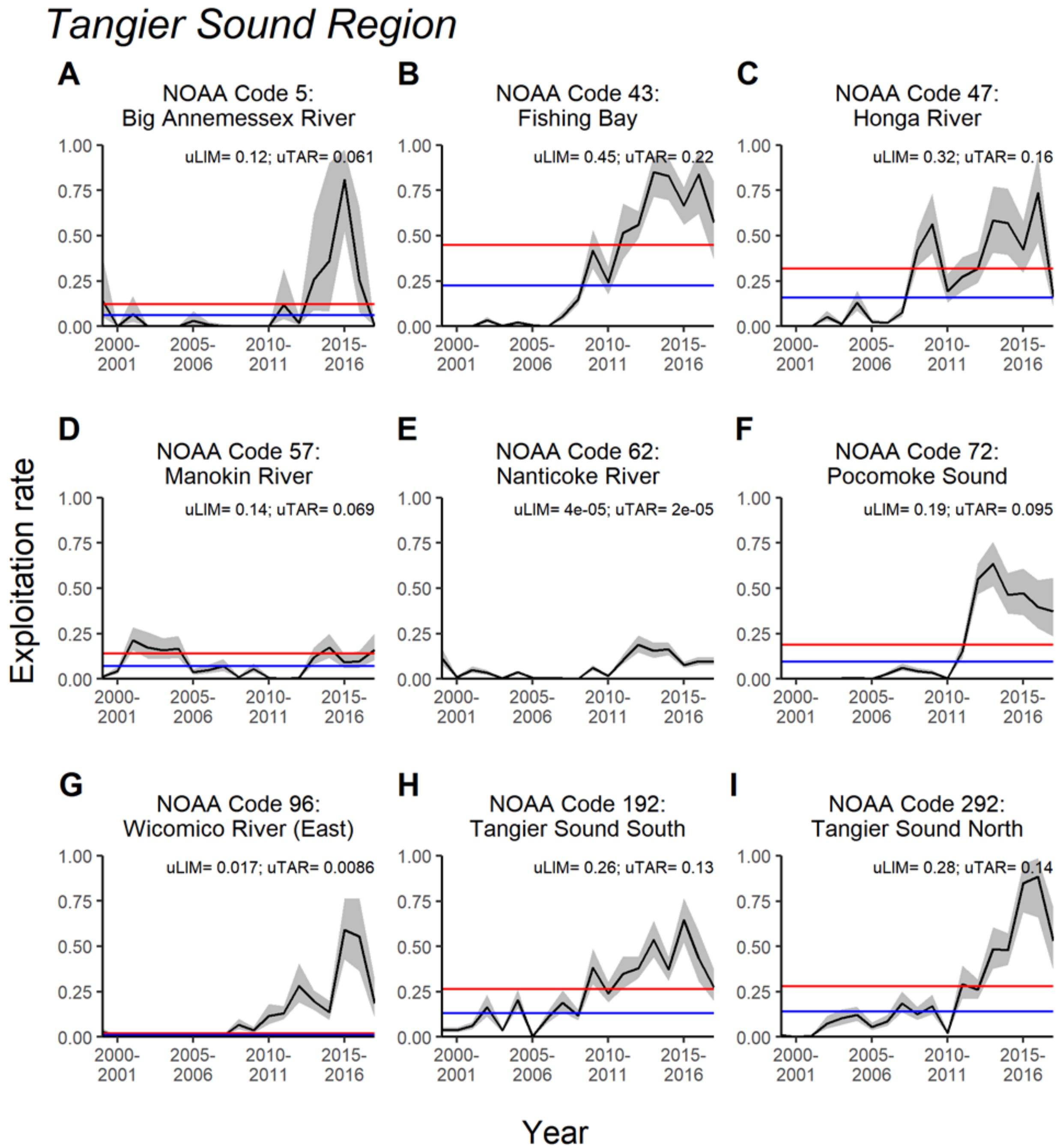

Figure 123. Estimated exploitation rate (black line) with approximate 95% confidence intervals (gray shaded region relative to the upper limit (red horizontal line) exploitation rate reference point and target (blue horizontal line) exploitation rate reference point for NOAA codes in the Tangier Sound region. The absence of red and blue horizontal lines indicates estimates very close to zero.

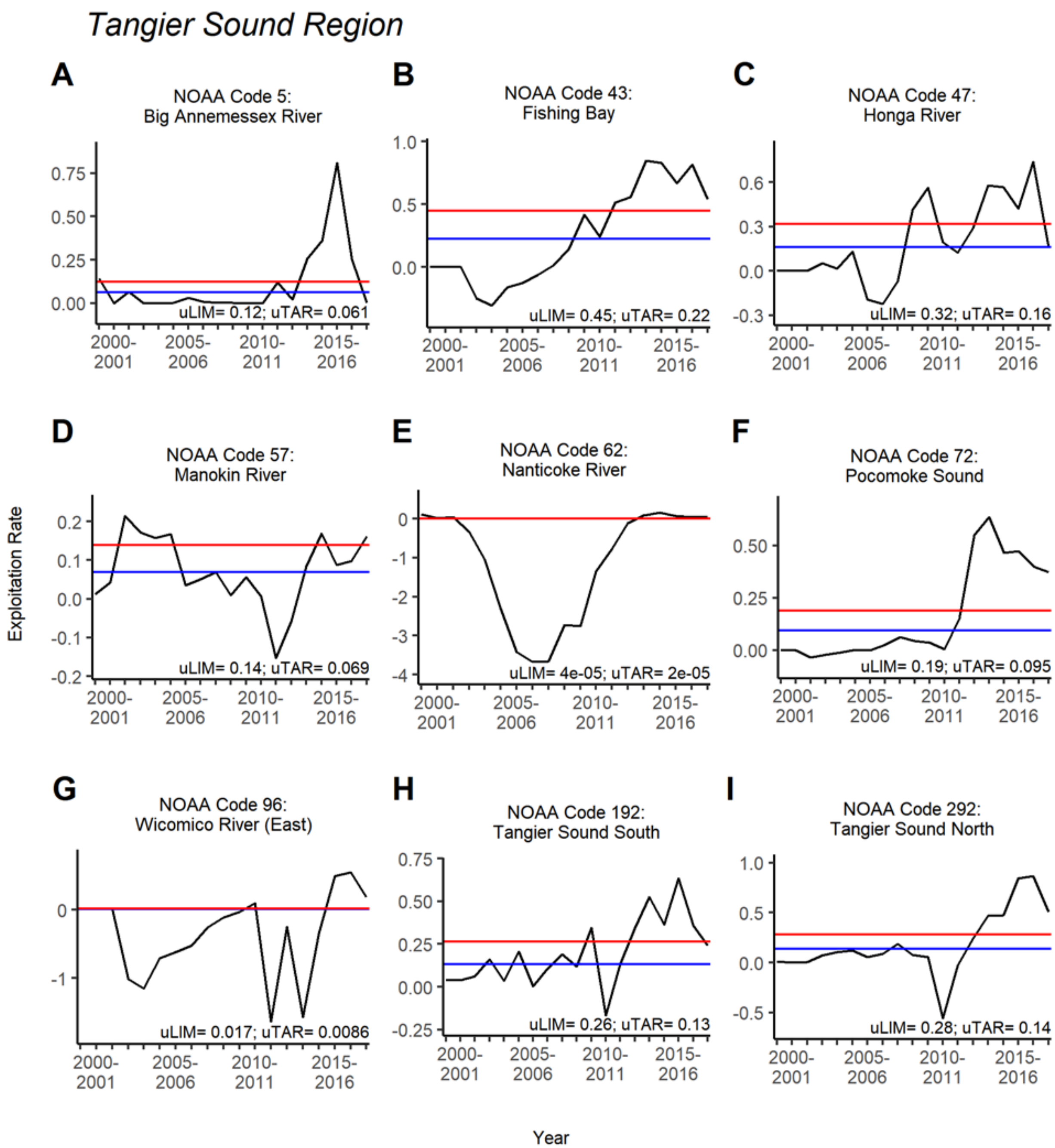

Figure 124. Comparison of the exploitation rate (adjusted for plantings) to the target (uTAR) and limit (uLIM) reference points over time for the Tangier Sound region. A negative exploitation rate indicates that harvest was less than the number of estimated market oysters from plantings.

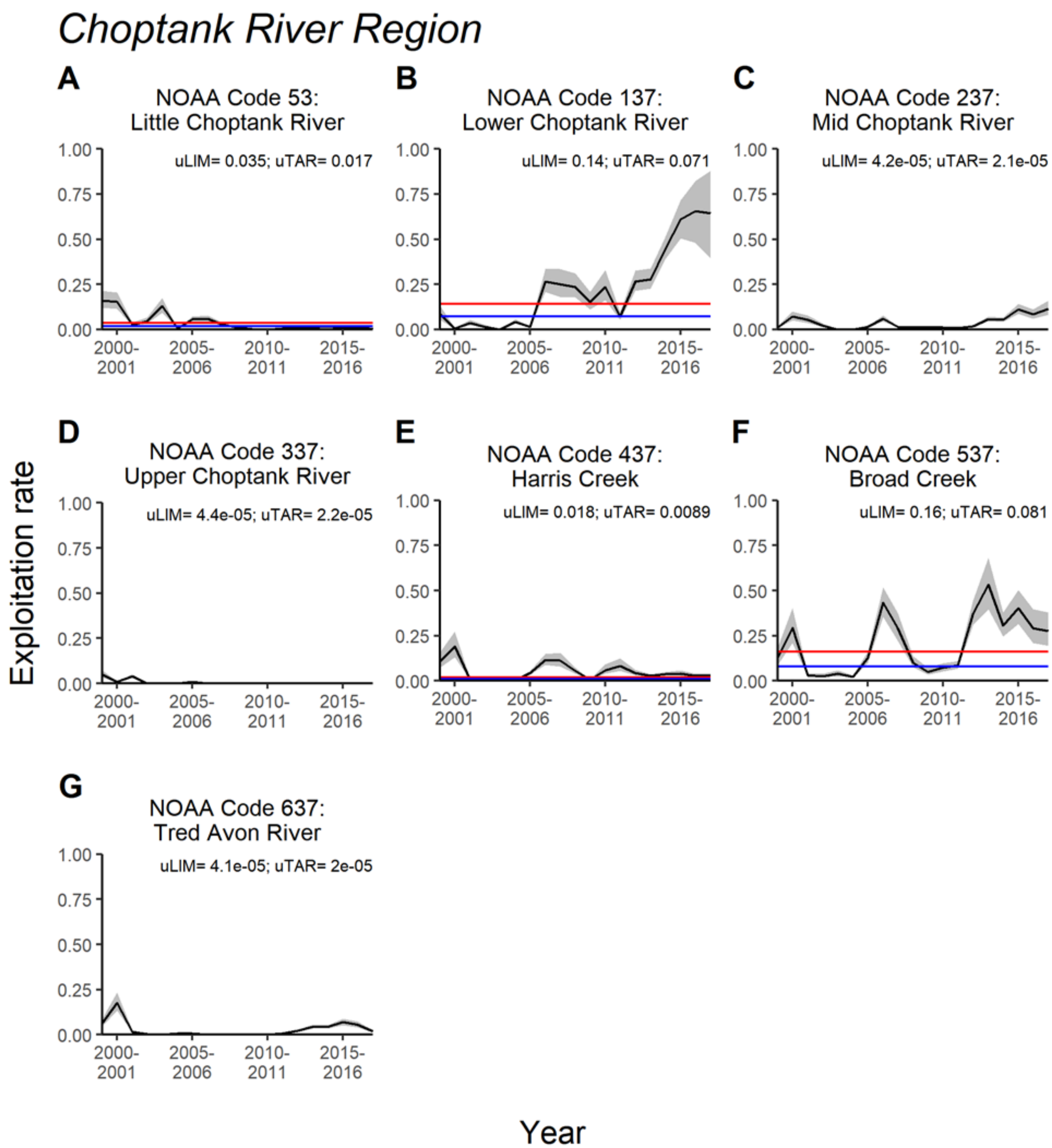

Figure 125. Estimated exploitation rate (black line) with approximate 95% confidence intervals (gray shaded region relative to the upper limit (red horizontal line) exploitation rate reference point and target (blue horizontal line) exploitation rate reference point for NOAA codes in the Choptank RIver region. The absence of red and blue horizontal lines indicates estimates very close to zero.

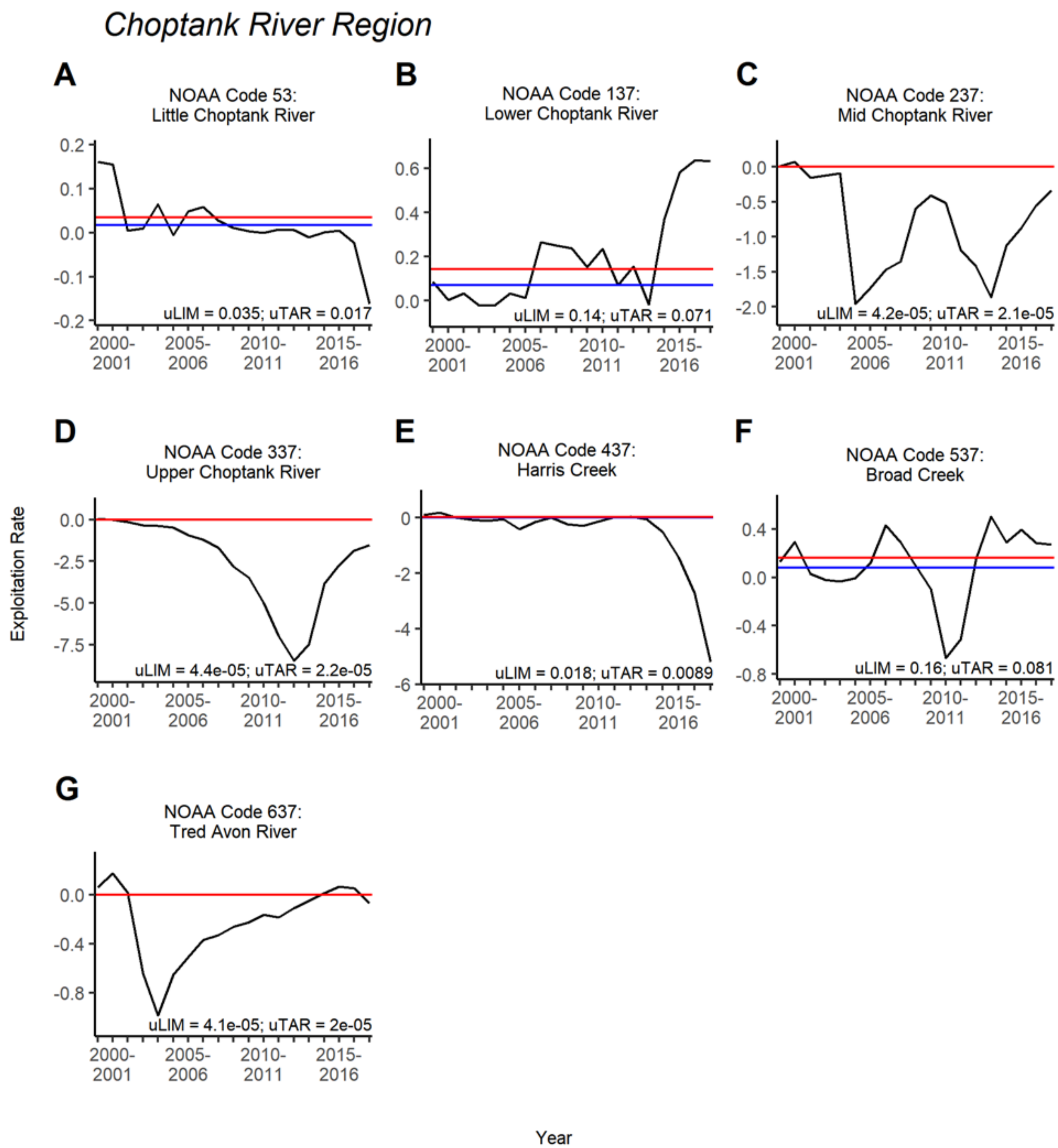

Figure 126. Comparison of the exploitation rate (adjusted for plantings) to the target (uTAR) and limit (uLIM) reference points over time for the Choptank River region. A negative exploitation rate indicates that harvest was less than the number of estimated market oysters from plantings.

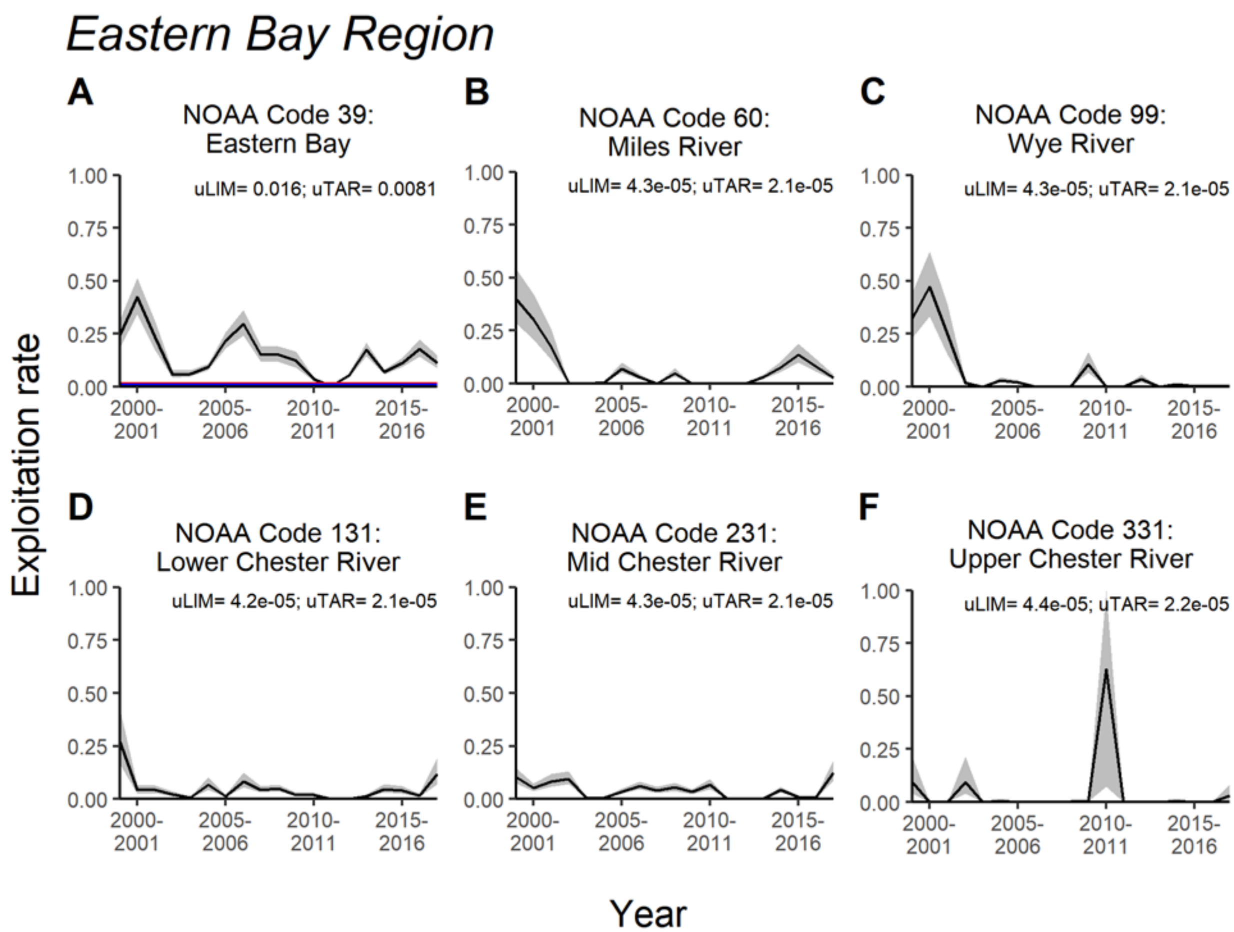

Figure 127. Estimated exploitation rate (black line) with approximate 95% confidence intervals (gray shaded region relative to the upper limit (red horizontal line) exploitation rate reference point and target (blue horizontal line) exploitation rate reference point for NOAA codes in the Eastern Bay region. The absence of red and blue horizontal lines indicates estimates very close to zero.

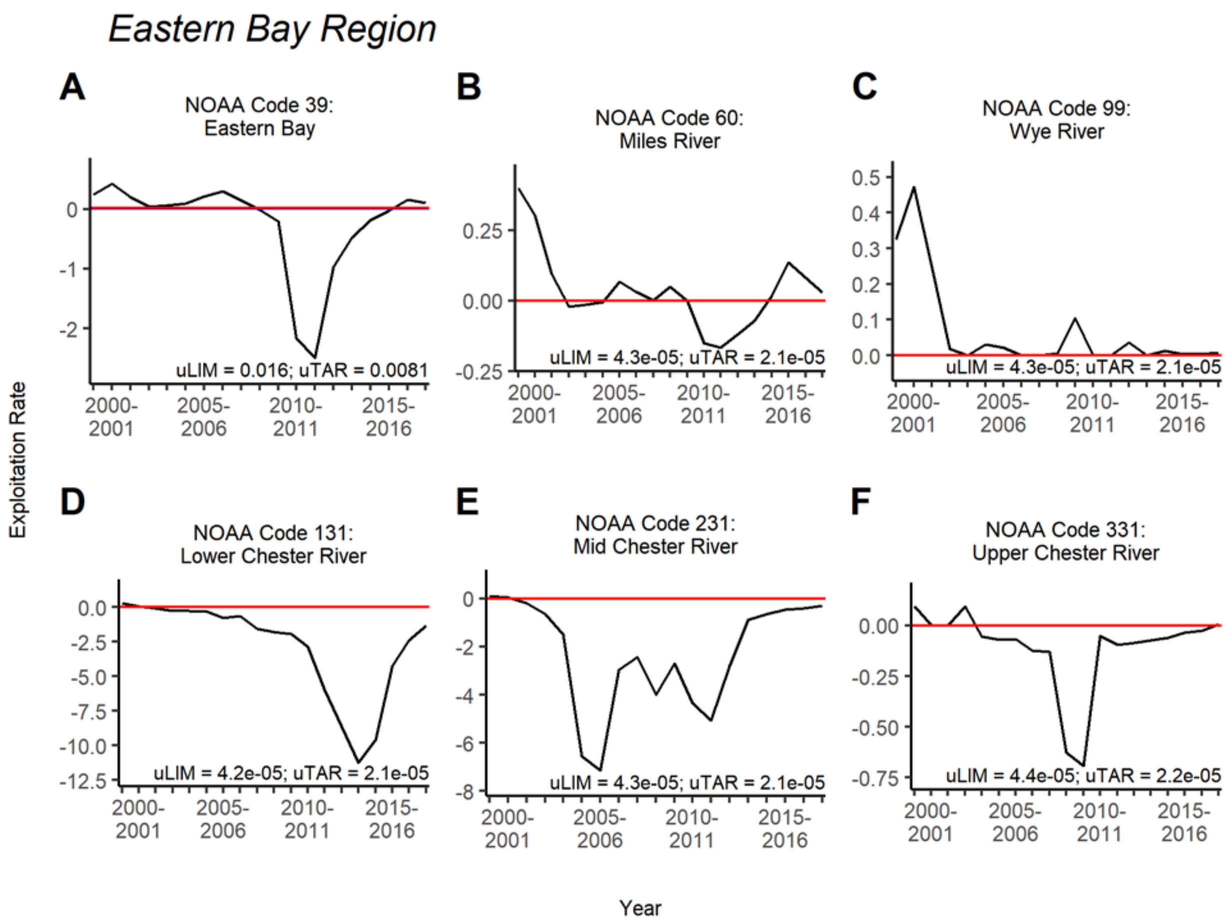

Figure 128. Comparison of the exploitation rate (adjusted for plantings) to the target (uTAR) and limit (uLIM) reference points over time for the Eastern Bay region. A negative exploitation rate indicates that harvest was less than the number of estimated market oysters from plantings.

