Fisheries Research 212 (2019) 196–207

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Population dynamics of eastern oysters in the Choptank River Complex, Maryland during 1989–2015

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ARTICLE INFO

Handled by George A. Rose

Keywords:
Chesapeake Bay
Stock assessment
Marine protected areas
Oyster restoration
Crassostrea virginica

ABSTRACT

The eastern oyster (*Crassostrea virginica*) fishery in the Choptank River Complex (CRC), Maryland supports a large fishery. The CRC is also host to some of the largest oyster restoration projects in the world. Yet the relative effects of harvest and restoration on the population dynamics of eastern oyster in the CRC have not been assessed. We developed stage-based population models for each region of the CRC in AD Model Builder using dredge survey and harvest data provided by Maryland Department of Natural Resources from 1989 to 2015. Patterns in exploitation rates over time varied among regions. Abundance generally decreased during 1989–2003 and increased thereafter. Recruitment was greatest in the late 1990s, 2010, and 2012, which led to increases in abundance. Natural mortality was low across all regions during 2004-2015. Habitat, recruitment, and abundance declined 50–70% during 1989–2015, but fishery effort increased in years with higher abundance.

1. Introduction

Eastern oysters (*Crassostrea virginica*) are a commercially and ecologically important species that inhabit coastal waters and estuaries along the North American Atlantic coast. They provide important ecosystem services such as improving water quality and clarity through seston reduction and nitrogen removal, providing complex hard-bottom habitat, and promoting biodiversity (Newell, 1988; Coen et al., 2007; Kellogg et al., 2014). Of these benefits, the eastern oyster's ability to reduce solids and phytoplankton in the water column through suspension feeding has been observed *in situ* in shallow, mesohaline waters in Chesapeake Bay (Coen et al., 2007). Eastern oyster reefs promote biodiversity by providing refuge to fishes and invertebrates (Coen et al., 1999), acting as a coupling between benthic and pelagic systems, and bolstering fishery production for other species (Lenihan and Peterson, 1998).

The Maryland fishery for eastern oysters in Chesapeake Bay has experienced a large decline due to overharvest, loss of habitat, and disease (Rothschild et al., 1994; Wilberg et al., 2011). The fishery reached peak harvest in 1884 at 615,000 t (Rothschild et al., 1994). Annual harvest in recent years has since dropped to approximately 3% of the fishery's peak (Tarnowski, 2016), while abundance has been estimated at 0.3% of the abundance before the onset of commercial fishing (Wilberg et al., 2011). More efficient harvest methods such as power dredging and hydraulic patent tongs have been introduced over time that allowed the Maryland fleet to expand into deeper waters and remove eastern oysters at a higher rate (Rothschild et al., 1994). Although eastern oyster management has restricted harvest to the use of particular gear types in certain regions, the use of power dredging, a more efficient dredge gear (Chai et al., 1992; Powell et al., 2007) expanded into upper Chesapeake Bay in 2003. In addition, exploitation rate increased from 5% yr^{-1} in 2003 to an average of 25% yr^{-1} during 2004–2008 (Wilberg et al., 2011). This is above the estimated range of the exploitation rate that would produce maximum sustainable yield (5–10% yr^{-1}) for Chesapeake Bay, Maryland (Wilberg et al., 2013).

The recent decline in oyster populations has also been attributed to increased natural mortality from the introduction of two diseases into Chesapeake Bay (Mann and Powell, 2007). The diseases MSX (caused by *Haplosporidium nelsoni*) and Dermo (caused by *Perkinsus marinus*) both caused extensive mortality events in eastern oysters in Chesapeake Bay during the 1960s in high salinity waters (Burreson et al., 2000). The spread of MSX is attributed to the introduction of infected Japanese oysters (*Crassostrea gigas*), while the origins of Dermo are more nebulous (Mann and Powell, 2007); Dermo may have been associated with eastern oysters in Chesapeake Bay before its discovery (Burreson and Ragon Calvo, 1996). Although both diseases tend to be found in areas with higher salinity, during years of drought, 1986–1987 and 1990–1992, Dermo expanded its range into the mesohaline parts of

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https://doi.org/10.1016/j.fishres.2018.12.023
Received 13 August 2018; Received in revised form 20 December 2018; Accepted 24 December 2018

Fig. 1. Map of regions of the Choptank River Complex. Sanctuaries established after 2010 are shown in light grey.

Chesapeake Bay, Maryland (Cook et al., 1998). Estimates of natural mortality during 1986–1987 were approximately 60% yr^{-1}, and 25% yr^{-1} during 1990–1992 in Maryland, albeit with substantial uncertainty (Wilberg et al., 2011). Dermo remains prevalent among eastern oyster populations in Maryland (Tarnowski, 2016), but widespread mortality events have not occurred since 2002–2003 when the average natural mortality rate was close to 50% (Wilberg et al., 2011).