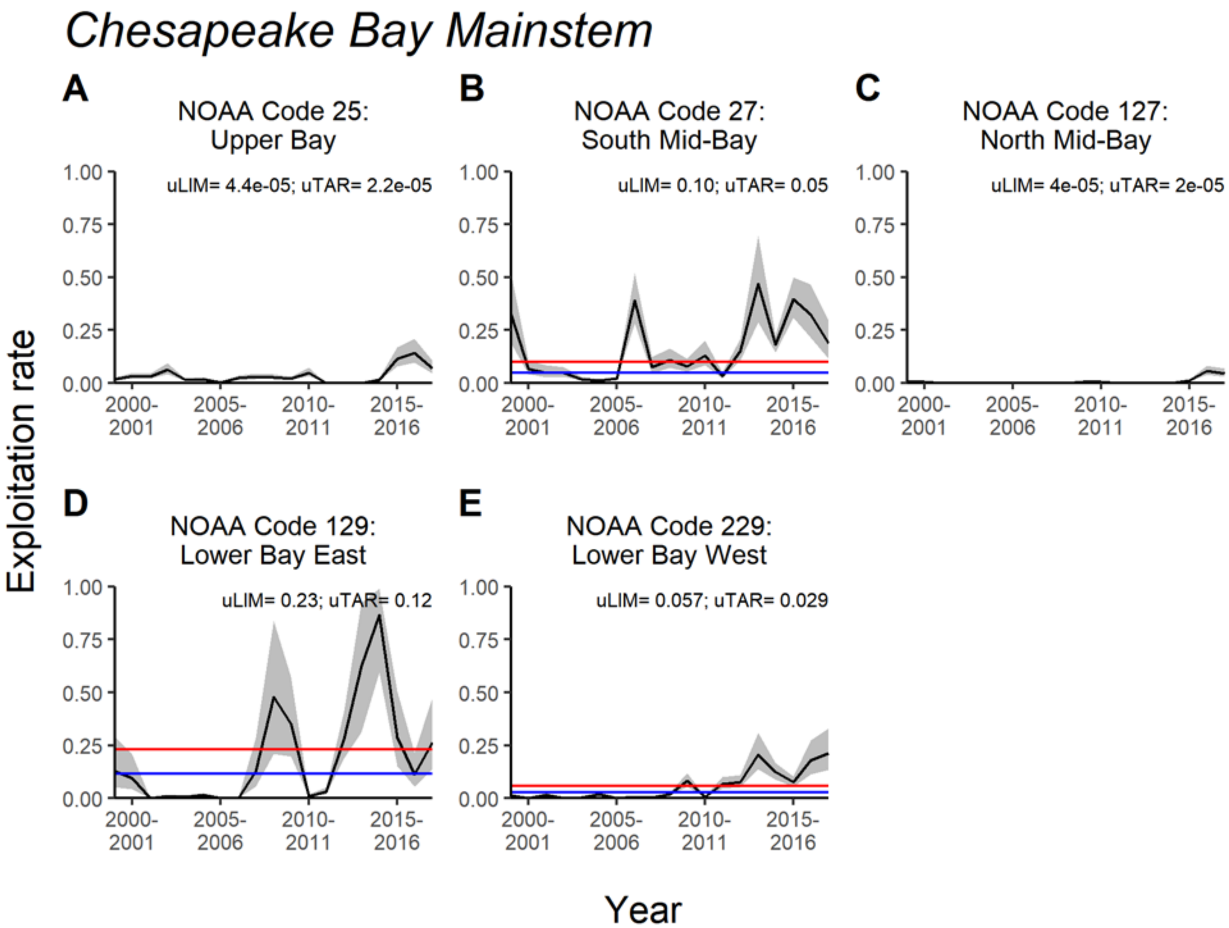

Figure 129. Estimated exploitation rate (black line) with approximate 95% confidence intervals (gray shaded region relative to the upper limit (red horizontal line) exploitation rate reference point and target (blue horizontal line) exploitation rate reference point for NOAA codes in the Chesapeake Bay Mainstem region. The absence of red and blue horizontal lines indicates estimates very close to zero.

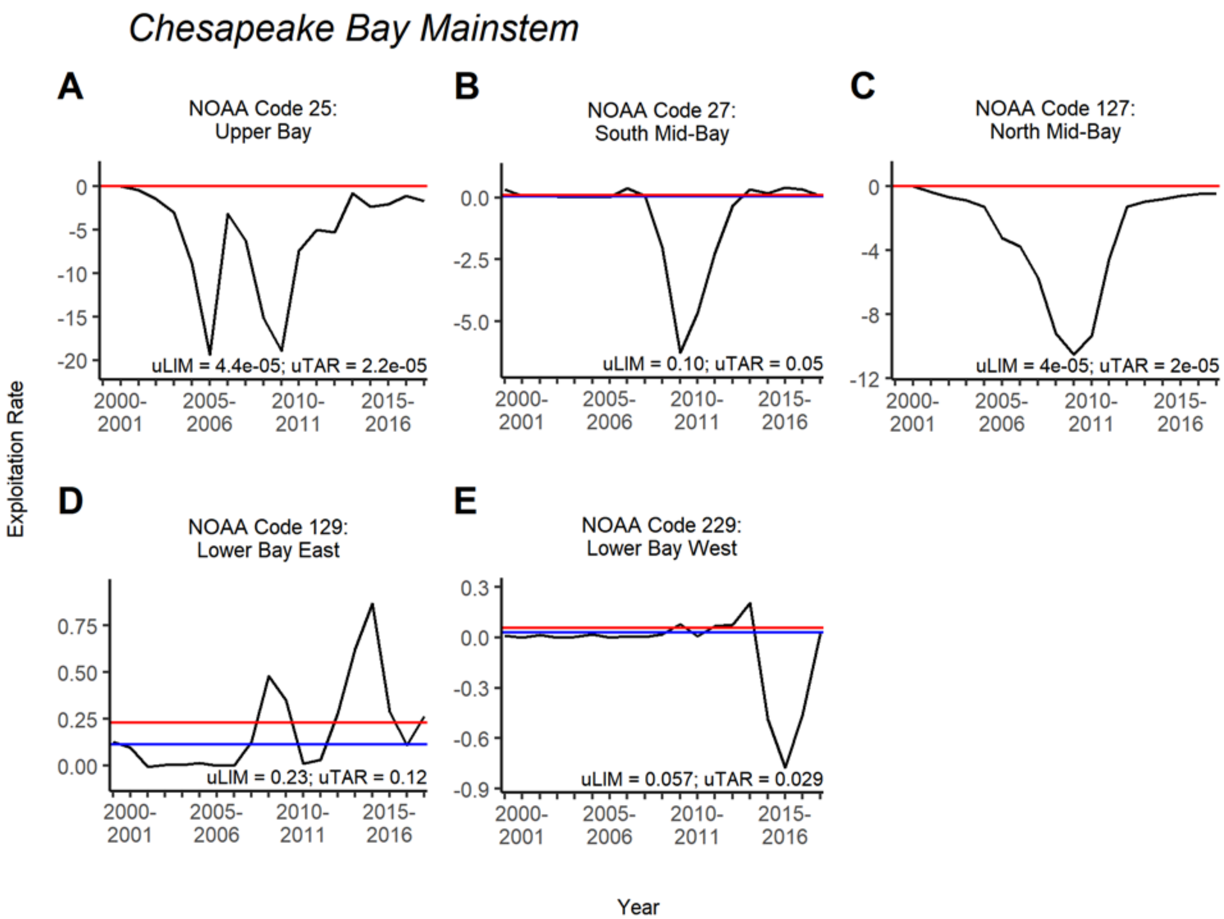

Figure 130. Comparison of the exploitation rate (adjusted for plantings) to the target (uTAR) and limit (uLIM) reference points over time for the Chesapeake Bay Mainstem region. A negative exploitation rate indicates that harvest was less than the number of estimated market oysters from plantings.

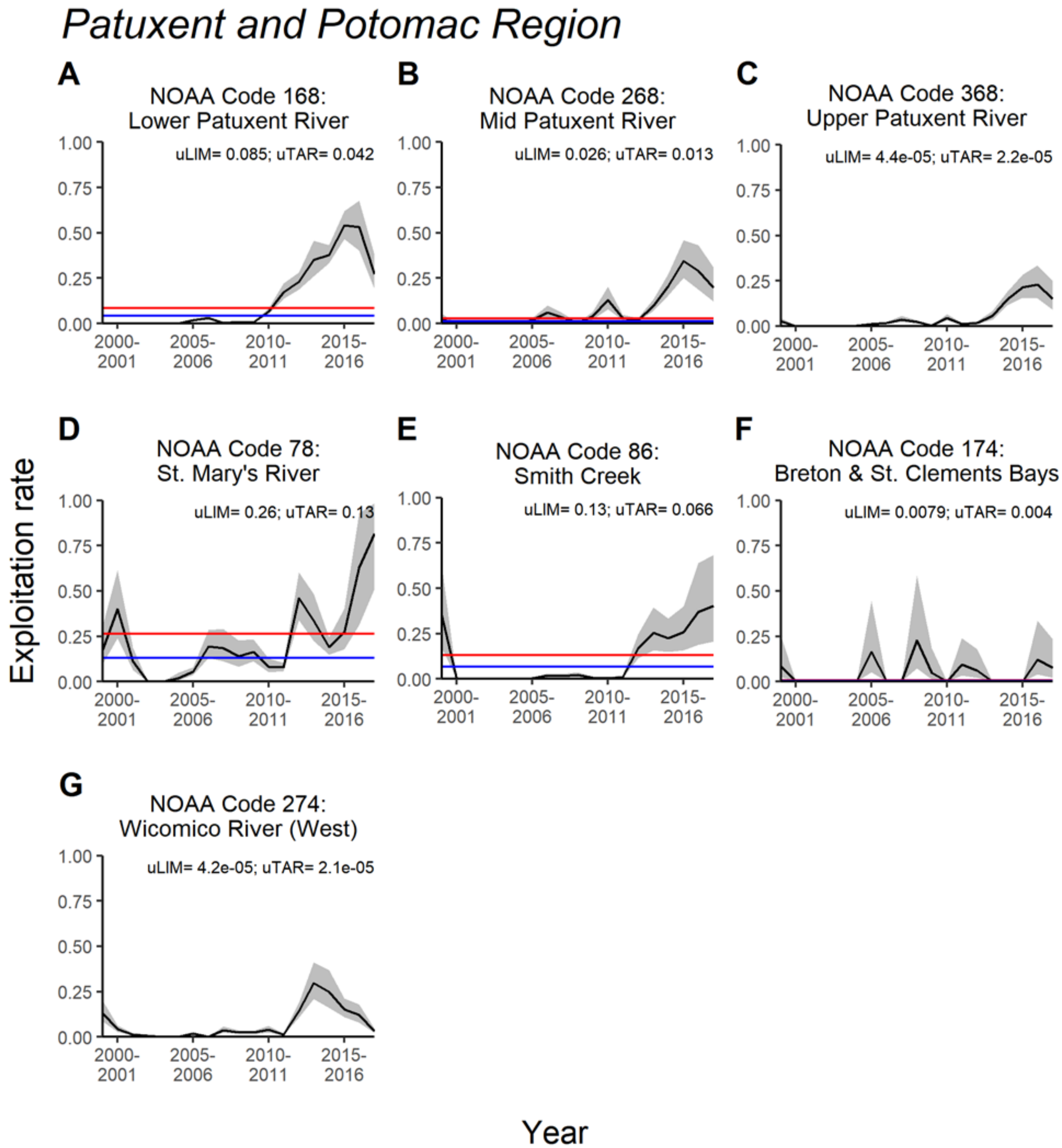

Figure 131. Estimated exploitation rate (black line) with approximate 95% confidence intervals (gray shaded region relative to the upper limit (red horizontal line) exploitation rate reference point and target (blue horizontal line) exploitation rate reference point for NOAA codes in the Patuxent and Potomac Rivers region. The absence of red and blue horizontal lines indicates estimates very close to zero.

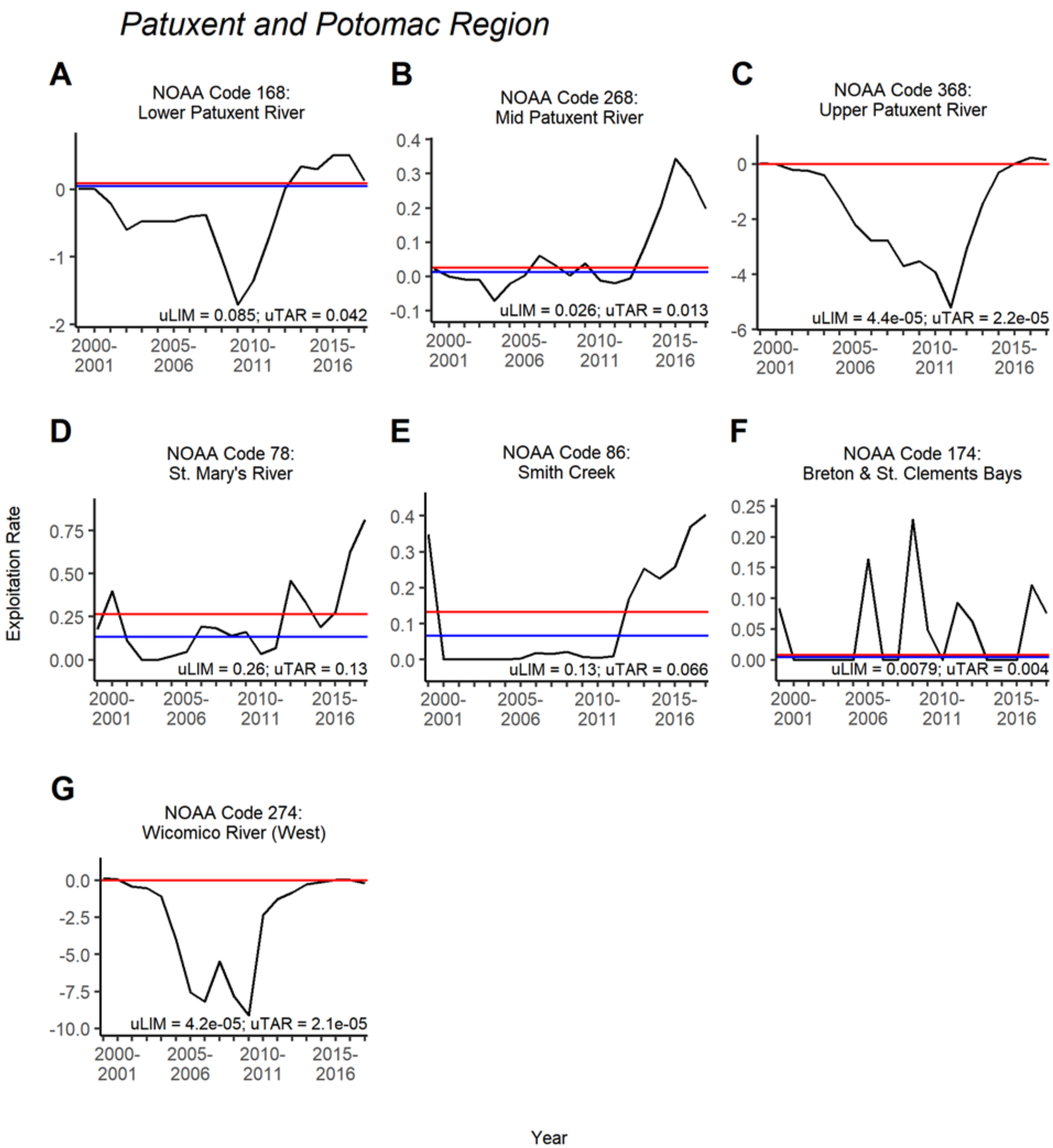

Figure 132. Comparison of the exploitation rate (adjusted for plantings) to the target (uTAR) and limit (uLIM) reference points over time for the Patuxent and Potomac rivers region. A negative exploitation rate indicates that harvest was less than the number of estimated market oysters from plantings.

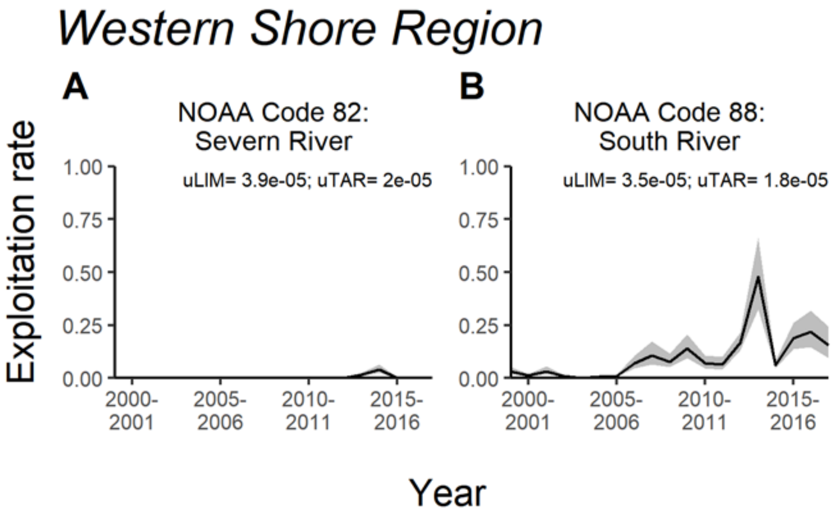

Figure 133. Estimated exploitation rate (black line) with approximate 95% confidence intervals (gray shaded region relative to the upper limit (red horizontal line) exploitation rate reference point and target (blue horizontal line) exploitation rate reference point for NOAA codes in the Western Shore region. The absence of red and blue horizontal lines indicates estimates very close to zero.

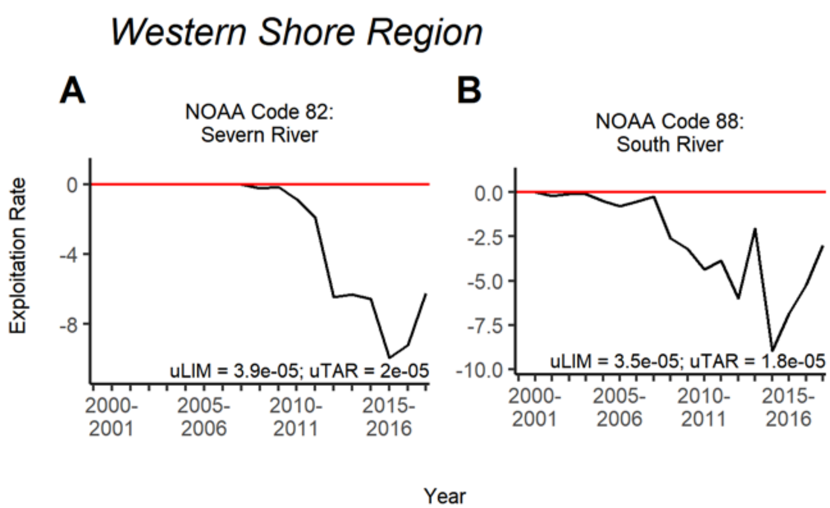

Figure 134. Comparison of the exploitation rate (adjusted for plantings) to the target (uTAR) and limit (uLIM) reference points over time for the Western Shore region. A negative exploitation rate indicates that harvest was less than the number of estimated market oysters from plantings.

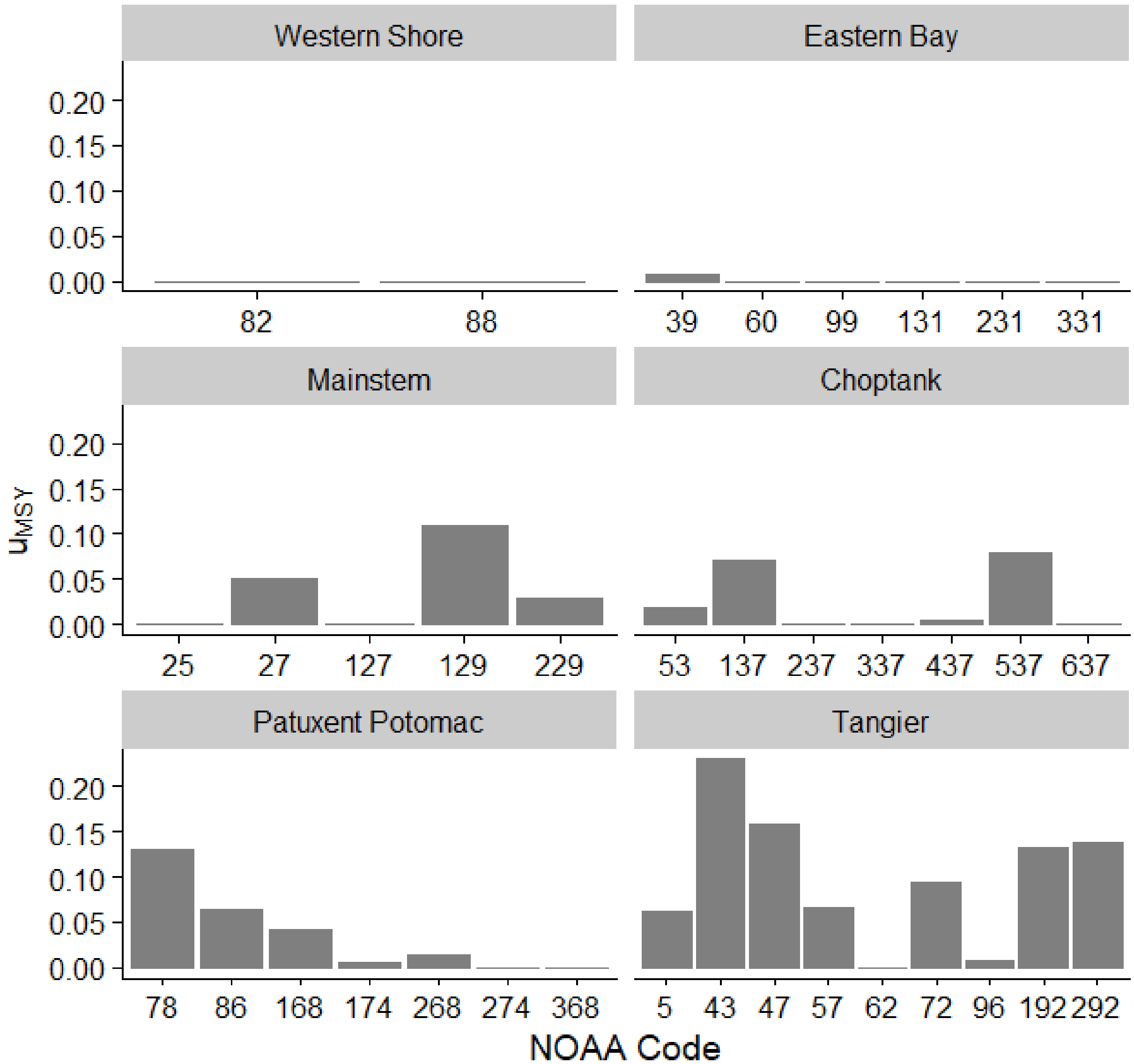

Figure 135. Estimates for the target exploitation reference point (U_{MSY}) for each NOAA Code in the sensitivity analysis when d = 0.08.

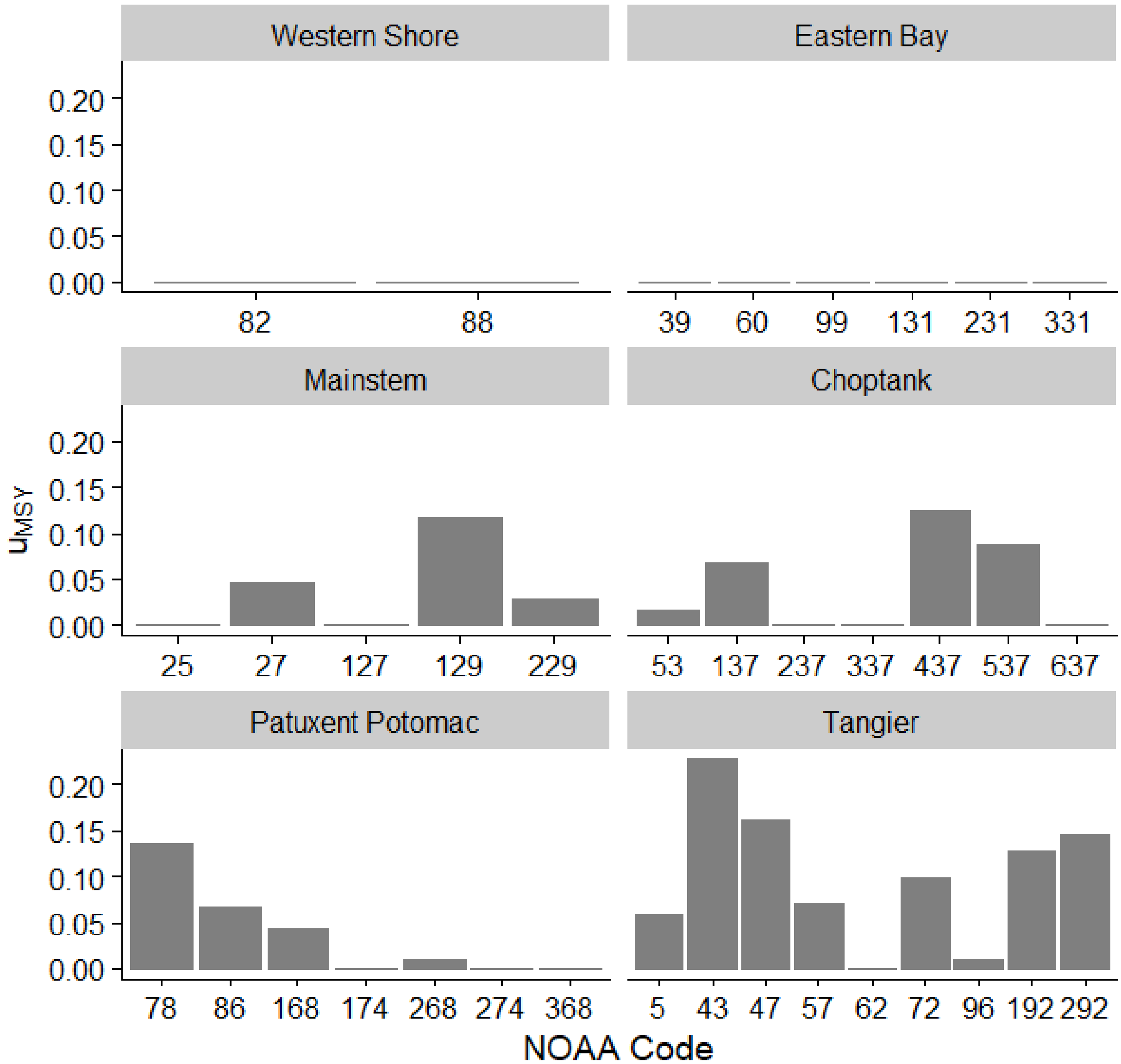

Figure 136. Estimates for the target exploitation reference point (U_{MSY}) for each NOAA Code in the sensitivity analysis when d = 0.32.

Figure 136. Estimates for the target exploitation reference point (U_{MSY}) for each NOAA Code in the sensitivity analysis when d = 0.32.

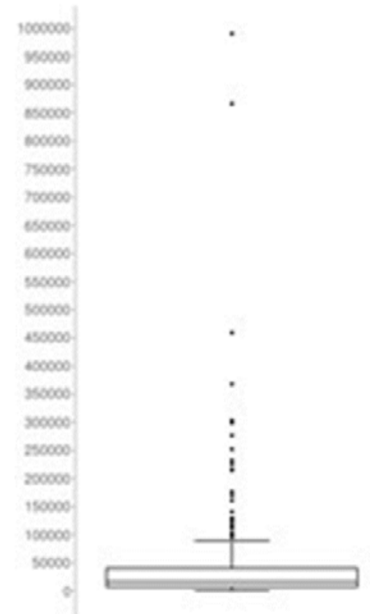

Figure 137. Distribution of initial abundance estimates of oysters in the Maryland portion of Chesapeake Bay derived from depletion analyses performed at the NOAA code level.

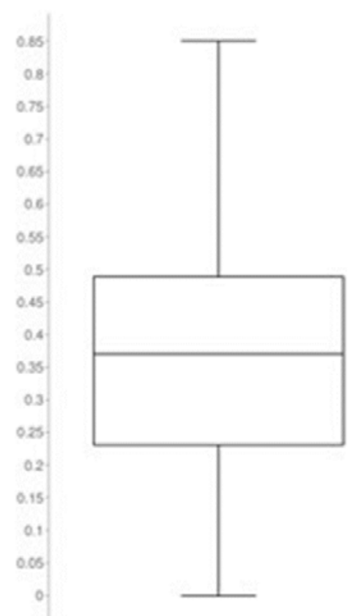

Figure 138. Distribution of exploitation rates of oysters in the Maryland portion of Chesapeake Bay derived from depletion analyses performed at the NOAA code level.

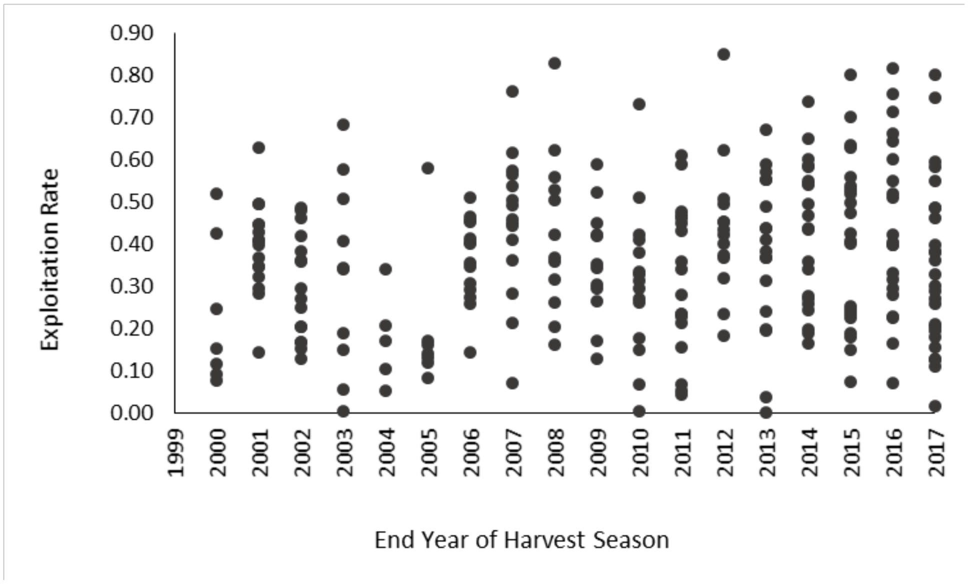

Figure 139. Estimates of exploitation rate of oysters in the Maryland portion of Chesapeake Bay derived from depletion analyses performed at the NOAA code level.

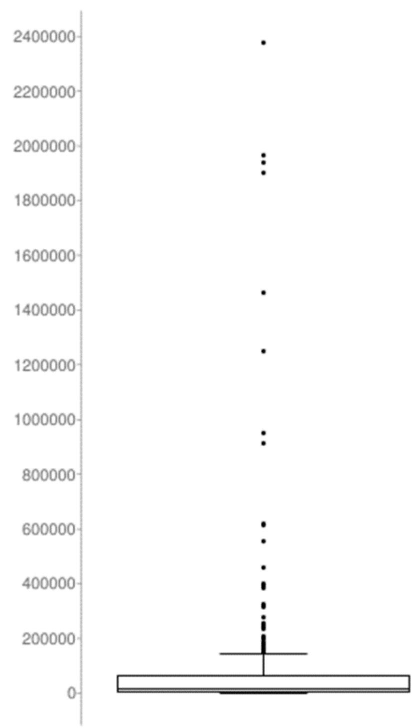

Figure 140. Distribution of widths of 95% confidence intervals of initial abundance estimates of oysters in the Maryland portion of Chesapeake Bay derived from depletion analyses performed at the NOAA code level.

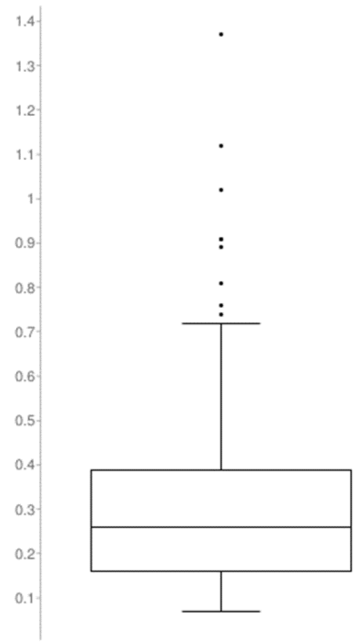

Figure 141. Distribution of widths of 95% confidence intervals of exploitation rate estimates of oysters in the Maryland portion of Chesapeake Bay derived from depletion analyses performed at the NOAA code level.

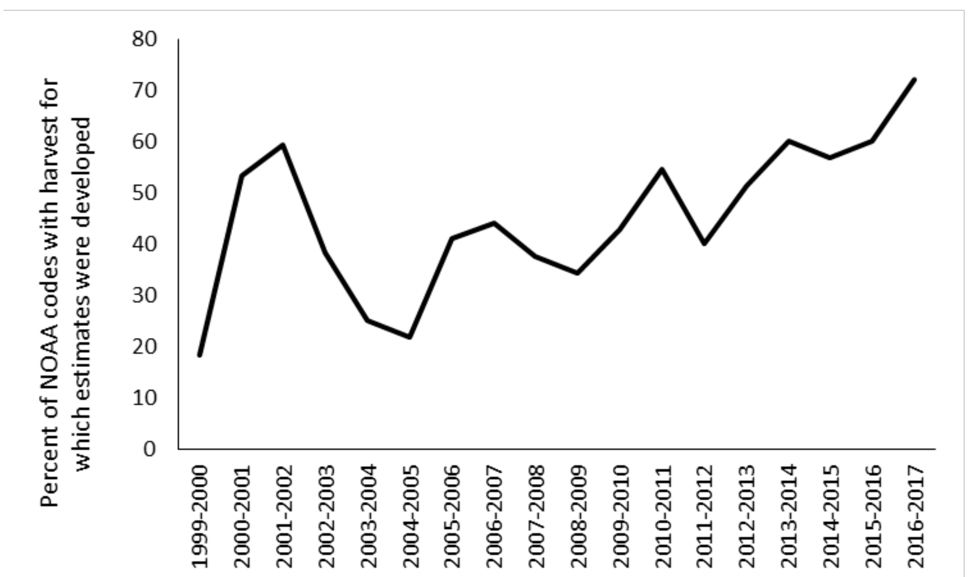

Figure 142. Percent of NOAA code harvest reporting areas within the Maryland portion of Chesapeake Bay with sufficient data to produce estimates of initial abundance and exploitation rate using depletion analyses.

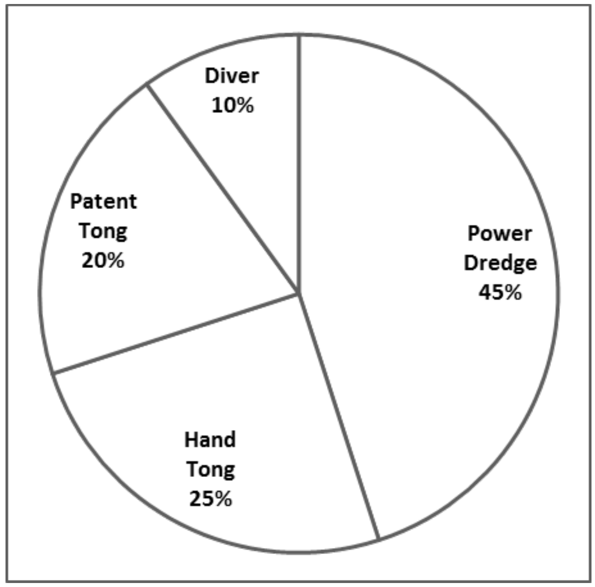

Figure 143. Percent of depletion analysis-generated estimates by dominant gear used for oysters in the Maryland portion of Chesapeake Bay.

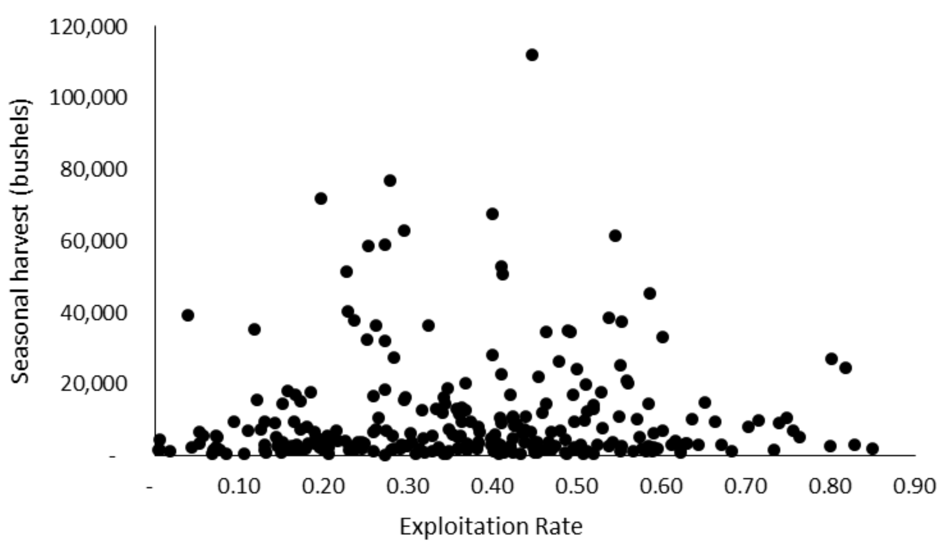

Figure 144. Depletion analysis- generated estimates of exploitation rate (in $Year_n$) vs. seasonal harvest (in $Year_n$) of oysters in the Maryland portion of Chesapeake Bay.

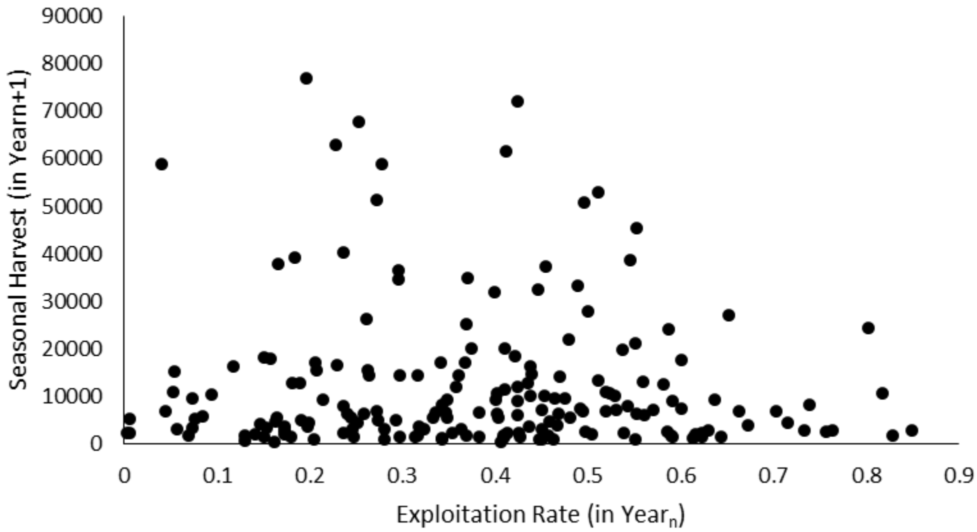

Figure 145. Depletion analysis- generated estimates of exploitation rate (in $Year_n$) vs. seasonal harvest (in $Year_{n+1}$) of oysters in the Maryland portion of Chesapeake Bay.

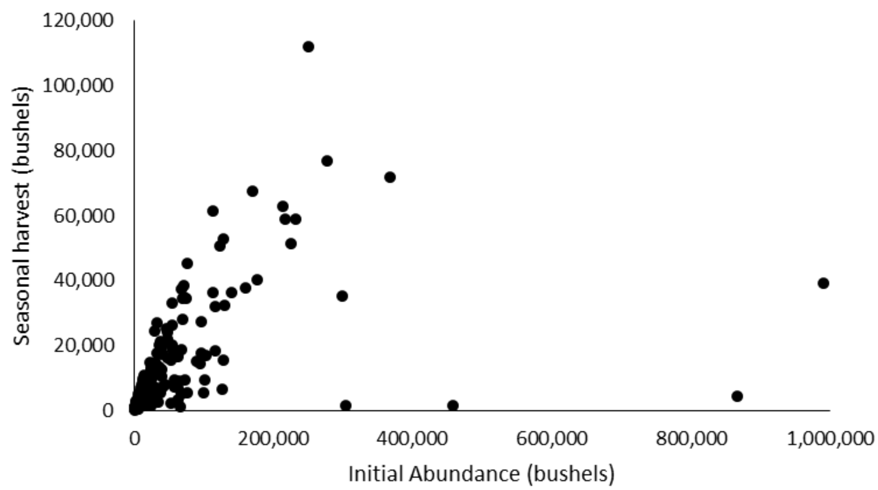

Figure 146. Depletion analysis- generated estimates of initial abundance (in $Year_n$) vs. seasonal harvest (in $Year_n$) of oysters in the Maryland portion of Chesapeake Bay, generated by depletion analyses of 30 NOAA codes.

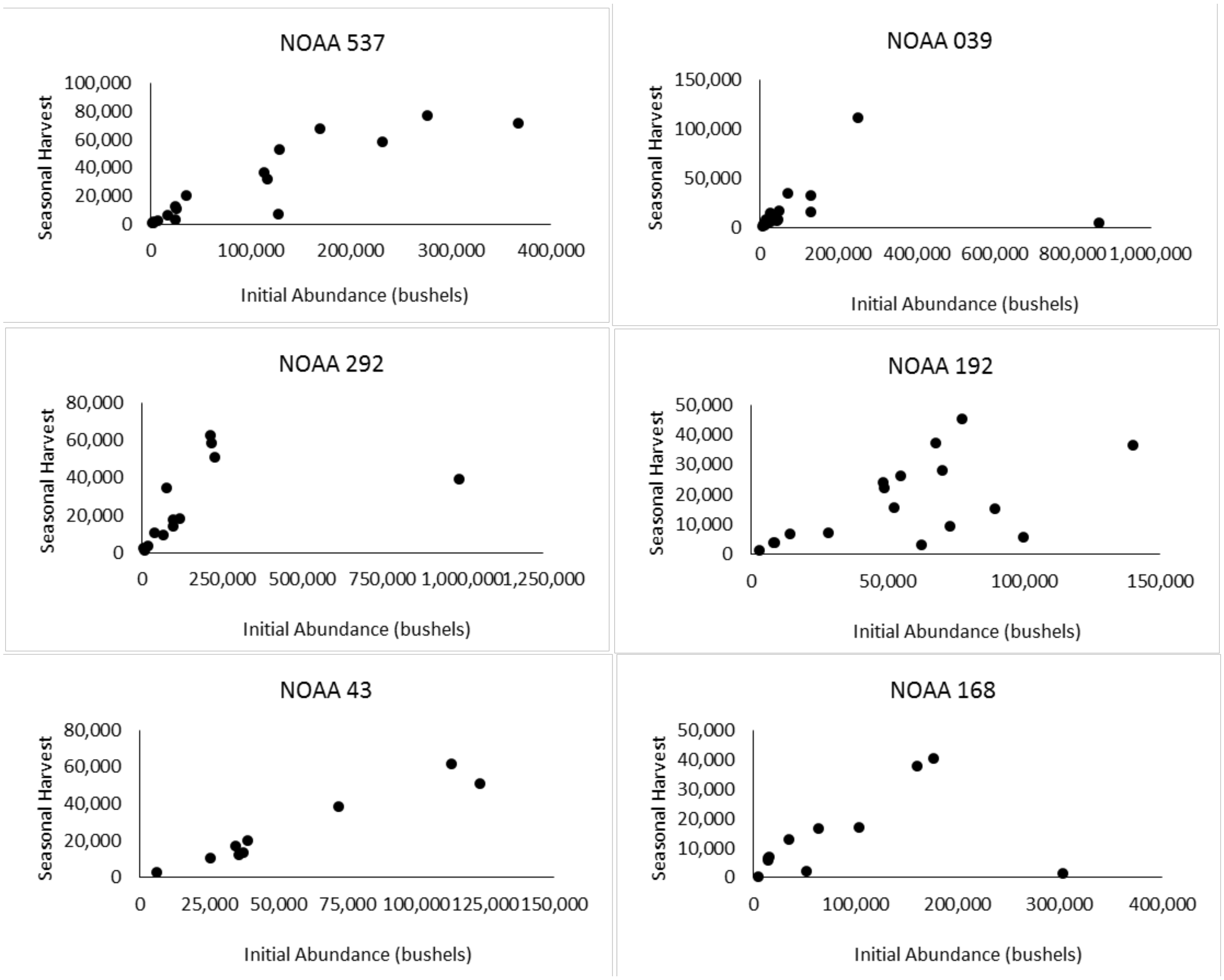

Figure 147. Initial abundance (in $Year_n$) vs. seasonal harvest (in $Year_n$) of oysters in the Maryland portion of Chesapeake Bay, generated by depletion analyses for 6 NOAA codes with highest time-series harvest.

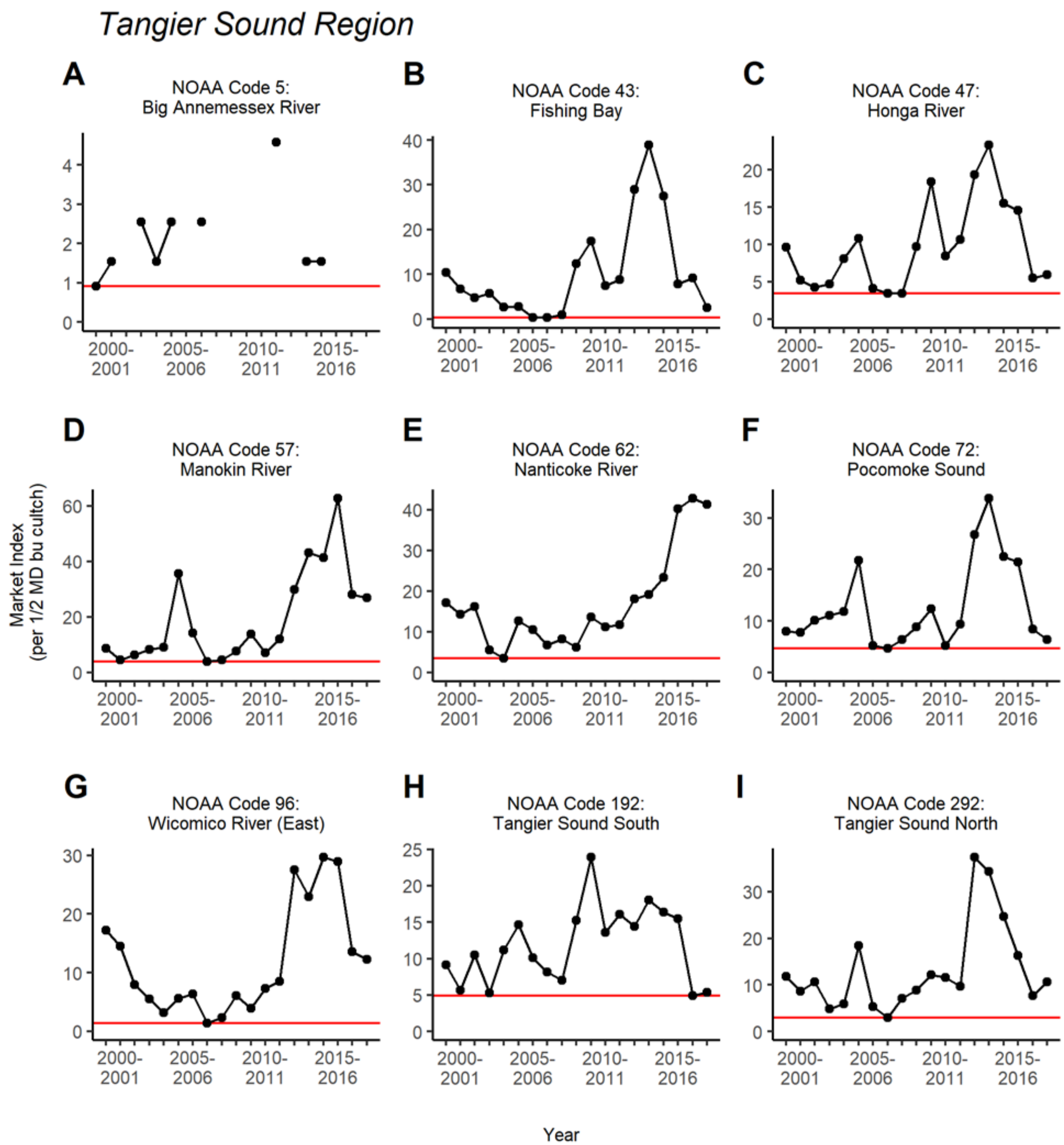

Figure 148. Standardized fall dredge survey indices of density (number of market oysters per ½ Maryland bushel (Md bu) of cultch) for market oysters in NOAA codes of the Tangier Sound region during 1999-2017. Points indicate the median estimates (log-scale back-transformed) and the red lines indicate the minimum number per bushel during the time series as a potential limit abundance reference point.

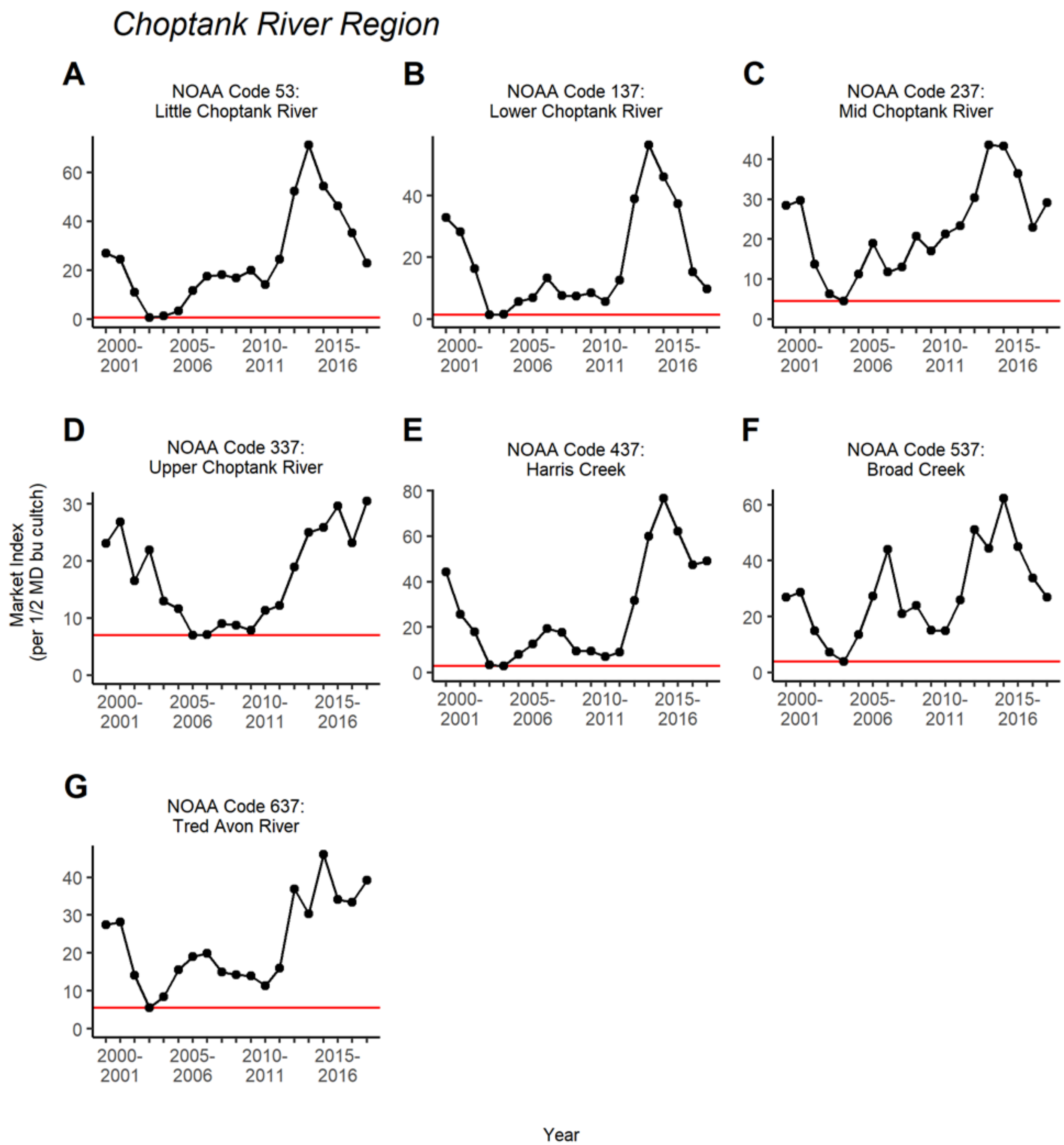

Figure 149. Standardized fall dredge survey indices of density (number of market oysters per ½ Maryland bushel (Md bu) of cultch) for market oysters in NOAA codes of the Choptank River region during 1999-2017. Points indicate the median estimates (log-scale back-transformed) and the red lines indicate the minimum number per bushel during the time series as a potential limit abundance reference point.