Management and restoration efforts have been implemented to counter the effects of overharvest and habitat loss. Current fishery regulations include a minimum size limit (76 mm), season limits, gear restrictions, and extensive stocking and habitat rehabilitation efforts (Kennedy and Breisch, 1983). In 2010, Maryland established 29 oyster sanctuaries (areas closed to oyster harvest), with the three largest sanctuaries established in the Choptank River Complex (Maryland Dept. of Natural Resources, 2016; Fig. 1). The Choptank River Complex sanctuaries were designed as part of an effort to protect 24% of the remaining oyster resource in Maryland. Additional restoration efforts have largely involved deploying young-of-the-year eastern oysters (spat) on shell in depleted eastern oyster habitat (Mann and Powell, 2007), although artificial reefs have been constructed in the three largest eastern oyster sanctuaries since 2010 (Westby et al., 2016). Implementing restoration and management strategies to counter the decline has been a contentious issue between natural resource managers and oyster harvesters (Bocking, 2011). Generally, commercial fishers have been against regulations that increasingly limit their fishing activities, such as the expansion of oyster sanctuaries (i.e., areas closed to oyster harvest) in 2010. In addition, requirements of some the funding sources used in the restoration efforts have meant that restored areas must remain closed to commercial harvest.

The CRC represents a substantial component of the Maryland fishery at 28% of annual yield (Tarnowski, 2016). Assessments have been performed to evaluate the effects of fishing and disease on eastern oysters in the Maryland portion of Chesapeake Bay, showing that populations within the area have been subject to substantial habitat loss and overfishing despite myriad regulations (Rothschild et al., 1994, Wilberg et al., 2011). However, the degree to which harvest, restoration, and natural mortality (including disease) have affected the abundance of eastern oysters in the CRC has not yet been assessed. Nor are current population estimates available for the CRC. Our research had two primary objectives: 1) to estimate abundance and rates of natural mortality and exploitation in all regions of the CRC, and 2) to compare estimates of natural mortality rates and recruitment among regions. To achieve these objectives, we implemented stock assessment models for each of the seven regions of the CRC to estimate how abundance and rates of natural mortality and exploitation have changed over time. Models were fitted to data from the Maryland Department of Natural Resources' (MD DNR) fall dredge survey, fishery catch per unit effort (CPUE) from the MD DNR buy ticket program, and estimated abundance derived from monitoring activities in Broad Creek, Harris Creek, and the Little Choptank River. These assessment models may provide managers with stock size information at a higher spatial resolution than has previously been possible and allow the evaluation of areas closed to harvest and restoration efforts.

2. Methods

2.1. Overview

We built nine statistical, stage-structured models for eastern oysters in the CRC similar to the one developed by Wilberg et al. (2011) for eastern oysters in the Chesapeake Bay, Maryland. Models were developed in AD Model Builder (Fournier et al., 2012) and estimated abundance by stage, natural mortality rates, amount of available habitat, and exploitation rates. The models were fitted to indices of density from the MD DNR fall dredge survey and fishery catch per unit effort (CPUE) during 1988 – 2016. The model year began on October 1st, corresponding to the beginning of the fishing season. Years in the model refer to the year of the end of the fishing season; for example, the model year for October 1, 1988 through September 30, 1989 was labeled as 1989.

2.2. Study area

The CRC is an estuary containing several smaller tributaries located in upper Chesapeake Bay, Maryland. The CRC is approximately 2000 km^2 with a salinity range of 5–20 depending on the location and time of year. The CRC was divided into seven regions by harvest reporting code (the lowest level of reporting for harvest and effort): Little Choptank River, Lower Choptank River, Middle Choptank River, Upper Choptank River, Harris Creek, Broad Creek, and Tred Avon River. Several regions contain areas closed to harvest for human health concerns or as oyster sanctuaries. Sanctuaries (i.e., marine protected areas) can cause bias in stock assessment model estimates because individuals within the sanctuary are likely subject to substantially lower mortality rates than those outside the sanctuary (Pincin and Wilberg, 2012). Therefore, to improve the accuracy of estimated parameters, we developed separate models for the Harris Creek and the Little Choptank River areas that were open and closed to harvest. Assessment models were developed for each of these nine regions (Fig. 1).