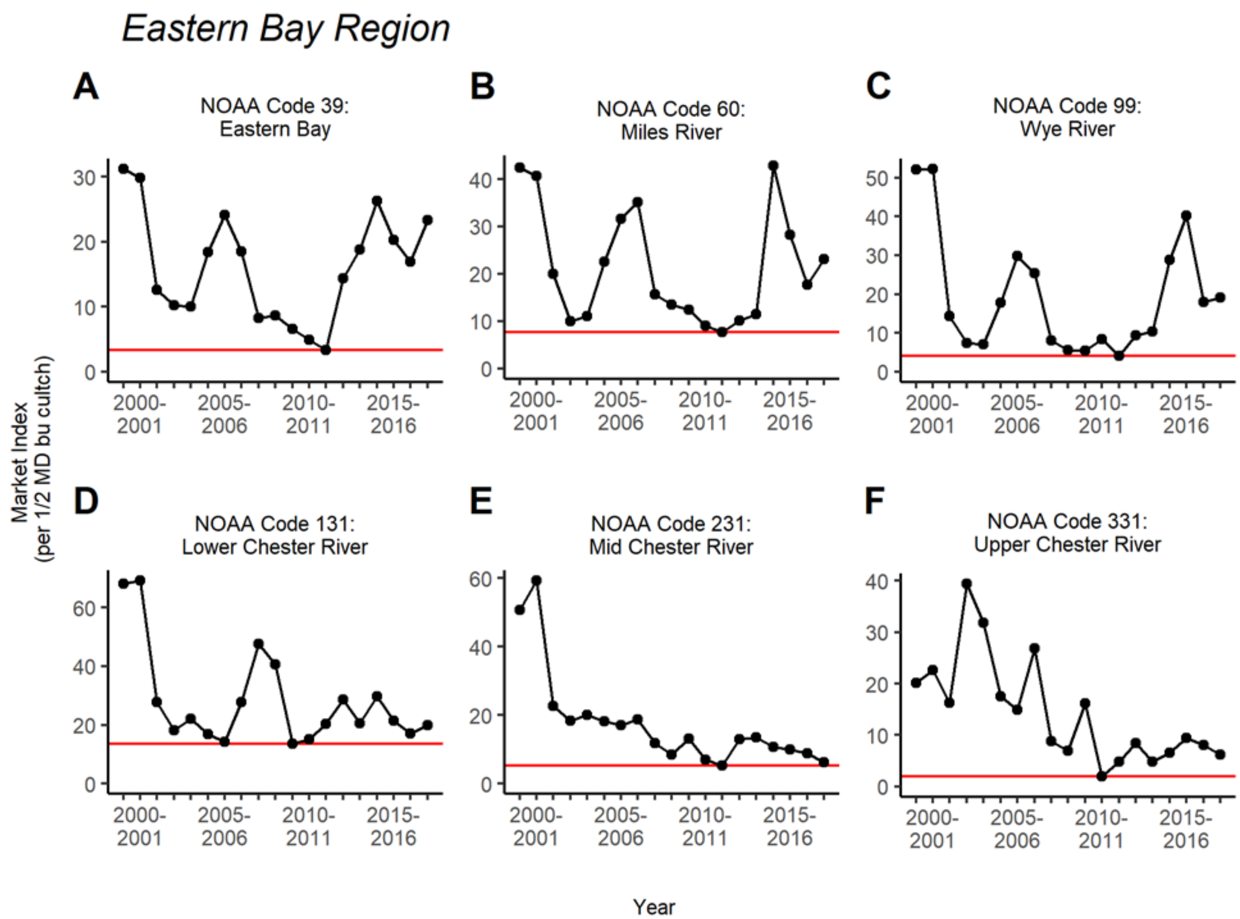

Figure 150. Standardized fall dredge survey indices of density (number of market oysters per ½ Maryland bushel (Md bu) of cultch) for market oysters in NOAA codes of the Eastern Bay region during 1999-2017. Points indicate the median estimates (log-scale back-transformed) and the red lines indicate the minimum number per bushel during the time series as a potential limit abundance reference point.

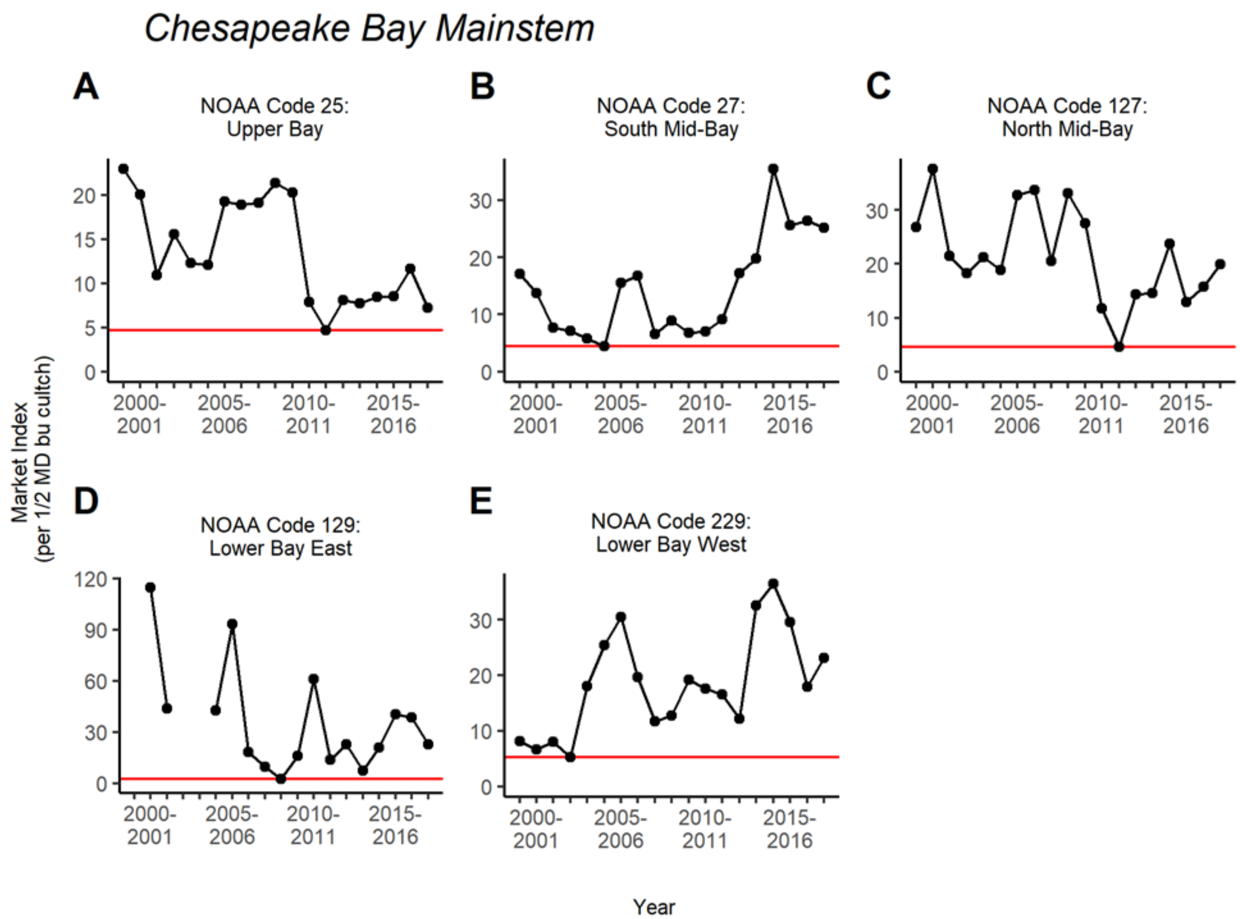

Figure 151. Standardized fall dredge survey indices of density (number of market oysters per ½ Maryland bushel (Md bu) of cultch) for market oysters in NOAA codes of the Chesapeake Bay Mainstem region during 1999-2017. Points indicate the median estimates (log-scale back-transformed) and the red lines indicate the minimum number per bushel during the time series as a potential limit abundance reference point.

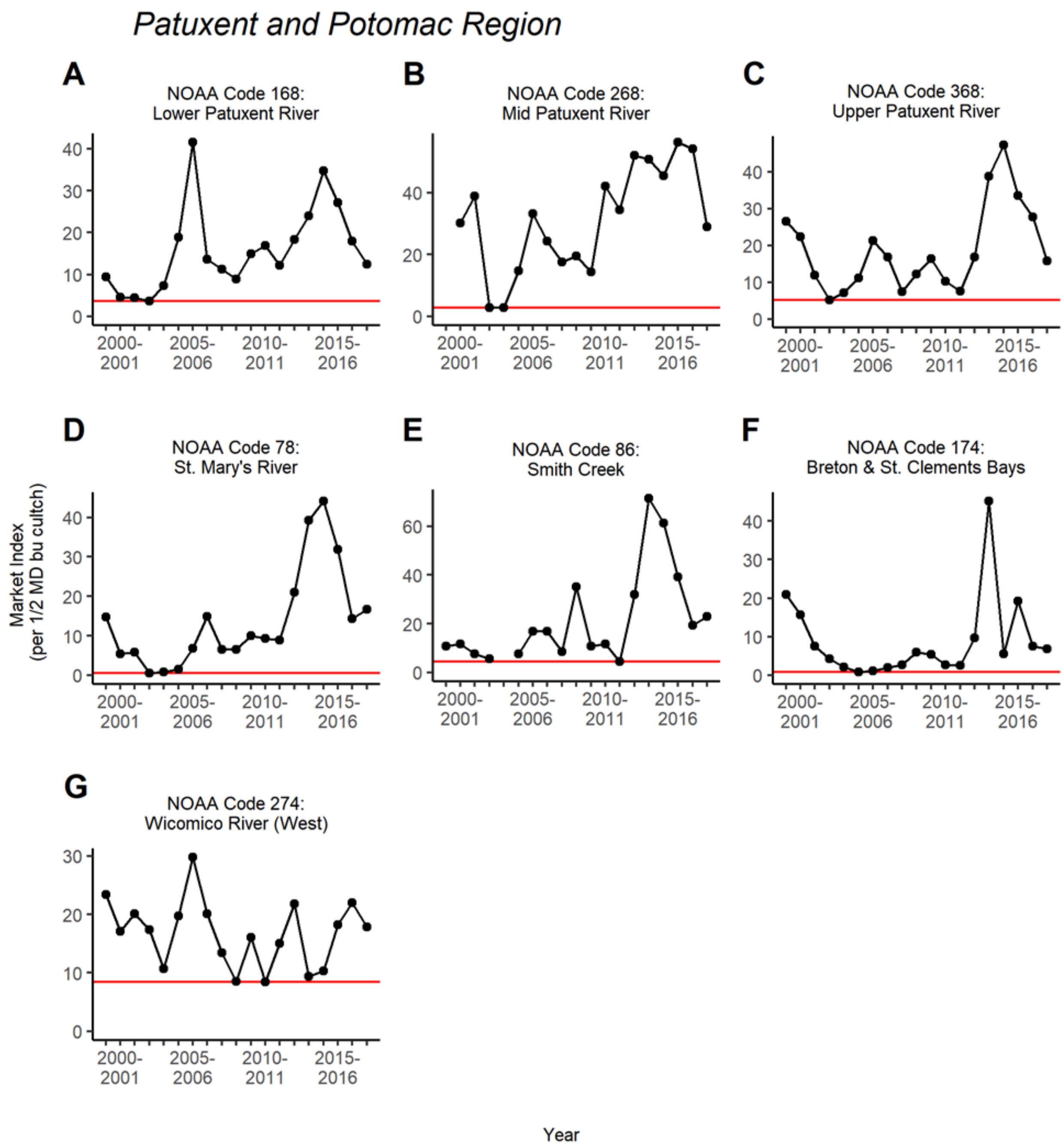

Figure 152. Standardized fall dredge survey indices of density (number of market oysters per ½ Maryland bushel (Md bu) of cultch) for market oysters in NOAA codes of the Patuxent and Potomac Rivers region during 1999-2017. Points indicate the median estimates (log-scale back-transformed) and the red lines indicate the minimum number per bushel during the time series as a potential limit abundance reference point.

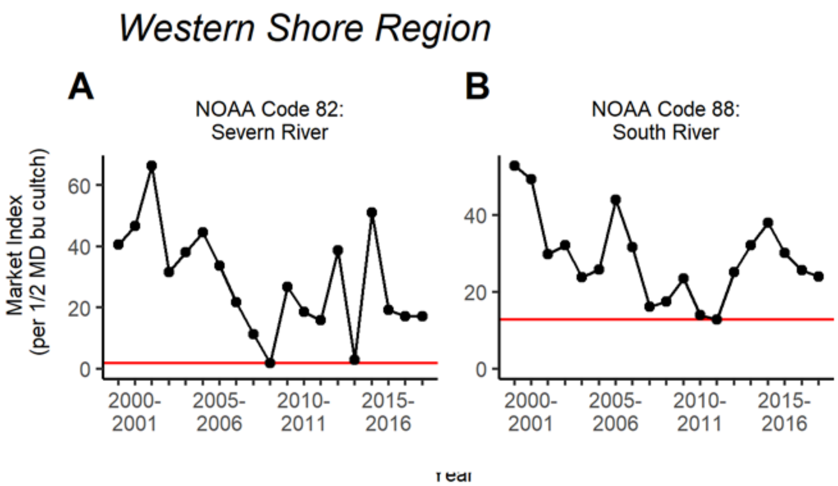

Figure 153. Standardized fall dredge survey indices of density (number of market oysters per ½ Maryland bushel (Md bu) of cultch) for market oysters in NOAA codes of the Western Shore region during 1999-2017. Points indicate the median estimates (log-scale back-transformed) and the red lines indicate the minimum number per bushel during the time series as a potential limit abundance reference point.

14.0 APPENDICES

14.1 Appendix I: Primary Data Sources for the 2018 Maryland Oyster Stock Assessment

This appendix contains a review of available data sources for eastern oysters *Crassosstrea virginica* that were used in the 2018 Maryland Oyster Stock Assessment. This review addresses TOR #1 (See Introduction Section 1.6). We limited the scope of this review to include data sources from the Maryland portion of the Chesapeake Bay because the 2018 Maryland Oyster Stock Assessment is focused exclusively on oysters in the portion of Chesapeake Bay under Maryland management.

A1.1 Fall Dredge Survey (Fishery Independent)

Data Source: Fall Dredge Survey

Location: Maryland DNR

Format: Electronic database (Microsoft Access)

Survey Objective: Provide indices related to the oyster population in Maryland, such as spatfall intensity, relative density, mortality, and biomass.

Potential Uses in Stock Assessment: The fall survey data can potentially be used to (1) examine changes in relative density over time for different sized and staged (spat, small, market) oysters, and (2) estimate natural mortality over time for small and market sized oysters.

Time Series: 1980 – 2016 for electronic database, but there are data available on oyster spat that goes back to the 1930s.

Spatial Scale: Statewide

Data Elements: The fall survey provides data on the number of live oysters (spat, small, and market) per bushel and the number of dead oysters (i.e., boxes) per bushel at each sample location. Size ranges and observed average size; 1 mm shell heights for individual oysters at ~30% of the stations since 2010.

Survey Design: Between 311 and 385 dredge samples are collected at fixed stations throughout Maryland each fall.

Sanctuary Information: Yes

Weaknesses:

Fixed site design only allows inference to sampled sites

Units of measurement (number per bushel)

Potential changes in dredge efficiency over space and time

Potential data quality issues with pre-1985 data

Strengths:

Good spatial coverage

Primary focus is oysters

Length of time series

Fixed site design allows following trends at same sites over time

Changes to Survey:

No major changes since 1980

A1.2 Disease Bars Fall Dredge Survey (Fishery Independent)

Data Source: Disease Bars Fall Dredge Survey (Conducted in conjunction with fall dredge survey described above)

Location: Maryland DNR

Format: Electronic database (Microsoft Access)

Survey Objective: Determine prevalence and intensity of disease (i.e., Dermo-disease and MSX) on oyster bars in Maryland.

Potential Uses in Stock Assessment: Disease data can potentially be used to correlate natural mortality with disease prevalence and intensity.

Time Series: 1990 - 2016, but there are data going back to the 1970s.

Spatial Scale: Statewide

Data Elements: Data on shell height and disease prevalence and intensity are collected from individual oysters.

Survey Design: Thirty oysters are collected from the same 43 sentinel bars in the fall survey every year. Fixed supplemental non-index sites were established to enhance spatial coverage.

Sanctuary Information: Yes

Weaknesses:

Fixed site design only allows inference about diseases to apply to sampled sites

Strengths:

Height data for individual oysters

Length of time series

Good spatial coverage

Fixed site design allows following disease trends at the same sites over time.

Changes to Survey:

No major changes

A1.3 Patent Tong Surveys (Fishery Independent)

Data Source: Patent Tong Surveys

Location: Maryland DNR, Annapolis

Format: Electronic database (Microsoft Access) and spreadsheets (Microsoft Excel)

Survey Objective:

1975-1978: Map oyster habitat in Chesapeake Bay

1989-1995: Investigate oyster population and disease trends in three salinity regimes

2011 - present: Assess oyster populations in sanctuaries

Potential Uses in Stock Assessment: The patent tong data can potentially be used to examine oyster populations within sanctuaries in more detail.

Time Series: 1975 - 1978; 1989 - 1995; 2011 - present

Spatial Scale:

1975- 1978: Individual bar scale

1989 - 1995: Individual bar scale

2011 - present: Individual sanctuary scale

Data Elements: Data on the number of live oysters (spat, small, and market), dead oysters (i.e., boxes), size (shell height in mm), habitat data expressed as cultch and grey shell volume for each sample site.

Survey Design:

1975 - 1978: Multiple systematic samples taken from individual bars

1989 - 1995: Multiple systematic samples taken from individual bars, from different habitat types within individual sanctuaries.

2011 - present: Multiple random samples taken from different habitat types within individual sanctuaries.

Sanctuary Information: Yes

Weaknesses:

Limited spatial and temporal coverage

Relatively small area per sample (1 meter squared)

Systematic design poses issues for statistical analyses

Strengths:

Individual Height Data for oysters.

Provides an estimate of density

Data at multiple times at some locations (e.g., 1975 and 1993)

Changes to Survey: No major changes within individual surveys but see entries above for differences among surveys.

A1.4 Shellfish Buy Tickets (Fishery Dependent)

Data Source: Maryland DNR Shellfish Buy Tickets

Location: Maryland DNR, Annapolis

Format: Electronic Database (Microsoft Access)

Survey Objective: Dealers report how many bushels of oysters are harvested in Maryland waters of the Chesapeake Bay to determine the amount of tax to be paid by dealers.

Potential Uses in Stock Assessment: The shellfish buy tickets can potentially be used to (1) estimate the amount of oysters harvested over time and (2) amount of effort used to harvest a given amount of oysters.

Time Series: 1988-1989 season through 2015-2016 season

Spatial Scale: Statewide

Data Elements: Data on area where harvest occurred, quantity of oysters harvested, and date of harvest.

Survey Design: Fishery dependent; self-reports from oyster dealers

Sanctuary Information: Data on areas before they were designated as sanctuaries.

Weaknesses:

Less than 100% reporting

Some data missing for records

Strengths:

Spatial and temporal scale of time series

Changes to Survey: No major changes over time

A1.5 Oyster Harvester Reports (Fishery Dependent)

Data Source: Maryland DNR Oyster Harvester Reports

Location: Maryland DNR, Annapolis

Format: Electronic Database (Microsoft Access)

Survey Objective: Oyster harvest reported by harvesters in greater detail than provided by dealers (e.g., bar-specific harvest).

Potential Uses in Stock Assessment: The oyster harvester reports can potentially be used to (1) estimate the amount of oysters harvested over time and (2) amount of effort used to harvest a given amount of oysters.

Time Series: 2009 - present

Spatial Scale: statewide

Data Elements: Data on bar-specific harvest location, quantity of oysters harvested, gear used, and the date of harvest.

Survey Design: Fishery dependent; self-reports from oyster harvesters

Sanctuary Information: No

Weaknesses:

Less than 100% reporting

Some data missing for records

Strengths:

Bar and gear specific harvest data

Changes to Survey: No major changes over time

A1.6 Oyster Severance Tax (Fishery Dependent)

Data Source: Oyster severance tax paid to the state of Maryland

Location: Maryland DNR, Annapolis

Format: Electronic database (Microsoft Access)

Survey Objective: Document amount of taxes paid for the total number of bushels harvested in Maryland each year.

Potential Uses in Stock Assessment: The oyster harvester reports can potentially be used to estimate the amount of oysters harvested over time.

Time Series: 2000 to present

Spatial Scale: Statewide

Data Elements: Data on the dollar amount of taxes paid each year for oyster bushels harvested in Maryland.

Survey Design: Fishery dependent; dollar amount reported is based on taxes paid by dealers for each bushel of oysters they report buying from watermen.

Sanctuary Information: No

Weaknesses:

Only statewide, cannot look at smaller scales

Strengths:

Provides additional estimate of statewide oyster harvest each year.

Changes to Survey: No major changes over time.

A1.7 Habitat Data (Fishery Independent)

Data Source:

Yates Survey

Bay Bottom Survey

Side Scan Sonar

Shell and Seed Plantings

Fall Oyster Survey

Location: Most of these can be found as GIS files online at http://data.imap.maryland.gov/ by searching for the appropriate terms (e.g., oysters, bay bottom survey)

Format: Electronic files

Survey Objective:

Yates Survey and Bay Bottom Survey: Map extent of oyster habitat in

Maryland portion of Chesapeake Bay

Side Scan Sonar: Map extent of oyster habitat in specific locations in

Maryland portion of Chesapeake Bay

Shell Plantings: track location of shell plantings over time

Potential Uses in Stock Assessment: The habitat data can potentially be used to estimate changes in the area of oyster habitat over time.

Time Series:

Yates Survey: 1906 – 1912

Bay Bottom Survey: 1975 - 1983

Side Scan Sonar: 2005-2013

Shell Plantings: 1960 - present

Fall Oyster Survey: 2005 – present

Spatial Scale:

Yates Survey: Statewide

Bay Bottom Survey: Statewide

Side Scan Sonar: Specific tributaries

Shell plantings: Statewide

Fall Oyster Survey: Statewide

Data Elements:

Yates Survey (From metadata online): Representation of historic oyster bottom as charted prior to the present, legally designated Natural Oyster Bars (NOB's), using source materials from 1906 to 1977

Bay bottom survey (From metadata online): Polygon dataset characterizing bottom type designations determined by MD DNR's Acoustic Bay Bottom Survey conducted from 1975 to 1983. Bottom type designations include cultch, mud, sand, leased bottom, hard bottom, mud with cultch and sand with cultch.

Side Scan Sonar: Polygon dataset characterizing bottom type designations determined by Maryland Geological Survey (MGS) and NOAA side scan sonar surveys. NOAA designated bottom types according to the Coastal and Marine Ecological Classification Standard and so Bay Bottom Survey categories of cultch, mud with cultch, and sand with cultch were all classified as oyster habitat. MGS categories of shell, mud with shell, and sand with shell were classified as oyster reef habitat.

Shell Plantings: Polygon dataset characterizing date, locations, and amount of shell or seed planted at sites throughout Maryland portion of Chesapeake Bay.

Fall Oyster Survey: total volume of substrate in dredge over a measured tow distance

Survey Design:

Yates Survey: systematic sampling

Bay Bottom Survey: systematic sampling

Side Scan Sonar: fixed sites

Shell Plantings: fixed sites

Fall Oyster Survey: fixed sites

Sanctuary Information: Yes

Weaknesses:

Most habitat data are now out of date and up to over 100 years old

Strengths:

Estimates of area of bottom occupied by oyster shell over long time period

Changes to Survey: No major changes within individual surveys, but see details above for differences among surveys.

14.2 Appendix II: Summary of oyster seed and shell planting data by NOAA code and year

This appendix provides a series of tables summarizing oyster seed and shell planting activity for each NOAA code in the Maryland Chesapeake Bay during 1999-2017. Habitat is the amount (acres) of material, primarily fresh or dredged oyster shell, placed on the bottom. Hatchery and Wild refer to the number (millions of individuals) of hatchery reared or transplanted wild seed placed on the bottom.

	NOAA Code	Year	Habitat	Hatchery	Wild
Tangier	5	1999	0	0	0
		2000	0	0	0
		2001	0	0	0
		2002	0	0	0
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	0	0	0
		2017	0	0	0
Tangier	43	1999	0	0	0
		2000	0	0	0
		2001	0	0	5.88
		2002	0	0	0
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	20	19	0
		2015	14.7	0	0
		2016	42.6	0	0
		2017	0	1	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Tangier	47	1999	0	0	0
		2000	0	0	0
		2001	0	0	0
		2002	10.6	0	0
		2003	0	0	0
		2004	0	0	8.76
		2005	27.3	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	55.13	0
		2010	0	0	0
		2011	0	0	0
		2012	40.5	0	0
		2013	4.4	0	0
		2014	63.4	0	0
		2015	23.2	0	0
		2016	21.8	0	0
		2017	0	0	0
Tangier	57	1999	0	0	5.03
		2000	0	0	0
		2001	12.6	0	0
		2002	0	0	0
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	10.24	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	0	0	0
		2017	0	0	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Tangier	62	1999	6.9	0	11.88
		2000	2.3	0	0
		2001	6.4	0	13.47
		2002	10.2	0.47	13.11
		2003	0	0	13.9
		2004	0	0	4.77
		2005	0	0	0
		2006	0	0	0
		2007	0	0	4.67
		2008	0	0	2.3
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	191.5	0	0
		2013	43.8	0	0
		2014	0	30.61	0
		2015	0	4.42	0
		2016	6.4	10.55	1.11
		2017	7.4	16.96	3.83
Tangier	72	1999	0	0	4.54
		2000	0	0	2.71
		2001	0	0	0
		2002	0	0	0
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	6.1	0	0
		2017	0	0	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Tangier	96	1999	0	0	0
		2000	0	0	0
		2001	0	0	4.85
		2002	0	0	0
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	19.81	0
		2010	0	0	0
		2011	0	47.48	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	13.1	0	0
		2016	0	8.35	0
		2017	0	0	0
Tangier	192	1999	81.6	0.33	4.52
		2000	118	4.14	0
		2001	45.2	0	0
		2002	122.8	0	0
		2003	177.8	0	0
		2004	191.3	0	0
		2005	76.4	0	0
		2006	110.1	0	0
		2007	1.1	0	0
		2008	0	4.49	9.56
		2009	0	0	58.98
		2010	0	0	0
		2011	0	0	0
		2012	157.6	0	0
		2013	5.6	14.86	0
		2014	0	26.04	0
		2015	16.9	0	0
		2016	0	0	0
		2017	0	0	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Tangier	292	1999	0	0	9.29
		2000	0	0	0
		2001	0	0	0
		2002	0	0	0
		2003	0	0	0
		2004	0	0	0
		2005	32.9	0	0
		2006	44.5	0	0
		2007	0	0	2.13
		2008	0	0	4.61
		2009	0	0	23.21
		2010	0	0	0
		2011	0	25.99	0
		2012	102.2	0	0
		2013	10.4	15.02	0
		2014	13.1	45.32	0
		2015	29	4.7	0
		2016	28.2	0	0
		2017	43.4	0	0
Choptank	53	1999	0	0	0
		2000	23.2	0	6.91
		2001	0	0	10.25
		2002	34	0.9	16.13
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	0	0
		2010	0	0	0
		2011	0	45.66	0
		2012	22.1	0	0
		2013	0	0	0
		2014	93.6	72.06	0
		2015	32.2	153.18	0
		2016	10.2	579.75	0
		2017	12.2	303.42	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Choptank	137	1999	26.4	0	9.14
		2000	11.6	9.48	0
		2001	0	0	0
		2002	0	0	0
		2003	0	0	0
		2004	0	0	0
		2005	20.9	0	0
		2006	11.2	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	0	0
		2010	0	39.44	0
		2011	0	93.09	0
		2012	71	0	0
		2013	0	0	0
		2014	10.4	0	0
		2015	5.6	0	0
		2016	8.5	0	0
		2017	0	0	0
Choptank	237	1999	0	0	39.09
		2000	24.9	0	14.54
		2001	25.4	0.84	0
		2002	18.1	0	0
		2003	0	12.7	22.28
		2004	0	0	0
		2005	0	0	0
		2006	0	1.2	0
		2007	0	0	0
		2008	0	30.2	0
		2009	0	105.37	0
		2010	0	44.24	0
		2011	0	81.06	0
		2012	0	1.37	0
		2013	0	18.82	0
		2014	0	11.03	0
		2015	0	0	0
		2016	0	13.69	0
		2017	0	13.54	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Choptank	337	1999	0	0	5.92
		2000	0	0	26.74
		2001	0	5.06	13
		2002	0	25.76	0
		2003	46.2	66.8	0
		2004	0	12	0
		2005	0	45.52	0
		2006	0	91.19	0
		2007	0	39.29	0
		2008	0	115.57	0
		2009	0	119.25	0
		2010	0	88.08	0
		2011	0	64.77	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	0	0	0
		2017	0	0	0
Choptank	437	1999	50	0	0
		2000	94.7	0	0
		2001	69.9	0	11.97
		2002	10.7	0	5.18
		2003	0	0	0
		2004	0	0	5.78
		2005	29.9	0	0
		2006	0	0	0
		2007	0	0	12.01
		2008	0	0	0
		2009	0	0	0
		2010	0	0	0
		2011	0	81.69	0
		2012	26.8	441.69	0
		2013	36.3	711.67	0
		2014	85	429.78	0
		2015	55.4	385.66	0
		2016	4.2	61.3	0
		2017	0	325.92	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Choptank	537	1999	12.1	0	0
		2000	10.2	0	0
		2001	31	0	11.95
		2002	30	0	9.07
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	38.1	0	0
		2007	0	0	0
		2008	0	0	12.21
		2009	0	0	48.84
		2010	0	0	0
		2011	0	0	0
		2012	75.4	0	0
		2013	8.9	0	0
		2014	2	0	0
		2015	80.8	0	0
		2016	20.6	19.4	0
		2017	38.2	0	0
Choptank	637	1999	9.9	0.15	0
		2000	4.4	0.03	0
		2001	5.5	0	17.22
		2002	1.3	0	8.62
		2003	4.8	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	14.07	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	16.1	20.36	0
		2016	6.2	279.54	0
		2017	7.4	230.17	3.08

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Eastern Bay	39	1999	120.9	0	6.85
		2000	159.8	6.04	7.14
		2001	140.3	0.04	0
		2002	76.4	1.48	0
		2003	0	0	0
		2004	36.7	0	0
		2005	42.9	0	0
		2006	0	0	0
		2007	0	8.68	7.2
		2008	0	40.8	4.61
		2009	0	42.72	20.62
		2010	0	0	0
		2011	0	21.33	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	20	0	0
		2016	0	10.31	0.59
		2017	0	10.19	16.86
Eastern Bay	60	1999	7.7	0.03	5.91
		2000	10.7	0	4.57
		2001	19.8	0	0
		2002	10.6	0	0
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	9.67	0
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	0	10.44	0
		2017	0	0	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Eastern Bay	99	1999	0	0	0
		2000	0	0.02	0
		2001	10.9	0	0
		2002	0	0	0
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	0	0	0
		2017	0	0	0
Eastern Bay	131	1999	0	0	0
		2000	0	0.03	11.72
		2001	10.9	1.45	7.97
		2002	15.2	17.72	0
		2003	86.4	48	0
		2004	26.5	9.1	0
		2005	55.9	100.56	0
		2006	0	16.96	0
		2007	0	10.1	0
		2008	0	47.04	0
		2009	0	109.72	0
		2010	0	80.36	0
		2011	0	71.98	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	7.54	0
		2016	0	0	0
		2017	0	9.12	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Eastern Bay	231	1999	0	0	48.17
		2000	0	0	62.05
		2001	0	0	82.66
		2002	0	0	31.07
		2003	7.9	1	88.96
		2004	0	6.7	0
		2005	6.8	22.24	0
		2006	29.5	119.31	0
		2007	0	35.87	0
		2008	0	116.98	0
		2009	0	16.81	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	8.8	0
		2016	0	40.73	0
		2017	0	27.94	0
Eastern Bay	331	1999	0	0	0
		2000	0	0	0
		2001	0	4.6	0
		2002	0	0.58	0
		2003	0	1	0
		2004	0	5.1	0
		2005	0	0	0
		2006	0	18.6	0
		2007	0	0	0
		2008	0	22.74	0
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	0	0	0
		2017	0	0	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Mainstem	25	1999	0	0.03	24.45
		2000	0	0.06	66.33
		2001	0	0	76.6
		2002	0	1.62	43.35
		2003	0	6.9	97.25
		2004	0.2	0	108.18
		2005	0	0	0
		2006	7	18.2	88.95
		2007	0	26.56	86.43
		2008	0	29.4	28.11
		2009	0	43.53	0
		2010	0	84.24	0
		2011	0	0	0
		2012	0	138.79	0
		2013	0	46.36	0
		2014	0.2	22.1	0
		2015	0	84.62	0
		2016	0	77.74	0.97
		2017	0	39.59	3.58
Mainstem	27	1999	0	0	13.08
		2000	0	0	0
		2001	0	0	0
		2002	0	0	0
		2003	8.2	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	7.6
		2008	0	0.55	11.75
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	85.6	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	12.3	9.77	1.27
		2017	0.4	0	1.5

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Mainstem	127	1999	15.3	2.5	10.8
		2000	0	0.06	72.91
		2001	0	0.54	36.67
		2002	0	0	14.18
		2003	0	0	33.22
		2004	0	0	63.58
		2005	0	0	0
		2006	0	0	45.15
		2007	0	0	43.16
		2008	0	0	9.45
		2009	0	0	4.26
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	8.87	0
		2015	0	17.45	0
		2016	0	13.08	0.59
		2017	0	0	7.74
Mainstem	129	1999	0	0.72	0
		2000	0	0	0
		2001	0	0	0
		2002	21.6	0	0
		2003	1.3	0	0
		2004	0	0	0
		2005	0	0	0
		2006	14.4	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	0	0	0
		2017	0	0	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Mainstem	229	1999	9.7	0	0
		2000	0	0	0
		2001	10.4	0	0
		2002	16.9	0	0
		2003	0.8	0	0
		2004	42.4	0	0
		2005	29.8	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	0	0
		2010	0	0	0
		2011	11.6	0	0
		2012	3.4	0	0
		2013	12.6	0	9.32
		2014	36.9	0	3.17
		2015	32.1	0	0
		2016	5.3	0	0
		2017	8.7	0	5.47
Patuxent Potomac	78	1999	7.3	0	0
		2000	12	0	0
		2001	0	0	0
		2002	0	0	0
		2003	0	0	0
		2004	0	0	2.63
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	0	2.53
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	5.79	0
		2015	0	10.54	0
		2016	0	6.72	0
		2017	0	0	0

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Patuxent Potomac	86	1999	0	0	5.03
		2000	0	0	0
		2001	0	0	0
		2002	0	0	0
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	0	0	0
		2017	0	0	0
Patuxent Potomac	168	1999	8.7	0	4.45
		2000	18.1	0	7.96
		2001	0	0	11.49
		2002	18.1	0	4.91
		2003	0	0	7.42
		2004	0	0	3.22
		2005	0	0	0
		2006	17.6	0	0
		2007	0	2.56	11.35
		2008	0	5.57	4.61
		2009	0	0	2.53
		2010	0	5.92	0
		2011	0	0	0
		2012	0	0	0
		2013	0	11.17	8.64
		2014	0	0	0
		2015	5.9	21.63	0
		2016	2.7	8.18	1.35
		2017	25.1	6.4	7.31

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Patuxent Potomac	174	1999	0	0	0
		2000	0	0	0
		2001	0	0	0
		2002	0	0	0
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	0	0
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	0	0	0
		2017	0	0	0
Patuxent Potomac	268	1999	2.9	1.2	3.25
		2000	0	0.02	0
		2001	0	0.62	0
		2002	0	0	0
		2003	0	0	0
		2004	0	0	0
		2005	0	0	0
		2006	0	0	0
		2007	0	0	0
		2008	0	10.23	0
		2009	0	0	0
		2010	0	0	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	0	0	0
		2017	0	0	1.54

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Patuxent Potomac	274	1999	0	0	13.69
		2000	0	0	34.01
		2001	0	0	12.31
		2002	0	0	21.89
		2003	0	0	34.35
		2004	0	0	26.67
		2005	0	0	0
		2006	0	2.43	0
		2007	0	3.37	20.28
		2008	0	6.76	5.07
		2009	0	19.5	0
		2010	0	12.04	0
		2011	0	0	0
		2012	0	17.3	0
		2013	0	16.81	0
		2014	0	21.39	0
		2015	0	29.76	0
		2016	0	25.15	0
		2017	0	31.61	0
Patuxent Potomac	368	1999	13.4	0	4.91
		2000	0	0	7.66
		2001	0	8.72	0
		2002	0	7.83	0
		2003	5.8	6.75	3.38
		2004	0	15.23	2.41
		2005	0	0	0
		2006	0	29	0
		2007	0	4.93	0
		2008	0	19.39	0
		2009	0	34.86	0
		2010	0	10.48	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	0
		2014	0	0	0
		2015	0	0	0
		2016	0	0	0
		2017	0	0	3.64

Region	NOAA Code	Year	Habitat	Hatchery	Wild
Western Shore	82	1999	11.9	4.73	2.15
		2000	0	0	0
		2001	0.4	1.55	0
		2002	0	1.23	0
		2003	0	0	0
		2004	0	0	0
		2005	2.9	0	0
		2006	0	7.08	0
		2007	0	1.67	0
		2008	0	44.86	0
		2009	0	46.51	0
		2010	0	60.53	0
		2011	0	0	0
		2012	0	16.94	0
		2013	0	44.43	0
		2014	0	0	0
		2015	0	0	0
		2016	0	0	0
		2017	0	0.37	0
Western Shore	88	1999	0	0.01	6.23
		2000	0	0.3	6.11
		2001	0	2.01	0
		2002	0	0	0
		2003	0.2	0	2.74
		2004	0	0	2.3
		2005	0	0	0
		2006	0	18.68	0
		2007	0	4.5	7.28
		2008	0	0	2.3
		2009	0	3.33	2.53
		2010	0	29.07	0
		2011	0	0	0
		2012	0	0	0
		2013	0	0	7.79
		2014	0	10.98	0
		2015	0	1.38	0
		2016	0	5.59	0
		2017	0	12.45	0

14.3 Appendix III Field study to estimate oyster per bushel conversion value

Background

The unit of harvest used by the assessment model is number of oysters. However, the harvest data provided by Maryland Department of Natural Resources oyster buy tickets and harvester reports are in the unit of bushels. Therefore, a conversion value for oysters per bushel was needed for the assessment.

Previously, the conversion value used was based on the Fourth Report of the Shell Fish Commission of Maryland (1912). This report found that the “average” number of “marketable oysters to fill a legal oyster bushel” was 329. This number was adopted by the Commission to represent one Maryland bushel (approximately 46 L) of marketable oysters, and was used as a constant factor in later calculations. However, the minimum legal size limit at that time was 2.5 inches. The present 3-inch minimum size limit went into effect in 1927.

Wilberg et al. (2011) used a value of 350 oysters per MD bushel in an analysis of the upper Chesapeake Bay. During the *OysterFutures* project, members of the fishing community stated that this value was too high and provided information that led to an estimate of 258 oysters per bushel. This value was used by Daminao (2017) in an analysis of the Choptank River complex.

The large discrepancy in these two values led to the decision to conduct a small study of the number of commercially harvested oysters per bushel in a contemporary and representative setting in the Maryland portion of the Chesapeake Bay.

Methods

Maryland Department of Natural Resources staff sampled oysters sold to a registered oyster buyer on Maryland's Eastern shore on December 20, 2017. Staff were divided into two teams of three staff – one person counted and measured oysters in a bushel basket, one person measured oysters, and one person recorded measurements. Two bushels were selected per harvester/location combination, one for each team.

Three types of data were recorded for each bushel (Table 1). Harvester data were harvest date, bar name, NOAA Code, and harvest gear type (Table 1). Size and number of oysters were recorded by measuring every 5th oyster and noting the total number of oysters per basket (Tables 1 and 2). With the exception of the first basket, measurements were made from the top to the bottom of the baskets. The volume of oysters per basket was determined by measuring the height of oysters in the bushel basket, the upper inner diameter at this height and lower inner diameter.

The volume of oysters per basket was calculated using the standard formula for a truncated cone:

$$V = (1/3) \cdot \pi \cdot h(R^2 + r^2 + R \cdot r) \qquad \textit{Equation 1}$$

where:

V = volume

R = larger radius (associated with upper inner diameter)

r = smaller radius (associated with lower inner diameter)

The distributions of all measurements were examined to determine whether the mean or median was the most representative typical value.

Results and Discussion

Samples collected

Ten paired samples were measured (2 baskets from each harvester/location combination) for a total of 20 samples. The 10th sample pair was from Howell Point, a bar near the edge of Sandy Hill sanctuary. The Maryland Department of Natural Resources was given anecdotal information that these oysters were harvested from a portion of the bar about 30-40 feet deep that was believed to be very close to the boundary of the Sandy Hill Sanctuary. Therefore, this sample may reflect an area that had not been subject to harvest pressure since 2009 (when Sandy Hill Sanctuary was established).

Harvest date, gears and locations

All bushels were harvested on December 19 or 20, 2017. The oysters sampled were harvested with a fairly even representation of harvest gears: diver (3 pairs of samples), patent tong (3 pairs of samples), power dredge (2 pairs of samples), and hand tong (2 pairs of samples). The oysters were harvested from a fairly wide distribution of NOAA codes in Chesapeake Bay: Patuxent River, Eastern Bay and Miles River, Choptank River and Broad Creek, and Tangier Sound and Fishing Bay (Figure 1). There were no samples from the Upper Bay or Potomac River tributaries.

Volume of oysters per bushel basket

The data describing the volume of oysters sold as a bushel are presented in Table 1. The median volume of oysters per basket was 37.4 liters (min 30.7, max 39.8, average 36.3, and standard deviation 2.8). The standard Maryland bushel is approximately 46 liters, so these “commercial oyster bushels” were approximately 81% of a standard Maryland bushel.

Number of oysters per bushel basket

The median number of oysters per bushel basket for all samples was 233 (min 85, max 328, average 214, standard deviation 67.1). The average number per bushel basket without sample #10 was 228 (median 223). The median number of oysters per liter was 6.3 (average 5.9, standard deviation 1.9, average without sample #10 was 6.3). The extrapolated median number of oysters per standard MD bushel = 292 (average 273, average without #10 was 291).

The population dynamics model (Section 3.2) used a value of 228 oysters per bushel.

Size distribution of oysters

Typical oyster size

A total of 893 oysters were measured. Oyster height ranged from 67 to 201 mm (Table 2). Due to right skew in the distribution caused by sample #10 (Figure 2), the median height of 87 mm is a better representative value for typical size than the mean (92 mm).

Small oysters

This study was not designed to measure legal percent undersized oysters, which are regulated by volume (COMAR 08.02.04.11A). However, the size measurements did support calculation of percent by number of the oysters below the legal minimum height of three inches (“small”).

The samples contained between 0% and 26% (by number) small oysters, with an apparent “gradient” by gear. Power dredge samples (n = 4) contained between 10% and 26%; hand tong samples (n = 4) contained a wide range (0%, 4%, 4% and 18%); half of the patent tong samples (n = 6) contained essentially none (0%, 0%, 2%, 9%, 9%, 20%); and half of the diver samples (n = 4) contained none, and had the lowest overall proportion of small oysters (0%, 0%, 5% and 6%).

The population dynamics model (Section 3.2) used a value of 8% small oysters per bushel.

Conclusions

This study was conducted on a single day approximately half-way through the 2017-2018 harvest season, at a single buyer centrally located in Maryland Chesapeake Bay. The samples collected represented harvest from all permitted gears, as well as a wide distribution of harvest areas throughout the Bay. Therefore, even though the sample sizes are relatively low, we believe the results represent current industry practices and are an improvement over estimates that have been previously used.

This study found approximately 230 oysters per bushel. This value is lower than the conversion factor from the Fourth Report of the Shell Fish Commission of Maryland (1912) for two possible reasons. The 1912 study was based on a legal minimum size of 2.5 inches, whereas the legal minimum size limit is now 3 inches. The current industry practice is to use a bushel basket approximately 20% smaller than the “standard Maryland bushel” (approximately 46 liters). Therefore, it is reasonable that there are fewer legal oysters “per bushel” sold in the current fishery.

This study also found that harvest gear used may have some effect on the number of small oysters per bushel – power dredge samples contained more small oysters than all other gears, and diver samples contained fewer small oysters than all other gears.

Table 1. Harvest date, location, gear type and bushel volume and oyster count summary statistics for oysters measured to determine volume of oysters per bushel in the current Maryland Chesapeake Bay oyster industry.

Sample Number	Tag Data Harvest Date	Tag Data Bar Name	Tag Data NOAA Code	Tag Data Gear Type	Calculated Volume (L)	Number of Oysters per Bushel	Extrapolated for Standard MD Bushel (46L)
01A	12/19/2017	Mears Bar	168	Patent Tong	39.76	252	291.54
01B	12/19/2017	Mears Bar	168	Patent Tong	35.26	233	304.00
02A	12/19/2017	Great Bar	537	Power Dredge	38.44	328	392.55
02B	12/19/2017	Great Bar	537	Power Dredge	33.13	290	402.70
03A	12/19/2017	Sandy Hill / Howell Pt	237	Diver	37.42	188	231.09
03B	12/19/2017	Sandy Hill / Howell Pt	237	Diver	35.29	163	212.48
04A	12/19/2017	Cedar Island	39	Hand Tong	37.42	222	272.88
04B	12/19/2017	Cedar Island	39	Hand Tong	33.87	230	312.38
05A	12/19/2017	Mud Rock	292	Patent Tong	38.59	284	338.51
05B	12/19/2017	Mud Rock	292	Patent Tong	32.78	276	387.35
06A	12/19/2017	Bugby	39	Diver	38.59	248	295.60
06B	12/19/2017	Bugby	39	Diver	35.93	256	327.72
07A	12/19/2017	ND	43	Power Dredge	38.52	239	285.41
07B	12/19/2017	ND	43	Power Dredge	33.23	250	346.07
08A	12/19/2017	Sharkfin Shoal	292	Patent Tong	39.76	243	281.13
08B	12/19/2017	Sharkfin Shoal	292	Patent Tong	33.87	223	302.87

Table 1 Continued

Sample Number	Tag Data Harvest Date	Tag Data Bar Name	Tag Data NOAA Code	Tag Data Gear Type	Calculated Volume (L)	Number of Oysters per Bushel	Extrapolated for Standard MD Bushel (46L)
09A	12/20/2017	Herring Island	60	Hand Tong	37.42	128	157.34
09B	12/20/2017	Herring Island	60	Hand Tong	33.32	139	191.88
10A	12/20/2017	Sandy Hill / Howell Pt	237	Diver	39.76	85	98.34
10B	12/20/2017	Sandy Hill / Howell Pt	237	Diver	38.74	90	106.86

Table 2. Harvest location, gear type and size summary statistics for oysters measured to determine volume of oysters per bushel in the current Maryland Chesapeake Bay oyster industry.