2.3. Data

2.3.1. MD DNR harvest data

Oyster buyers are required to submit reports to MD DNR that include number of eastern oysters purchased (in bushels), hours spent fishing, location, and number of crew aboard the vessel (Tarnowski, 2016). We used an average number of eastern oysters per bushel of 258 oysters at or above the legal size limit (76 mm shell height) based on estimates from eastern oyster buyers and harvesters. Up to 5% of a bushel may be composed of sub-legal eastern oysters (Tarnowski, 2016). We estimated that there were 360 smalls per bushel from estimates of the number of eastern oysters per bushel at different sizes using an average size for an undersized eastern oyster of 64 mm. We assumed that 5% of the harvest by volume was sub-legal based on discussions with harvesters and buyers.

We corrected the harvest estimates for underreporting. We assumed a rate of 24% underreporting for years prior to 2010 based on discussions with MD DNR (Frank Marenghi, MD DNR, personal comm.). On average, 86% of expected harvest reports were submitted during 2010–2015; we assumed that non-reporting was random and used 14% as an estimated underreporting rate for 2010–2015 (Frank Marenghi, MD DNR, unpublished data).

We calculated catch per unit effort (CPUE; bushels per man hour) for the hand tong and power dredge fisheries at the beginning and end of the season to provide the models with information on the amount of depletion during the fishing season. Hand tong and power dredge gears accounted for 91% of landings in the CRC during 1989–2015. Power dredging is more efficient at removing eastern oysters than other gears (Chai et al., 1992), so we calculated CPUE indices separately for the two gears. CPUE was calculated as the geometric mean number of bushels harvested per person hour for each year by gear type from the first month of harvest (October for hand tong, November for power dredge), and the last month of harvest (March). CPUE data were not always available for each month and gear either because information was missing on the buy ticket to calculate effort or no fishing occurred during that period for a gear. For years with CPUE data available for the beginning or end of the season, only one index was calculated.

2.3.2. Maryland fall dredge survey

Fall dredge survey data were available for 1989–2015. The fall dredge survey has been conducted annually from October through December using an 81-cm-wide oyster dredge over 259 natural oyster bars, including public fishery bars and bars located within sanctuaries. A 1/2 Maryland bushel (23 L) sub-sample was taken from the dredged material (cultch) after each tow. Eastern oysters in the subsample were sorted by stage and counted. The stages included young-of-the-year eastern oysters (spat), small adult eastern oysters (smalls; > 1 yr and < 76 mm shell height), and market-sized adult eastern oysters (markets; > 76 mm shell height). Additionally, the articulated shells (valves still attached at the hinge ligament) of dead eastern oysters (boxes) were recorded for the same size categories as live eastern oysters (smalls, markets; Jordan et al., 2002; Tarnowski, 2016). Spat boxes were also recorded but were very rare due to their fragility. All counts were then recorded as number per Maryland bushel.

We used the fall dredge survey data to develop indices of relative density (Wilberg et al., 2011) for each stage. Because the metric recorded over much of the fall dredge survey was number of oysters $23L^{-1}$ of cultch material, it is likely more closely related to density than abundance (Wilberg et al., 2011). If the area of oyster habitat was constant over time, indices of density and abundance would be equivalent. However, oyster habitat has declined substantially in the Maryland portion of Chesapeake Bay (Rothschild et al., 1994; Smith et al., 2005).

We fitted generalized linear mixed effects models (GLMM) to the fall dredge survey count data (Maunder and Punt, 2004; Bolker et al., 2009). The GLMMs included year as a fixed effect, and site (i.e., oyster reef) as a random effect to correct for changes in sites sampled over time and potential differences in catchability among sites (Wilberg et al., 2011), The model included a log link function and a negative binomial distribution to account for the over-dispersion of counts in the fall dredge survey (Linden and Mantyniemi, 2011). The model was applied separately to data for each region to develop indices of relative density by stage.

2.3.3. Patent tong population estimates

Data were available for Harris Creek, Broad Creek and the Little Choptank from patent tong surveys conducted to validate the side-scan SONAR bottom maps in 2010 and provide estimates of oyster population size and density. Data were collected during summer months using a stratified random sampling approach with four strata classified by bottom type. Thirty to 314 points per stratum were sampled. Estimates of abundance in each habitat classification were calculated as the product of mean density and the area of each habitat classification. The total abundance of eastern oysters in a region was the sum of the abundance estimate in each habitat classification. Nonparametric bootstrapping was used to estimate the precision of the estimates by resampling the data (with replacement) 10,000 times, calculating the abundance per stratum, and summing abundance over strata. This process was done separately for each region. Sample sizes for each stratum and region were fixed at the same levels as were achieved in the field sampling. The estimated number of live adult eastern oysters (smalls and markets) was 10 million for the Little Choptank Closed region 23 million for the Harris Creek Closed region, and 66 million for the Broad Creek region (K. Paynter, University of Maryland Center for Environmental Science, unpublished data). The models for Harris Creek, Broad Creek, and the Little Choptank River were fitted to these patent tong estimates of abundance for 2010.