Sample Number	Tag Data Bar Name	Tag Data NOAA Code	Tag Data Gear Type	Bushel A						Bushel B					
				Number of Oysters Measured	Min Size (mm)	Max Size (mm)	Median Size (mm)	Average Size (mm)	% Undersize (by number)	Number of Oysters	Min Size (mm)	Max Size (mm)	Median Size (mm)	Average Size (mm)	% Undersize (by number)
01	Mears Bar	168	Patent Tong	51	70	123	85	88	20%	46	71	120	85	87	9%
02	Great Bar	537	Power Dredge	65	67	125	79	81	26%	58	70	131	80	81	14%
03	Sandy Hill / Howell Pt	237	Diver	37	68	127	93	96	5%	32	72	150	98	99	6%
04	Cedar Island	39	Hand Tong	44	71	120	86	87	18%	46	72	140	86	88	4%
05	Mud Rock	292	Patent Tong	56	75	125	87	89	2%	55	77	128	89	90	0%
06	Bugby	39	Diver	49	72	150	88	91	6%	51	77	115	85	90	0%
07	ND	43	Power Dredge	47	72	121	84	88	15%	50	71	134	86	89	10%
08	Sharkfin Shoal	292	Patent Tong	48	76	128	89	92	0%	44	70	126	91	93	9%
09	Herring Island	60	Hand Tong	25	73	130	96	99	4%	27	82	125	97	101	0%
10	Sandy Hill / Howell Pt	237	Diver	17	110	160	133	135	0%	18	100	201	134	140	0%

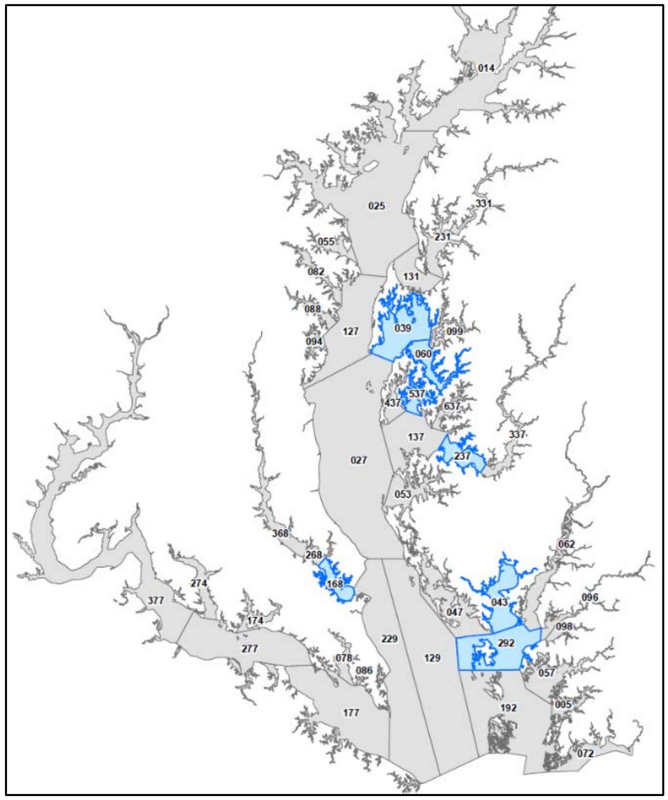

Figure 1. Distribution of harvest locations of sampled oysters – samples were harvested in the highlighted NOAA codes.

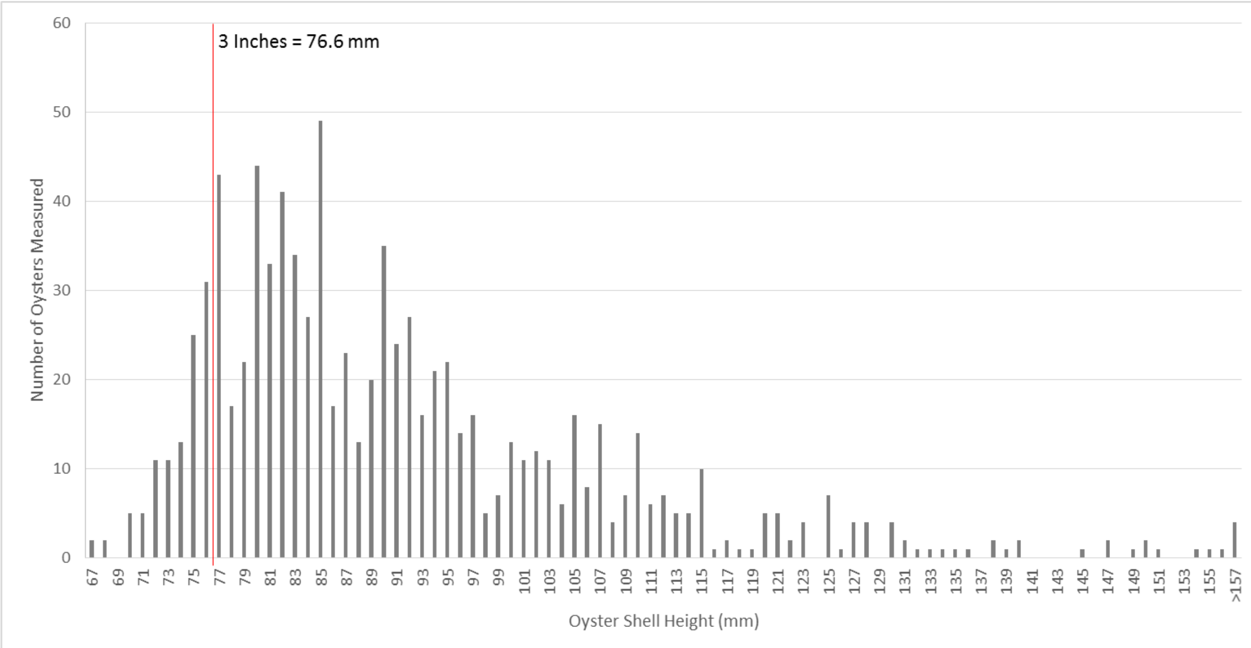

Figure 2. Size distribution of sampled oysters. The minimum legal size is 3 inches.

14.4 Appendix IV : Trend Analysis of the Fall Survey Data

Methods

Our goal was to understand how the density of oysters by stage changed in the Maryland Department of Natural Resources fall dredge survey during 1999-2017. Generalized additive models (GAMs) were used to estimate non-linear trends over time in the numbers of spat, small, and market oysters collected in the survey per half Maryland bushel cultch. This was done for the Maryland portion of Chesapeake Bay in aggregate and by NOAA code.

First, a model was created to estimate non-linear trends for each stage (spat, small, and market). A model for the number of oysters per half bushel cultch at time t (days) and in NOAA code j included a combination of a smoothed term representing a non-linear trend common across the bay, autoregressive effects, and a random effect by NOAA code:

$$Y_{t,j} = f(D_t) + b_1 Y_{t-1,j} + b_2 Y_{t-2,j} + \alpha_{t,j} + \epsilon_{t,j},$$

where t is time index (t = 1, …, T); j is NOAA code index (j = 1, …, J); D_t is the day of sampling (from 1 being the first day of the analyzed period to 6630 being the last day), b_1 and b_2 are coefficients on the autoregressive terms, $Y_{t-1,j}$ and $Y_{t-2,j}$ are the number of oysters per half bushel cultch at the same NOAA code at lagged times, α_j is the random intercept per region (NOAA code), and $\epsilon_{t,j}$ are uncorrelated residuals. This model allowed us to estimate smoothed non-linear trends for each stage across the Maryland Portion of Chesapeake Bay.

Next, an analysis was also done where separate non-linear trends $f_j(D_t)$ were estimated for each NOAA code and each stage:

$$Y_{t,j} = f_j(D_t) + b_1 Y_{t-1,j} + b_2 Y_{t-2,j} + \epsilon_{t,j}.$$

Note that this model is similar to the first model, but with a smooth term that is different for each NOAA code and a random effect by NOAA code is no longer needed.

Both models were fit separately for spat, small, and market oysters per half bushel cultch averaged by date of collection and NOAA code. The models were estimated in the R package mgcv (Wood, 2018) accounting for the weights of the observations (weights were the number of dredge tows averaged), assuming a Box–Cox t distribution for the data (Rigby and Stasinopoulos, 2006; Stasinopoulos and Rigby, 2007), and estimating smoothed trend functions using penalized regression splines, where the penalty term penalizes functions that are less smooth. P-values were reported to assess the approximate significance of the smoothed function compared to no trend.

For the models by NOAA code, we compared the magnitude of the smoothed term by NOAA code in the lowest year to the last year of the time series, so approximate 95% confidence intervals were calculated for the smoothed non-linear trend. However, although confidence intervals of this type have close to nominal coverage probabilities (Marra and Wood, 2012; Wood, 2018), the coverage is studied by averaging across the observation points ("across-the-function") and not point-wise. Wood (2006) and Marra and Wood (2012) mention that point-wise intervals are expected to have poorer coverage and obtaining intervals for smooth functions with good point-wise coverage in the GAM framework is a challenging problem. Intuitively, intervals for extrema might have the worst coverage compared with other points, which is problematic for comparing the minimum of the time series of the recent year. Hence, a visual comparison of the recent year with a year of the lowest observed catch is provided just for illustration purposes. The ultimate goal of this analysis was to be able to compare an index only method for monitoring abundance relative to the minimum of the time series, similar to the approach for the stage-structured assessment model.

Note that differences in gear efficiency for a dredge of spat, small, and market oysters could be a confounding factor when looking at difference in magnitude of these smoothed functions. Dredge efficiency is highly variable and can differ based on bar or on size of oysters (Powell et al., 2007; Marenghi et al., 2017). Thus, comparing magnitude of these indices among bars and among stages of oysters is not meaningful without considering efficiency to scale these to absolute density instead of an index of density.

Results

Maryland Bay-wide smoothed functions

The smoothed function for spat varied over time and the magnitude was small (between -2 and 2; Figure 1A). The value at the end of the time series was slightly below the value at the beginning, which was a peak in the time series. The smoothed function for small oysters had a linear increase over the time series and a small magnitude (approximately -1.75 at the beginning of the time series and approximately 1.75 by the end; Figure 1B). The smoothed function for market oysters was similar in pattern to the one for spat but was lagged by approximately 1000 d (~2.7 yrs; Figure 1C). However, the range of the function for markets was larger (between -4 and 7.5) than those of either spat or small oysters.

Smoothed functions by NOAA code

Comparison of spat, small, and market smoothed functions within the same region

Regional smoothed functions for spat, small, and market were estimated for 34 NOAA codes (Figures 2-19). Of these 102 functions, 20 had p-values greater than 0.1, and thus were considered to not have significant trends. These NOAA codes are thus not discussed in the section below.

For many NOAA codes, years of high density as seen in the spat smoothed function could also be seen in the small and market smoothed functions, lagged by 1-2 and 2-4 years, respectively. In addition, the peaks were often wider in the market smoothed functions (e.g., NOAA code 57, Figures 2, 8, and 14). This pattern occurred in all regions of the bay, but not in all NOAA codes. In some NOAA codes, the lagged pattern among stages was apparent in spat and small oysters, but not in markets (e.g., NOAA code 231, Figures 4, 10, and 16) or in smalls and markets, but not in the spat smoothed function (e.g., NOAA code 25, Figures 5, 11, and 17).

Comparison of time series minimums to the last year

By stage (and not including smoothed functions where $p \geq 0.1$), 36%, 55%, and 65% of spat, small, and market models by NOAA code were above the confidence intervals of the minimum in the last year (as indicated by confidence intervals in the last year not overlapping with those in the minimum year; Table 1).

Spat

In Tangier Sound, considering only functions with $p < 0.1$, the trends were similar in pattern and degrees of freedom used (~8) among NOAA codes, except for NOAA code 96 (Wicomico River East; Figure 2). The common pattern was relatively low density at the beginning of the time series, with some fluctuations in the middle of the time series before increasing to a high value around 2011. The pattern after 2011 was not consistent among NOAA Codes. In all NOAA codes, the lowest point in the time series was in 2004. Despite the similarities in pattern, the magnitude of these functions varied by NOAA code. NOAA code 096 (Wicomico River East) had a different function shape, a monotonic increase from about -10 to 8 during 2001 to 2017.

In the Choptank Region, the NOAA codes with $p < 0.1$ (53, 337, 437, and 637) had trends that were unique to each NOAA code (Figure 3). However, 337 and 437 both had time series minimums in 2004.

In the Eastern Bay region, all smooth functions had p values < 0.1 except for NOAA code 39 (Fishing Bay; Figure 4). The year when the function was at a minimum varied by region. NOAA codes 231 and 331 had similar trends, with minimums in 2002 and 2003, low values during 2007 to 2017, and a peak in 2004 or 2005. NOAA code 60 had a unique pattern from the other Eastern Bay region NOAA codes, with a minimum in 2006 after a decline. NOAA codes 99 and 131 had different patterns, but both had minimums in 2015, and the end of the time series was similar in value to the minimum.

In the Chesapeake Bay Mainstem region, only 25 and 229 had smoothed functions with p-values < 0.1 (Figure 5). These NOAA codes had minimums in different years (2009 and 2005, respectively), but both NOAA codes had low values in the beginning of the time series and large peaks near the end (in 2013 and 2015, respectively).

The Patuxent River only had 1 NOAA code (368) that had a smoothed function with $p < 0.1$ and the Potomac river had 3 NOAA codes (86, 174, and 274; Figure 6). The minimum in NOAA code 368 was in 2013, while 86 and 174 had minima in 2006, and 274 had a minimum in 2010. NOAA codes 86 and 174 had similar trends, but they differed in magnitude. NOAA codes 368 and 274 had unique patterns.

The Western Shore NOAA codes had smoothed functions with $p < 0.1$ and minimums in 2005 (Figure 7). Both NOAA codes had low values in the beginning of the time series and increases in 2008, but NOAA code 82 decreased to low values around 2011, whereas NOAA code 88 had a second higher peak in 2011 before decreasing and reaching a trough in 2013.

Small Oysters

In Tangier Sound, all smooth functions had $p < 0.1$ (Figure 8). The minimum in these time series all occurred between 2004 and 2008, except for NOAA code 5 (Big Annemessex River), which had its minimum in 2017. NOAA code 5 had a unique pattern (decreasing monotonic function). However, there were some similarities between the trends in all other NOAA codes; the most distinctive similarity was a peak around 2012 or 2013. The magnitude of the smooth functions varied among NOAA codes.

All Choptank region NOAA codes had a smoothed function with $p < 0.1$ (Figure 9). These time series all had similar patterns, including high values in 2000 or 2001 and in 2011, 2012, or 2013. Time series minimums occurred at different times depending on the NOAA code, but all occurred in the 2000s.

In the Eastern Bay region, all smooth functions had p values < 0.1 except for NOAA code 131 (Lower Chester River; Figure 10). The patterns among the smooth functions (for $p < 0.1$) were not consistent, although there were some similarities. The time series all had relatively high values at the beginning of the time series that then decreased, although there were fluctuations in some of the time series. The year in which the time series was a minimum was not consistent among the regions, varying between 2007 and 2017.

All four NOAA codes of the Chesapeake Bay Mainstem region had smoothed functions with p values < 0.1 (Figure 11). NOAA codes 129 and 229 had similar patterns (including a minimum in 2000 in both time series) that used similar effective degrees of freedom (~7.5), but the range of the functions was different. The two other NOAA codes, 25 and 27, had minimums in 2011 and 2017, respectively, and had unique patterns.

Only 2 of the NOAA codes in the Patuxent and Potomac rivers had smoothed functions with $p < 0.1$ (NOAA codes 168 and 274; Figure 12). These NOAA codes had unique patterns and had minimums at different times (2006 and 2012, respectively. The degrees of freedom used by the smoothed function and the magnitude of fluctuations were similar.

Both western shore NOAA codes had smoothed functions with $p < 0.1$ and peaks in 2009 (Figure 13). However, while the minimum for NOAA code 82 was in 2006, it was in 2016 (the last year of this time series) in 88.

Market Oysters

In Tangier Sound, the NOAA codes had commonalities, including lower values at the beginning of the time series compared to the end, peaks around 2004/2005 in five of nine NOAA codes, and peaks around 2014 in six NOAA codes (Figure 14). Four NOAA codes had minima in 2006 or 2007. The range of the smoothed function varied by NOAA code.

The Choptank River region NOAA codes had similar patterns, including minima in 2002 or 2003 (except for 337 which had a minimum in 2006), low values at the beginning of the time series, and a large peak around 2013 or 2014 (Figure 15). Most NOAA codes also had a slight peak between 2005 and 2007. The ranges of the smoothed functions were within the same order of magnitude.

In the Eastern Bay region, minimums for the time series were between 2010 and 2012 for all NOAA codes except for 99, which had a minimum in the first year of the time series, 2001. There were some similarities between NOAA codes 39 (Fishing Bay) and 99 (Wye River), with peaks around 2005 and 2014/2015 (Figure 16). The range for all NOAA codes were within the same order of magnitude.

The Chesapeake Bay Mainstem NOAA codes had unique trends by NOAA code, although there were some similarities among them (Figure 17). The minimums were in 2010 and 2011 in 25 and 27, respectively, but 229 had a minimum earlier in the time series, in 2000. NOAA codes 27 and 229 had some similarities in their patterns, with peaks or increases in 2005, 2009, and 2014. The smoothed functions all had similar ranges.

There were some similarities in trends of the Patuxent and Potomac Rivers (Figure 18). Many NOAA codes had peaks in 2005 or 2006 and 2014, and all time series increased during 2012-2014. NOAA code 86 was the only smoothed function that was a monotonic increasing function, whereas the other NOAA codes used approximately 8 degrees of freedom. Minimum values were between 2001 and 2006, with minimums in most NOAA codes were in 2002 or 2003.

Western shore NOAA codes shared similar patterns, although NOAA code 82 had its minimum in 2008, while 88 had it in 2011 (Figure 19).

Discussion

While there were often commonalities in trends in the fall survey indices among NOAA codes, these results also reveal that the indices have varied substantially in their trends over time, sometimes even within a region. This trend analysis using GAMs highlights the importance of considering the oyster population in the Maryland portion of Chesapeake Bay on the NOAA code level instead of on a broader scale.

Furthermore, peaks of recruitment can be followed into the small and market stages in some NOAA codes, in others there may not be lagged patterns among the stages. This could be for a variety of reasons, including sampling variability, years of high natural mortality, harvest or plantings of small oysters moved from other regions. Some of these processes (like natural mortality events, harvest or plantings) can be accounted for in the assessment model.

While the confidence intervals included in this analysis may not correctly represent all uncertainty to compare among years, there was a large proportion of indices that overlapped with the minimum in the last year, suggesting densities are at levels similar to the minimum of the time series. Calculating confidence intervals within the GAM framework is not a trivial exercise; however, if done properly, the density in the last year can be compared to the minimum of the time series more confidently. The minimum is useful as a comparison, especially for the market index, as it is analogous to the limit abundance reference points used with the stage-structured assessment model.

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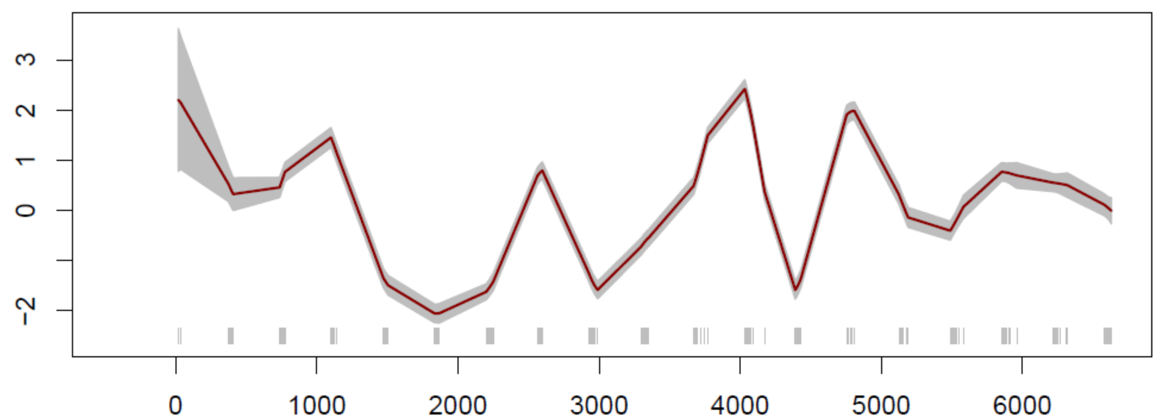
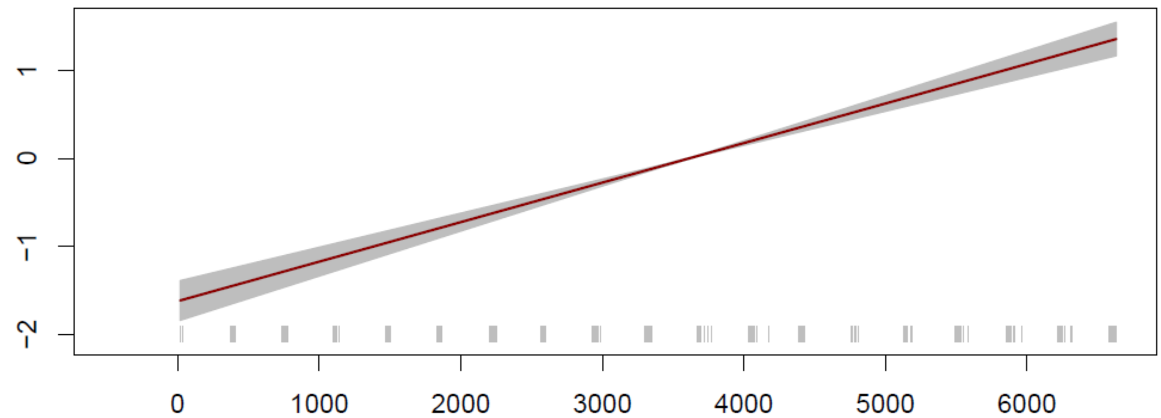
A. Spat



B. Small



C. Market

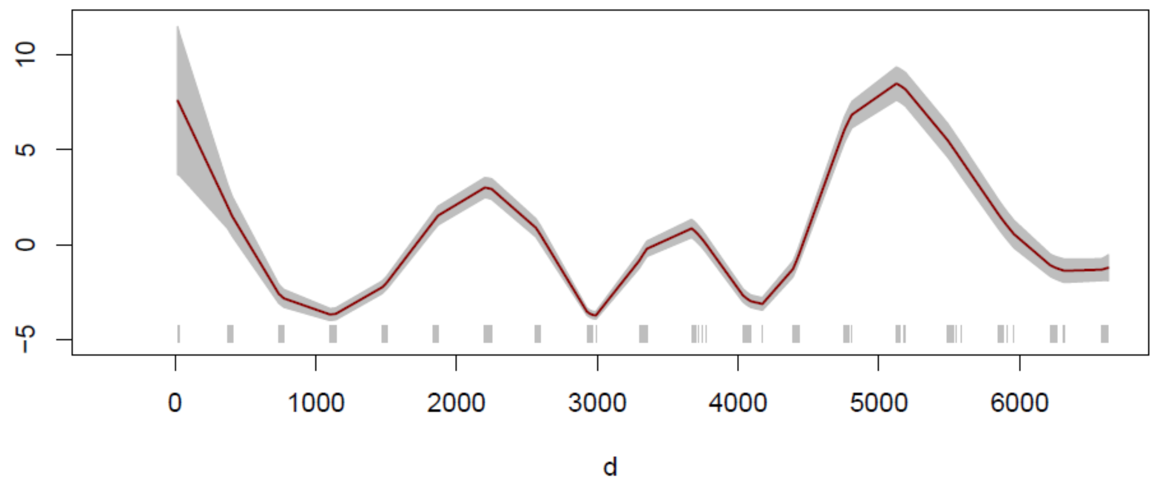


Figure 1. Smooth non-linear functions for spat (A), small (B), and market (C) oysters in the Maryland Portion of Chesapeake Bay. The x axes are labeled in terms of days since the start of the 1999 fall dredge survey, and the units for the y axes are in number per half bushel cultch.

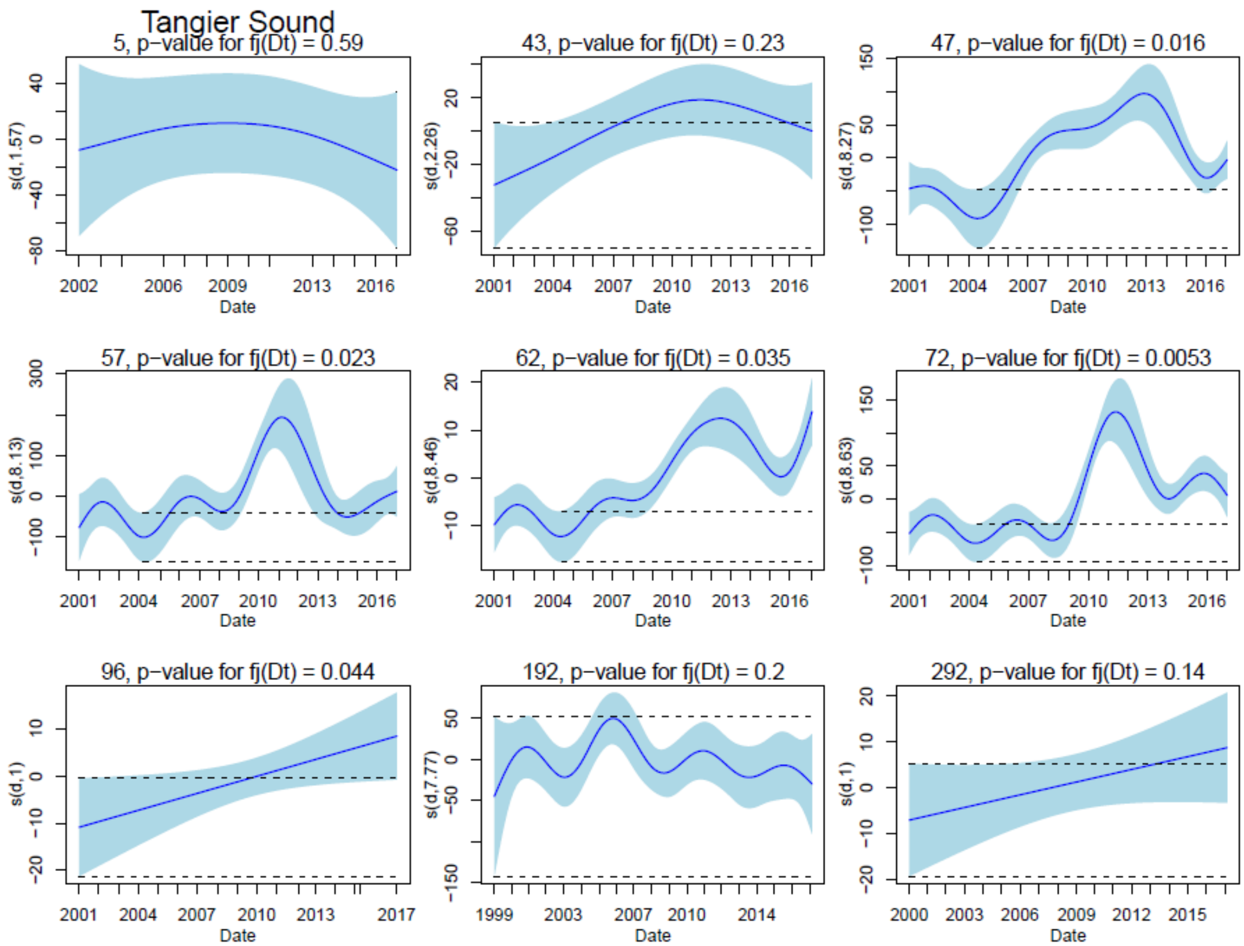


Figure 2. Regional smooth functions for spat by NOAA code in the Tangier Sound region. The NOAA code number is shown at the left above each plot, followed by the p-value for the significance of the smooth (compared to no trend). The y axes have units of oysters per half bushel cultch and the numbers on the y axes labels represent the effective number of degrees of freedom used by the smoothed function (where large numbers reflect higher non-linearity). The line represents the smoothed function and the shaded regions the approximate 95% confidence intervals that include uncertainty about the overall mean. The dotted lines represent the lower and upper confidence intervals in the year when the smoothed function has the lowest value, included to compare to the estimates in the last year of the time series. If the minimum is in the last year, the confidence intervals are represented by two dots.

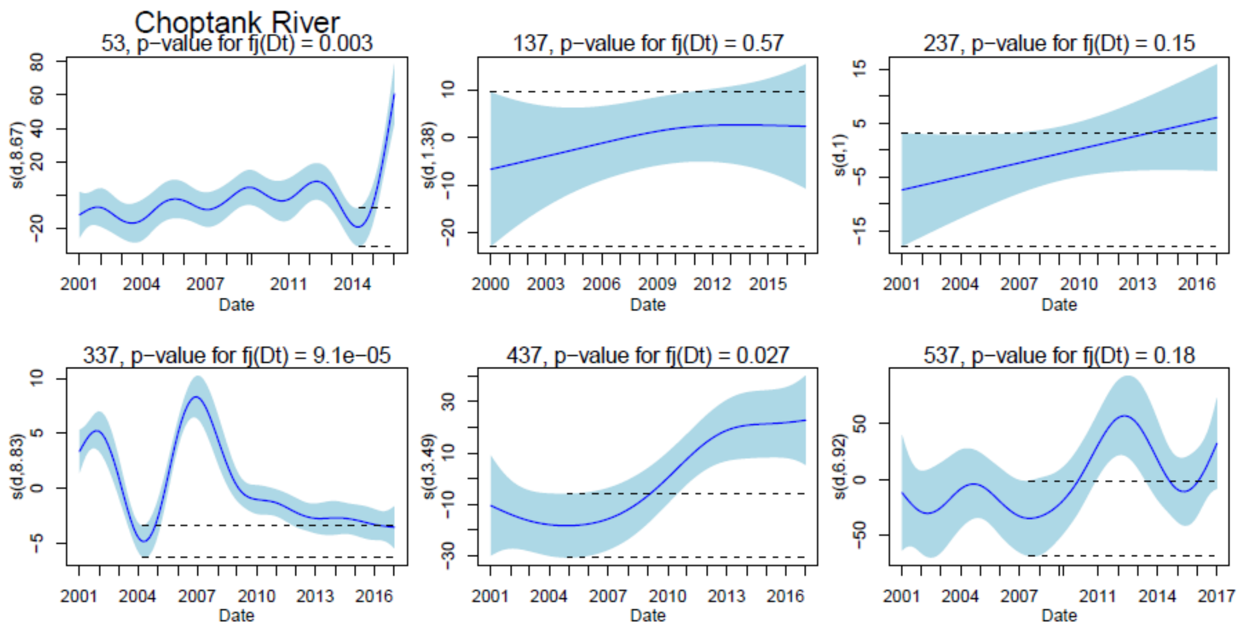


Figure 3. Regional smooth functions for spat by NOAA code in the Choptank region. Symbology is as described in Figure 4.

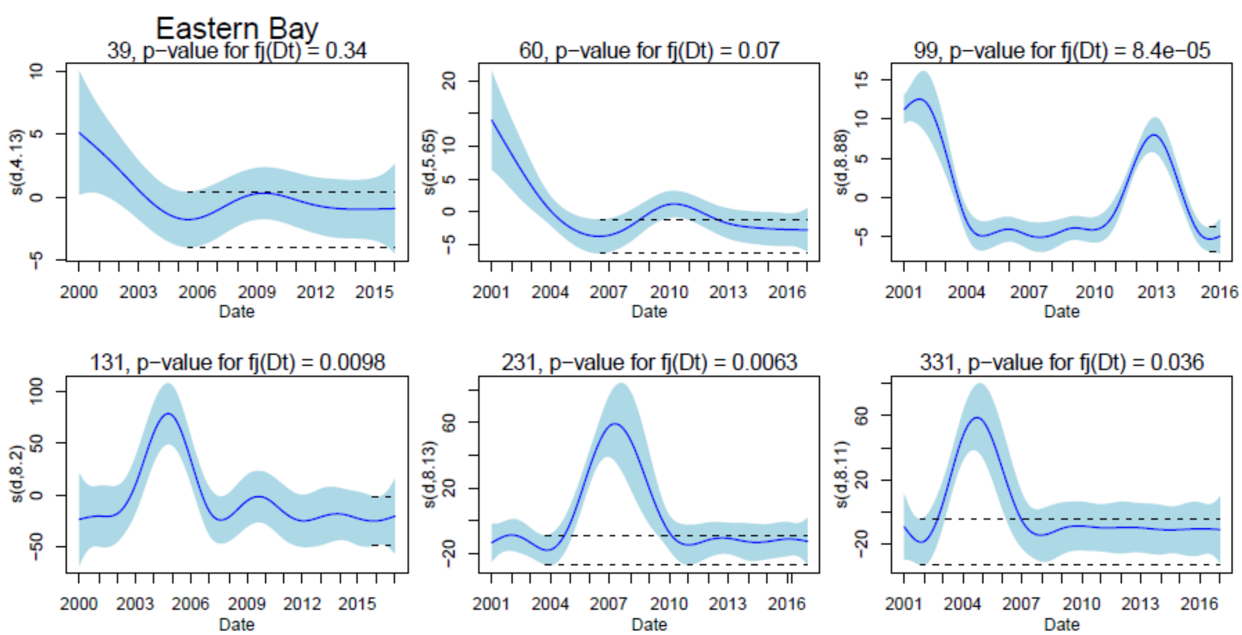


Figure 4. Regional smooth functions for spat by NOAA code in the Eastern Bay region. Symbology is as described in Figure 4.

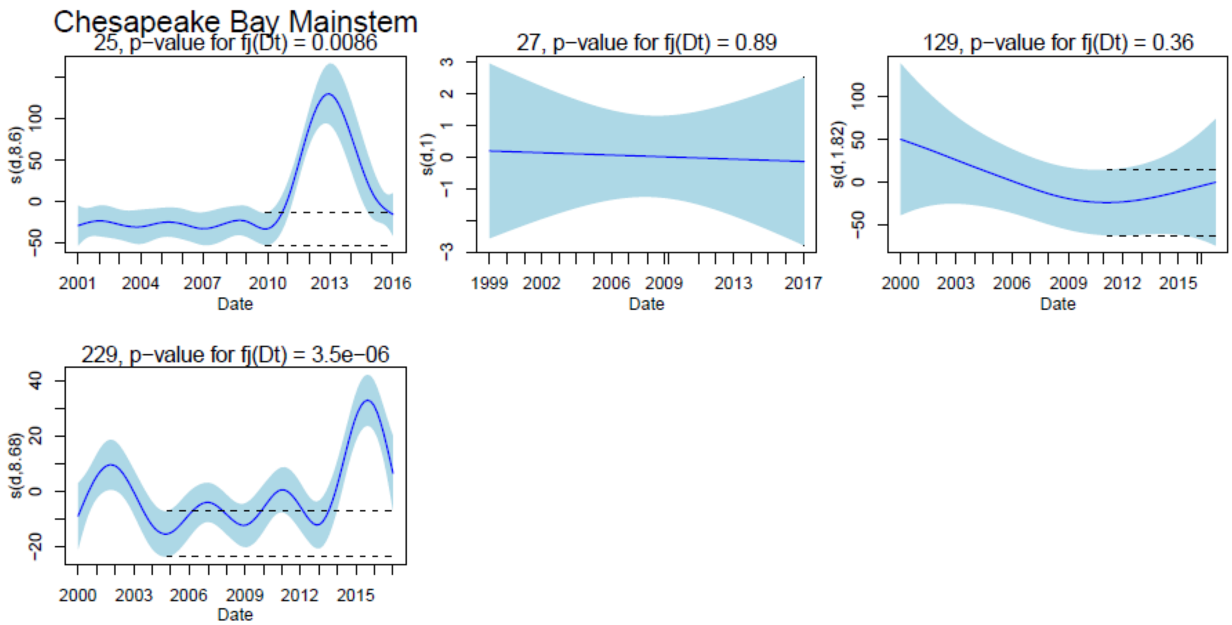


Figure 5. Regional smooth functions for spat by NOAA code in the Chesapeake Bay Mainstem region. Symbology is as described in Figure 4.

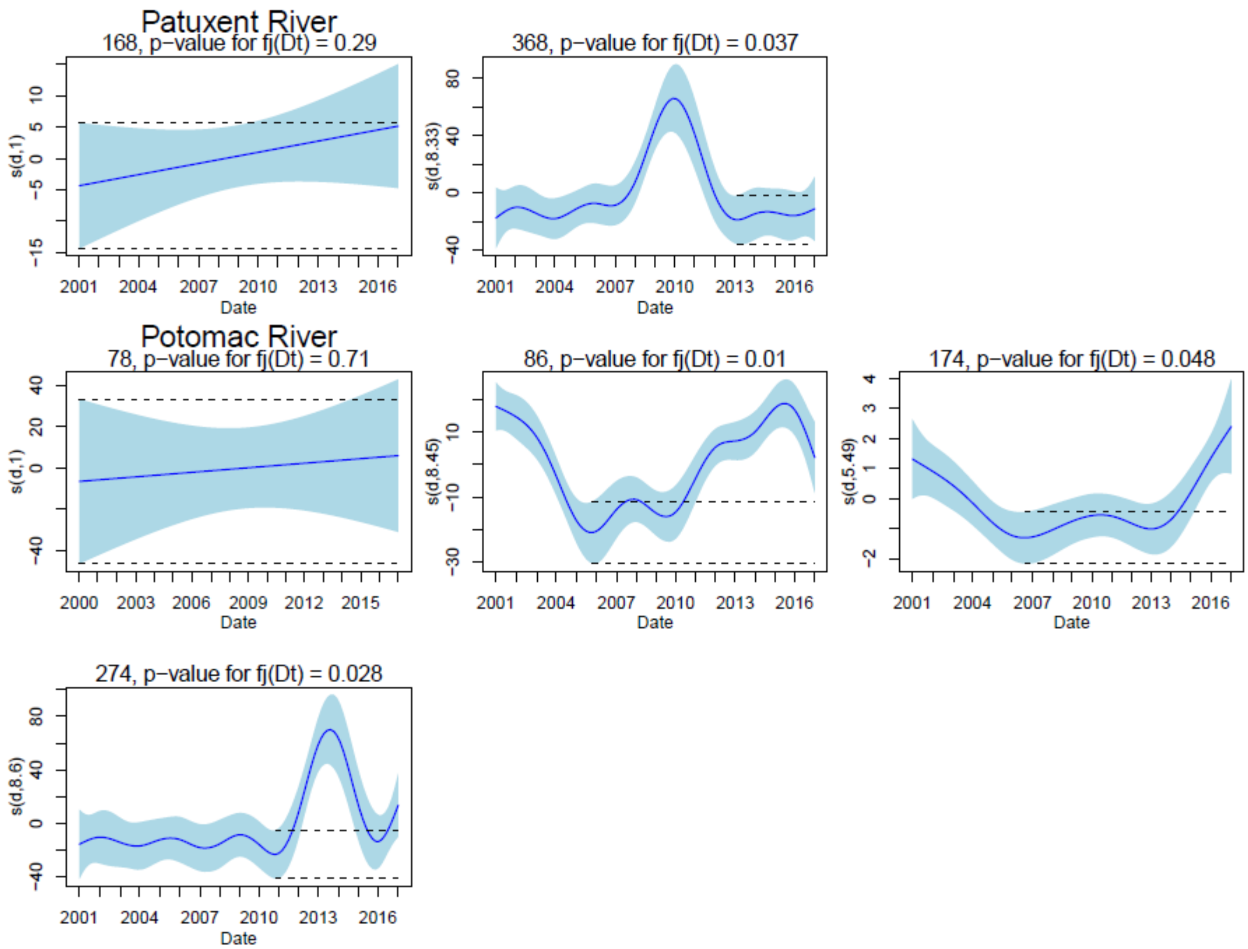


Figure 6. Regional smooth functions for spat by NOAA code in the Patuxent and Potomac River region. Symbology is as described in Figure 4.

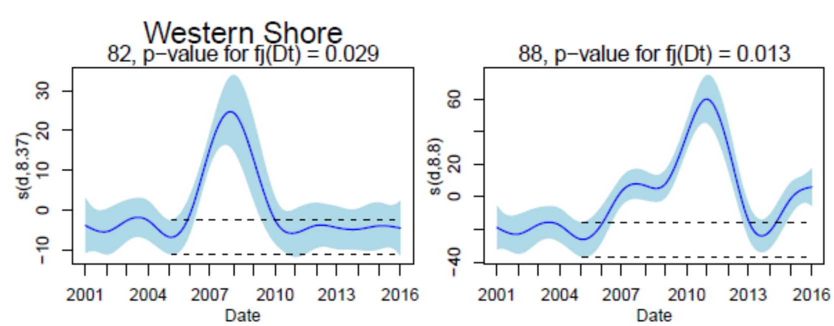


Figure 7. Regional smooth functions for spat by NOAA code in the Western Shore region. Symbology is as described in Figure 4.

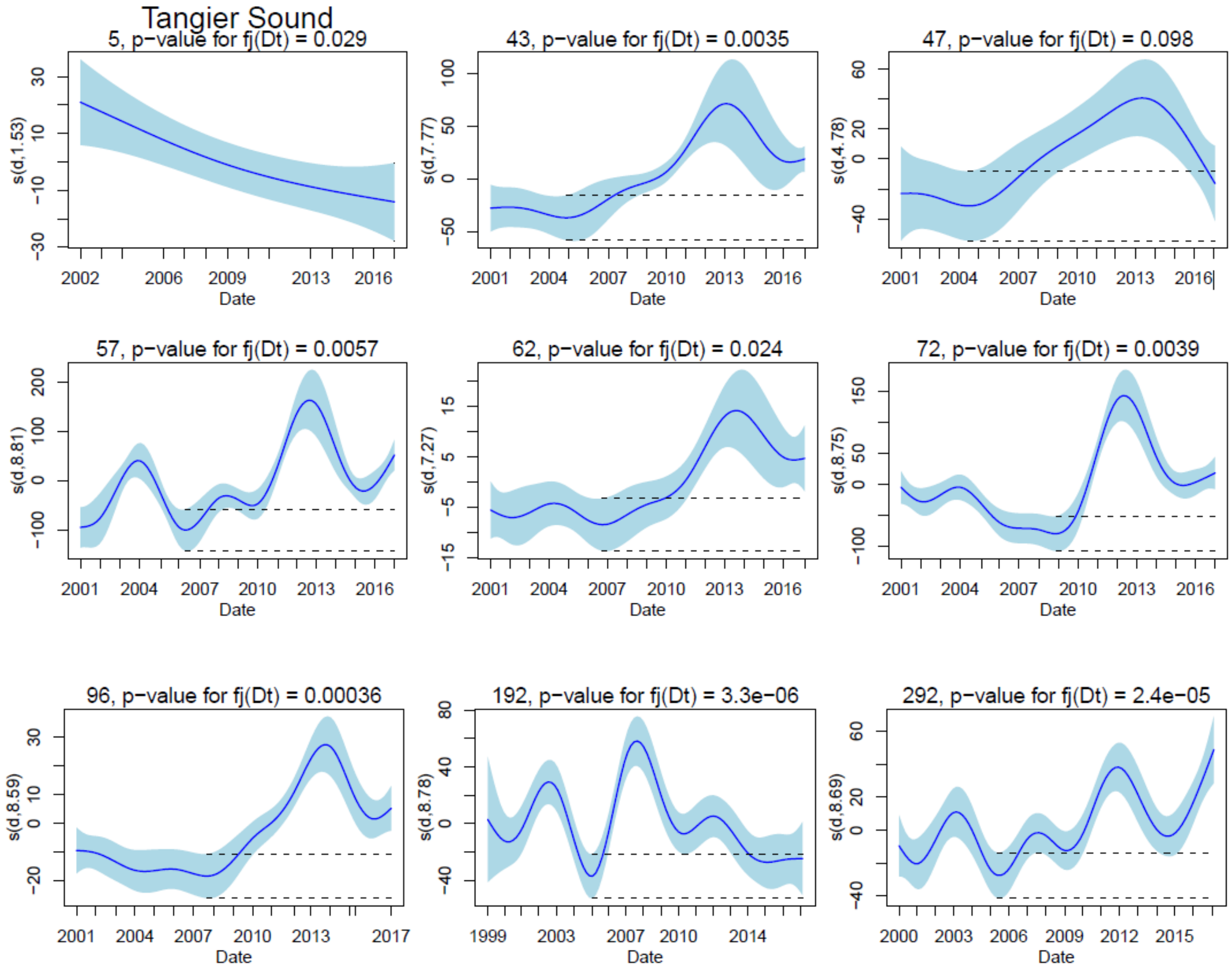


Figure 8. Regional smooth functions for small oysters by NOAA code in the Tangier sound region. Symbology is as described in Figure 4.

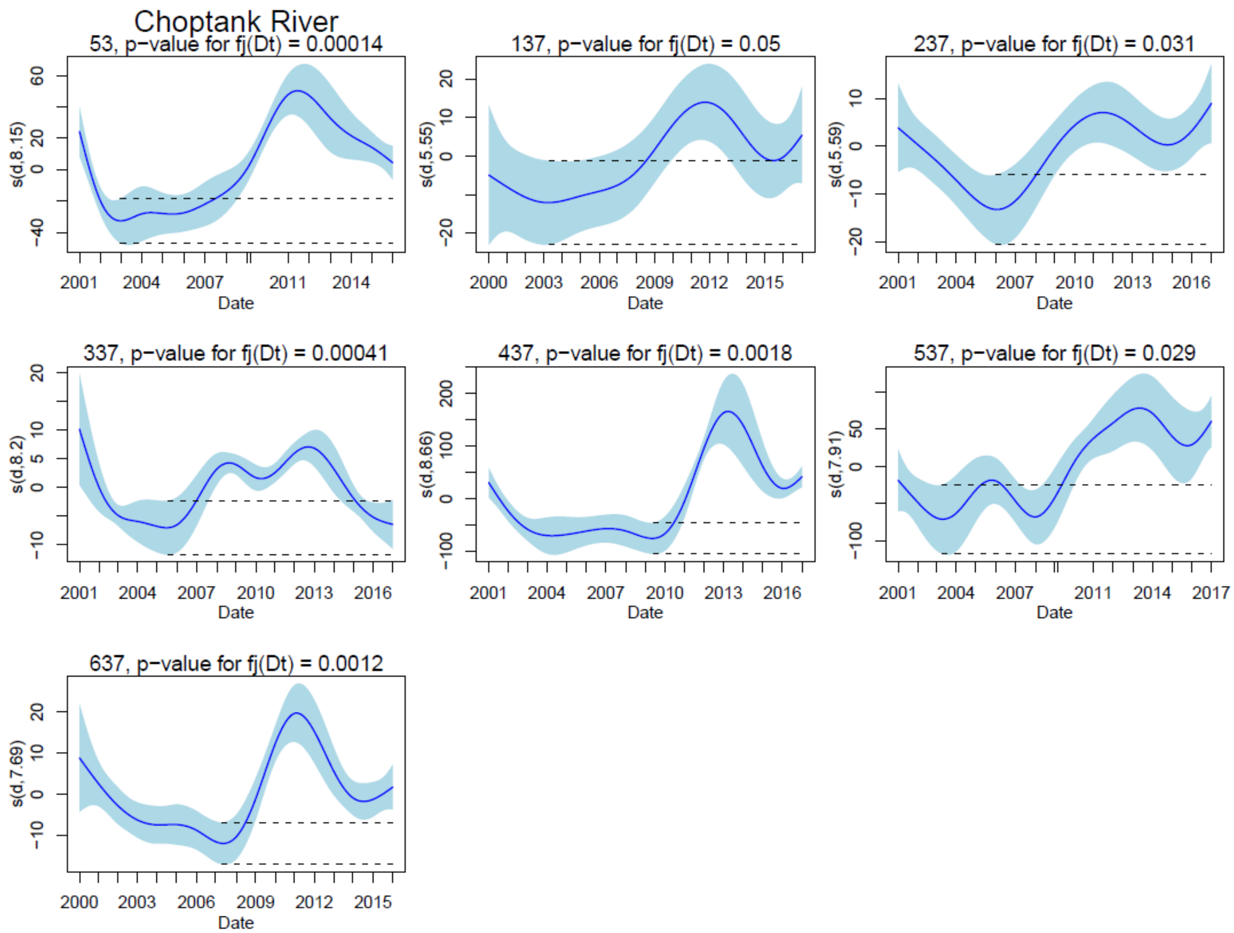


Figure 9. Regional smooth functions for small oysters by NOAA code in the Choptank region. Symbology is as described in Figure 4.

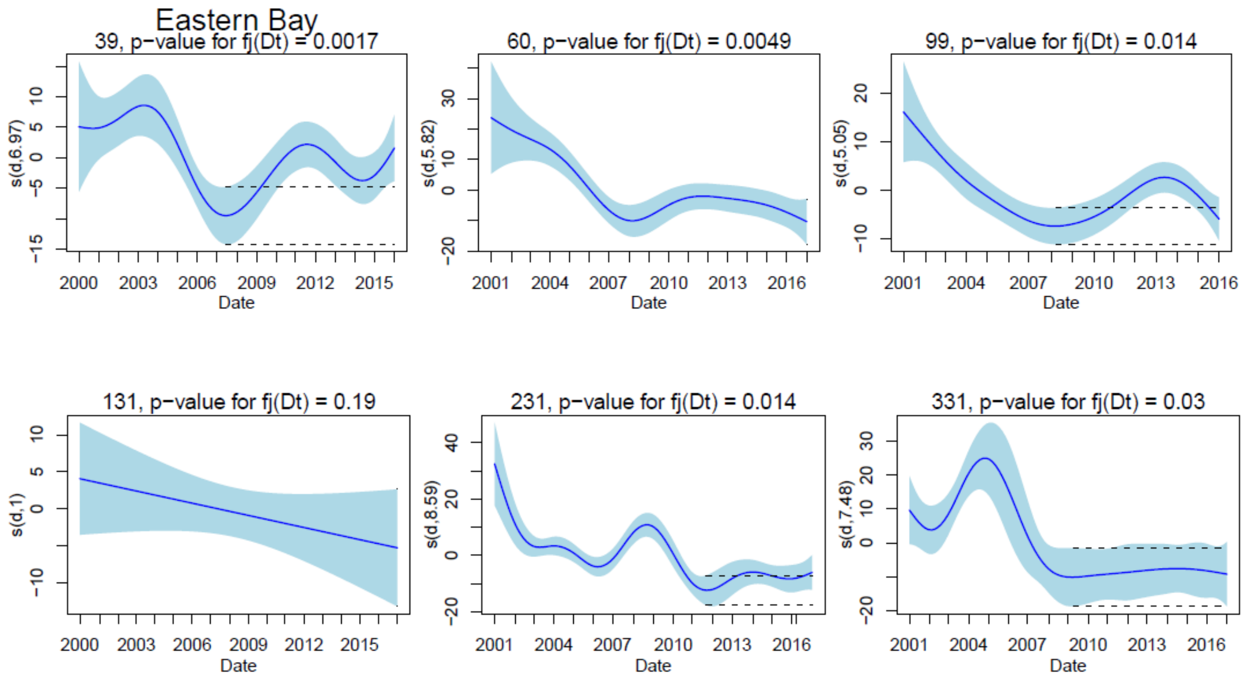


Figure 10. Regional smooth functions for small oysters by NOAA code in the Eastern Bay region. Symbology is as described in Figure 4.

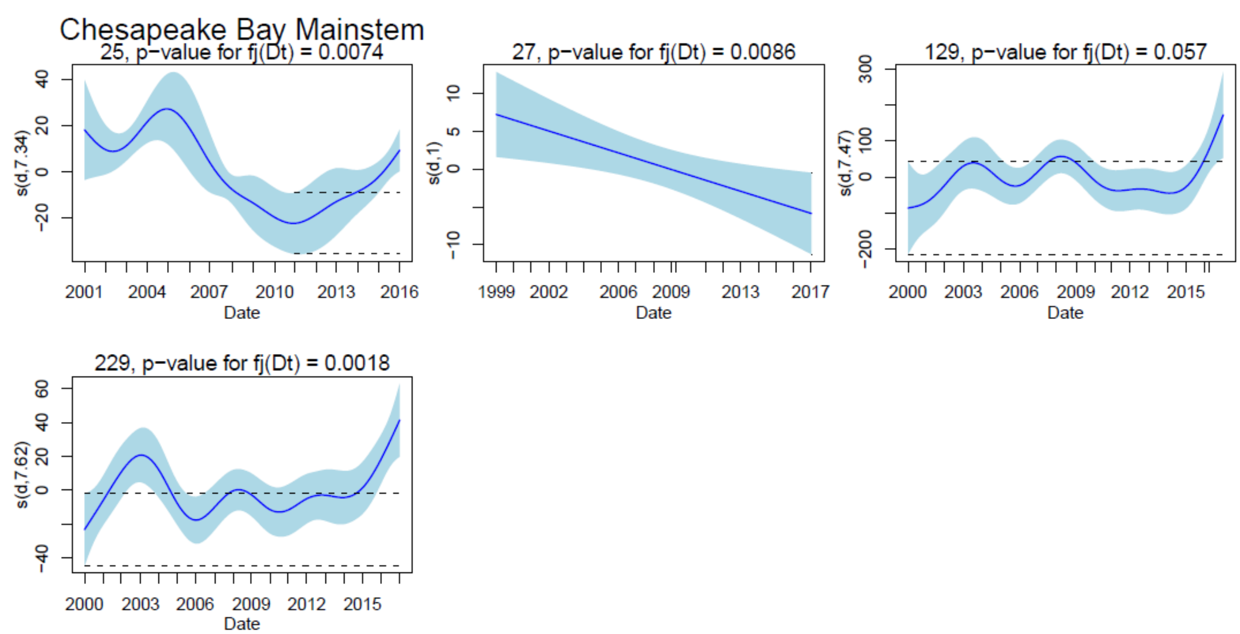


Figure 11. Regional smooth functions for small oysters by NOAA code in the Chesapeake Bay Mainstem region. Symbology is as described in Figure 4.

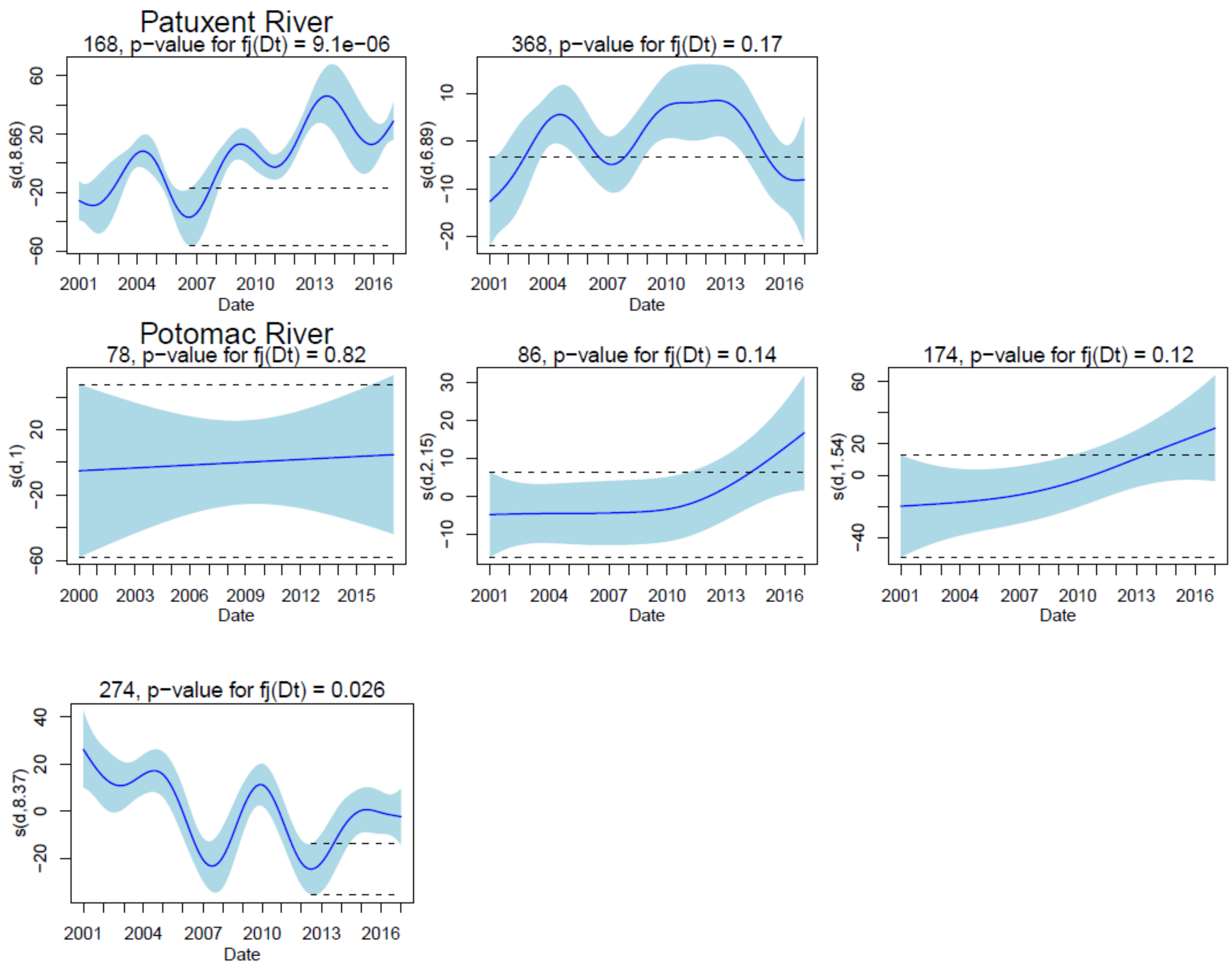


Figure 12. Regional smooth functions for small oysters by NOAA code in the Patuxent and Potomac River region. Symbology is as described in Figure 4.

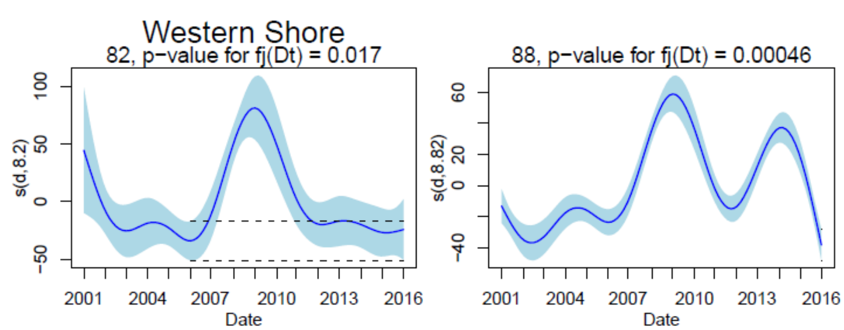


Figure 13. Regional smooth functions for small oysters by NOAA code in the Western Shore region. Symbology is as described in Figure 4.

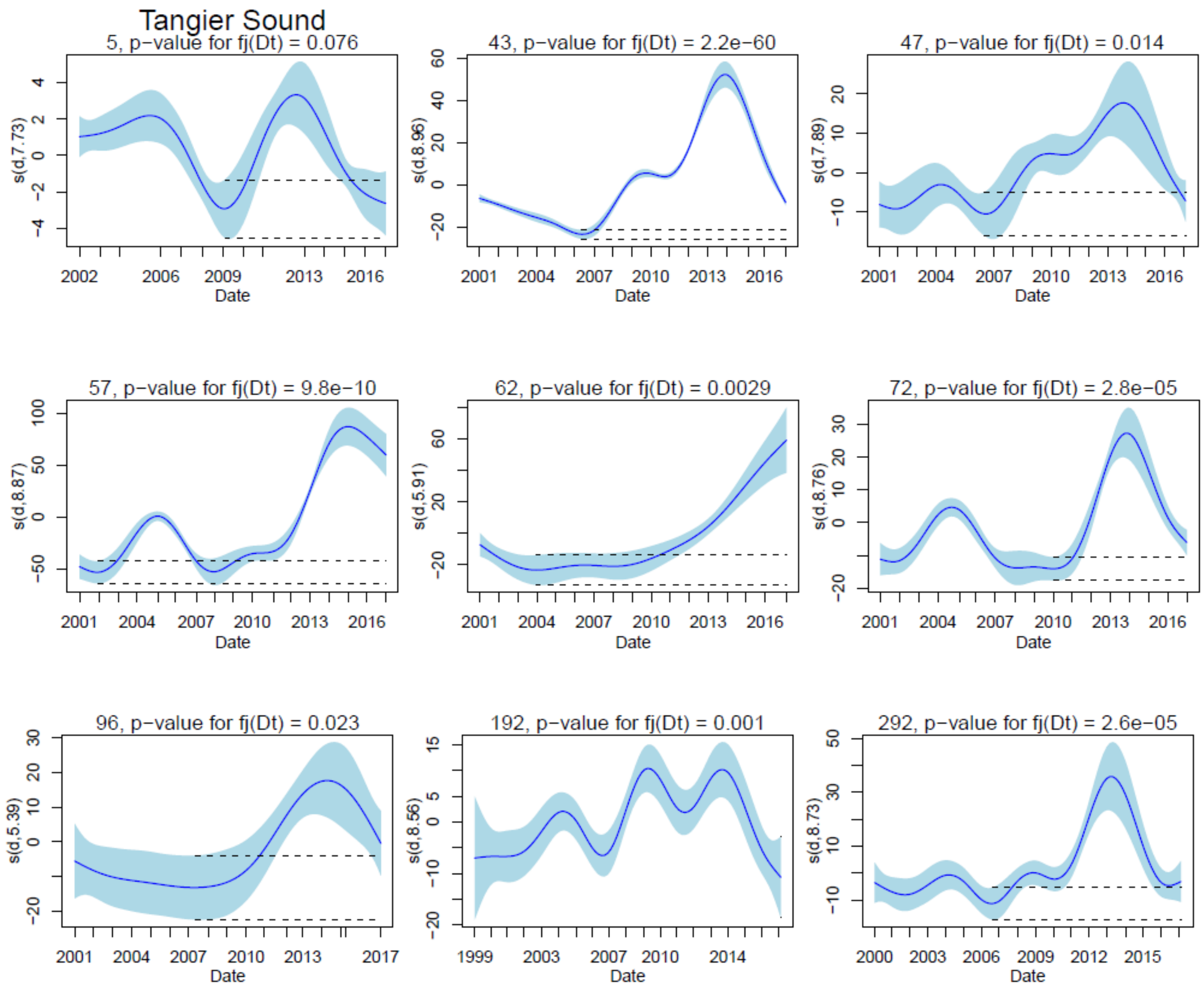


Figure 14. Regional smooth functions for market oysters by NOAA code in the Tangier sound region. Symbology is as described in Figure 4.

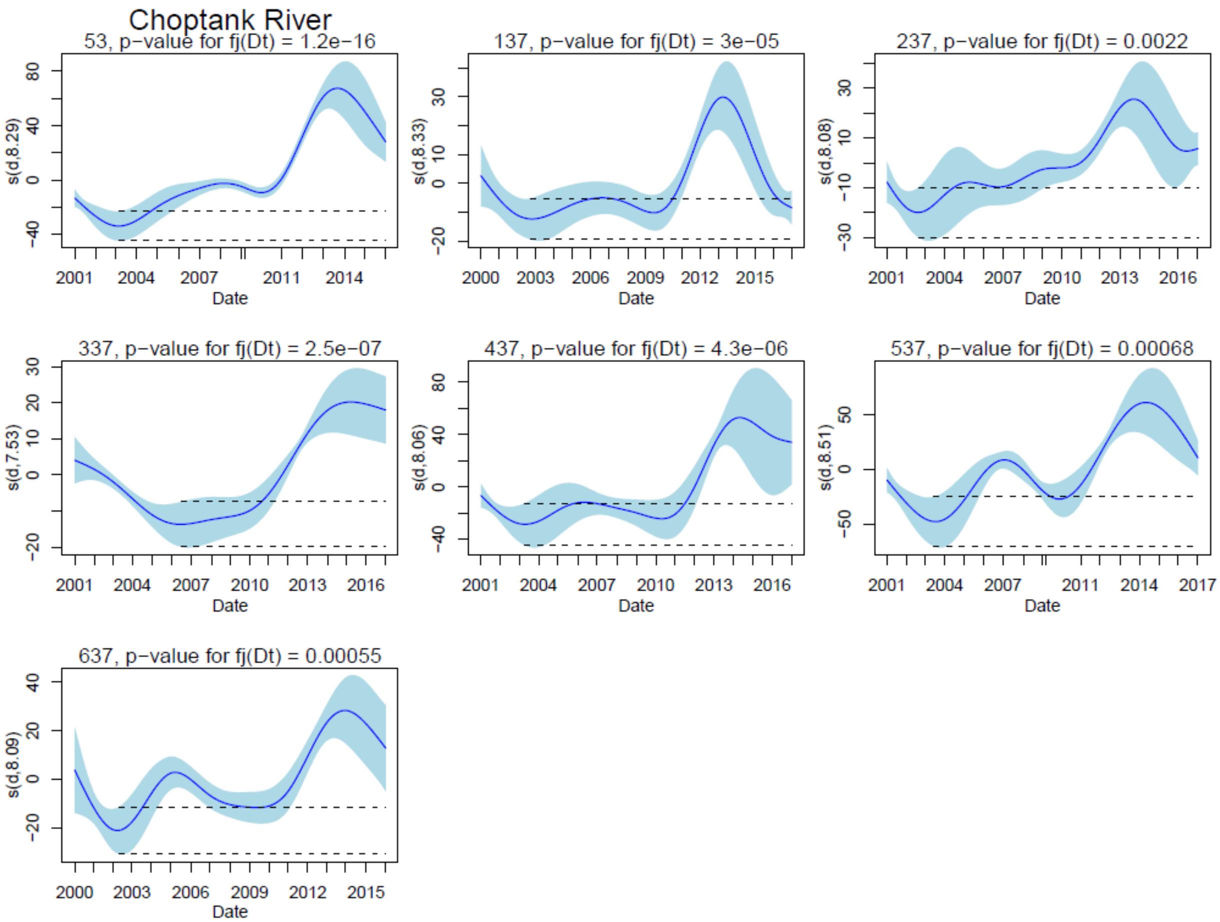


Figure 15. Regional smooth functions for market oysters by NOAA code in the Choptank Region. Symbology is as described in Figure 4.

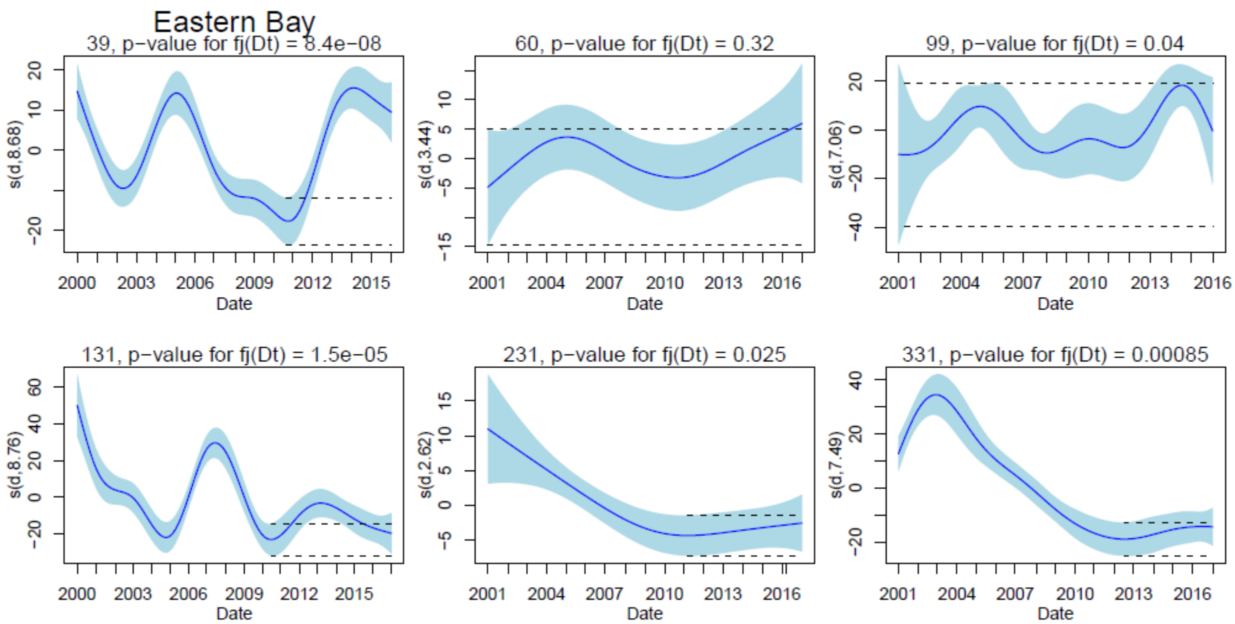


Figure 16. Regional smooth functions for market oysters by NOAA code in the Eastern Bay region. Symbology is as described in Figure 4.

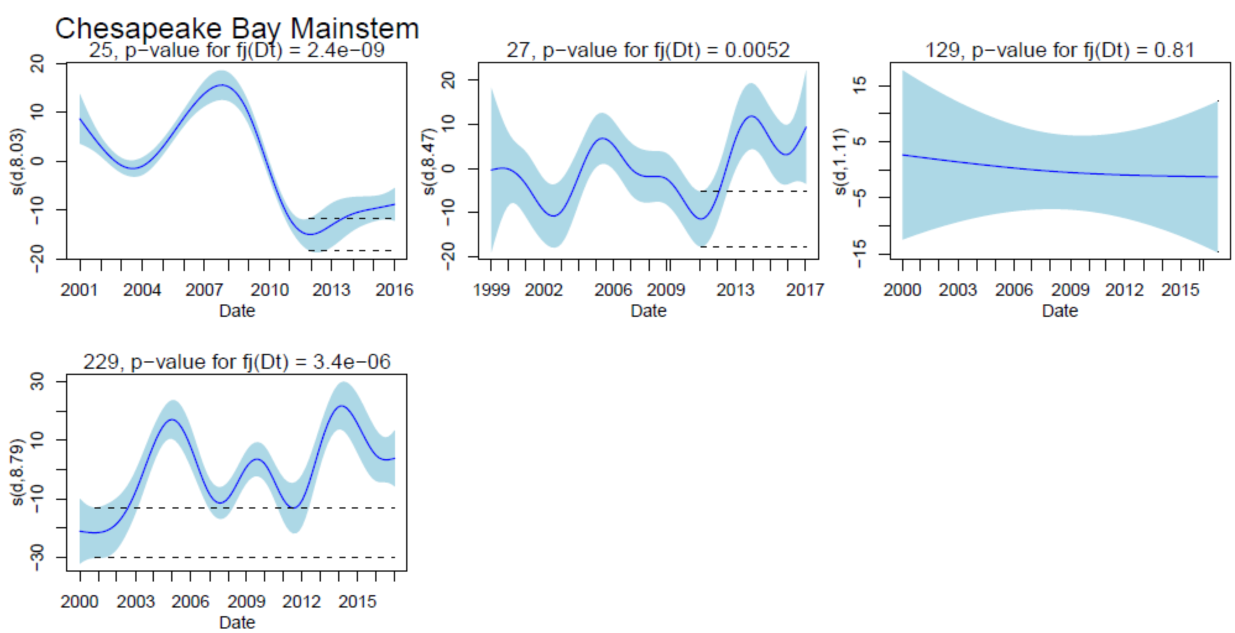


Figure 17. Regional smooth functions for market oysters by NOAA code in the Chesapeake Bay Mainstem region. Symbology is as described in Figure 4.

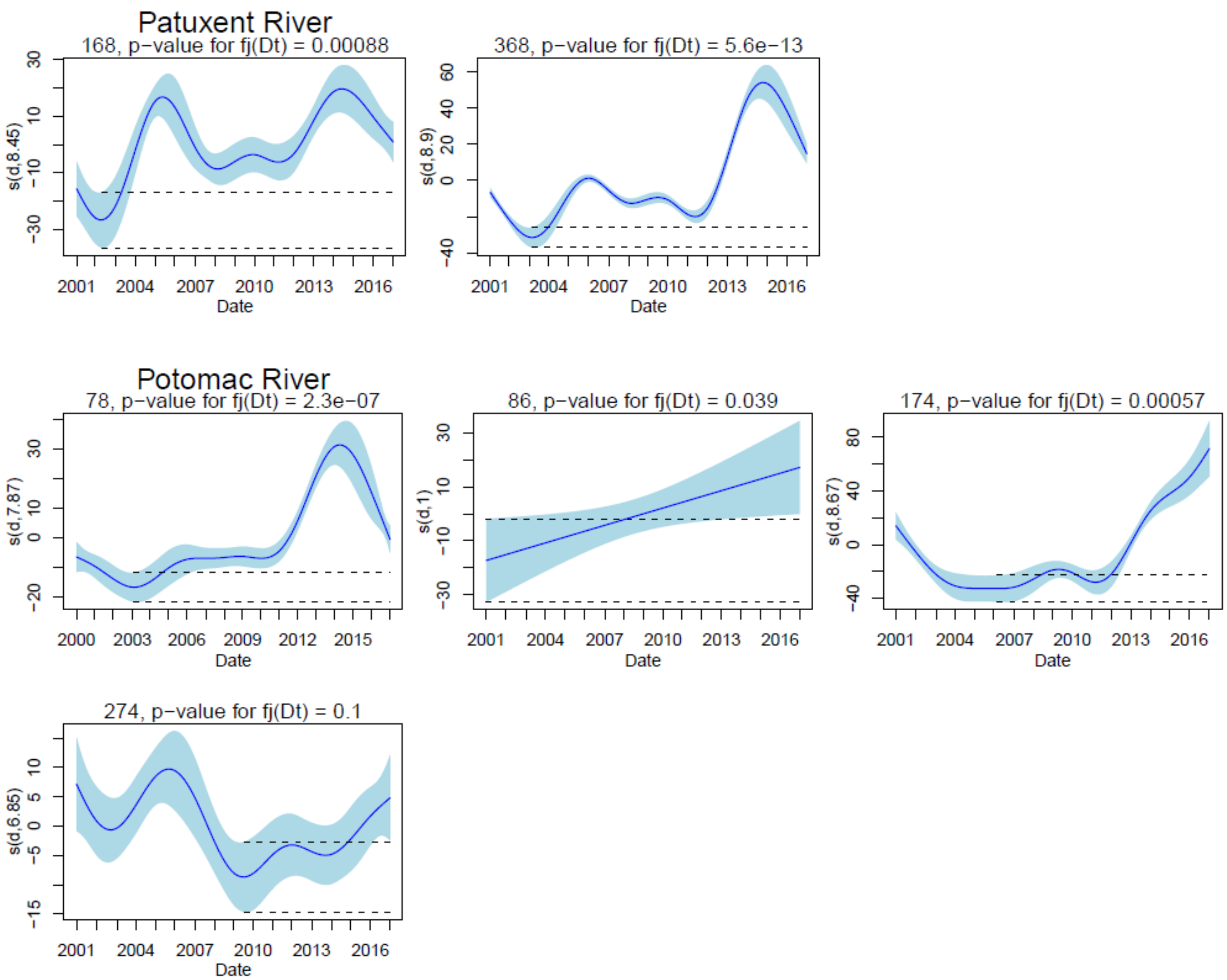


Figure 18. Regional smooth functions for market oysters by NOAA code in the Patuxent and Potomac River region. Symbology is as described in Figure 4.

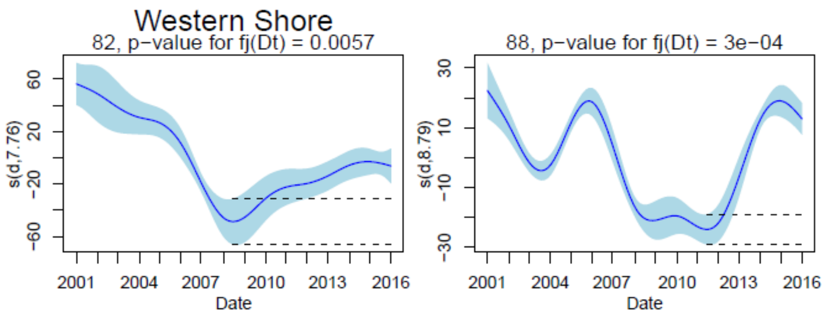


Figure 19. Regional smooth functions for market oysters by NOAA code in the Western Shore region. Symbology is as described in Figure 4.

Table 1. Number of NOAA codes by stage with the last year smoothed function confidence intervals overlapping (within) or not overlapping (above) with the confidence intervals in the minimum year of the time series. N/A represents NOAA codes with a smoothed function p-value ≥ 0.1.

Stage	**Within**	**Above**	**N/A**
Spat	14	8	12
Small	13	16	5
Market	11	20	3