2.3.4. Spat on shell planting

Hatchery-reared spat-on-shell have been planted as part of restoration activities in the CRC since 1998 (Appendix 1). The spat were approximately one-month old (1–2 mm shell height) when planted (Paynter et al., 2010). The number of eastern oysters planted varied by region and year. During 1998–2008, 15 million spat were planted in the Middle Choptank, and 460 million in the Upper Choptank (ORP, unpublished data). During 2011–2015, 2 billion spat were planted in Harris Creek, 130 million in the Little Choptank River, and 10 million in the Tred Avon River (Westby et al., 2016). Survival of spat from planting to October in the model was assumed to be 15% based on estimated survival from dive surveys in Harris Creek (K. Paynter, University of Maryland Center for Environmental Science, unpublished data).

2.3.5. Habitat restoration

Major restoration activities began in the CRC in 2010 in which oyster reefs were restored by planting hatchery-reared spat-on-shell, and hard bottom substrate was rebuilt using stone, clam shell, and oyster shell. As of the last year used in the models (2015), 0.55 km^2 of oyster reefs had been constructed from rock and bivalve shell and seeded with spat in Harris Creek, 0.52 km^2 in the Little Choptank River, and 0.06 km^2 in the Tred Avon (Westby et al., 2016). Estimates of repletion activities by MD DNR using fossil shell during 1984–1999 were not included in the models because these habitat plantings comprised approximately 0.02% of the estimated 90 km^2 of hard bottom habitat in the CRC as of 2001 (Smith et al., 2005) and 0.03% of the estimated 51 km^2 of habitat in the CRC as of 2010 (Allen et al., 2013). Shell from these activities was rapidly lost to sedimentation within about five years after planting (Smith et al., 2005).

2.3.6. SONAR bottom mapping

The area of available hard bottom habitat for eastern oysters in the CRC was estimated with side-scan SONAR by harvest reporting region in 2010. GIS polygons of oyster habitat were created by combining the SONAR data with patent tong survey data, ponar grabs, and acoustic classifications (Allen et al., 2013).

2.4. Assessment model

2.4.1. Population model

The models were stage-based using the five stages from the fall dredge survey: spat, smalls, markets, small boxes, and market boxes. The model year began on October 1, at the beginning of the hang tong season, and coincided with the timing of the fall dredge survey. The processes being modeled included recruitment to the fishery (natural and planted), growth from small to market, natural mortality (that includes disease) of spat, smalls and markets, the effect of fishing on small and market-sized eastern oysters (fishing mortality), changes to habitat over time, and the disarticulation of small and market boxes. Model variables and parameters are described in Table 1.

The initial abundance of spat, smalls, and markets in the first year were estimated as parameters for each region. We did not include a stock-recruitment relationship in the model because recruitment is affected by environmental factors as well as egg production and habitat availability (Kimmel and Newell, 2007). 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 (Eq. (1)),

$$N_{y+1,0} = e^{\bar{r}+\check{r}_y} + N_{y,a} S_{y,a} \tag{1}$$

The number of spat planted was multiplied by a survival rate of 15% 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 to become smalls and

Table 1
Definition of model variables and parameters in the stage-structured eastern oyster assessment model.

Parameter	Definition
	Indicator variables and subscripts
y	Year
s	Stage (0 = spat, 1 = small, 2 = market)
g	Gear (hand tong, power dredge)
	Estimated parameters
$\bar{r}$	Mean recruitment
$\bar{M}$	Average rate of natural mortality for small and market oysters
b	Rate of disarticulation of small boxes and market boxes
G	Mean growth parameter
d	Rate of habitat decay
d_{sm}	Rate of disarticulation of small boxes
d_{mk}	Rate of disarticulation of market boxes
$\check{r}$	Annual recruitment deviations
$\check{M}$	Annual deviations in natural mortality for small and market oysters
$N_{1989,s}$	Estimated number of live oysters by stage during the first year
$B_{1989,s}$	Estimated number of boxes by stage during the first year
$q_{N,s}$	Catchability of spat, small, and market oysters
$q_{B,s}$	Catchability of small boxes and market boxes
q_g	Catchability by gear: hand tong, power dredge
	Calculated quantities
$N_{y,s}$	Abundance of spat, small, and market oysters
$\bar{N}$	Average abundance of small and market oysters
M	Natural mortality of small and market oysters
$B_{y,s}$	Abundance of small and market boxes
H	Area of habitat
u	Rate of exploitation
$\hat{I}_N$	Estimated index of relative density of spat, small, and market oysters
$\hat{I}_B$	Estimated index of relative density of small boxes and market boxes
$\hat{I}_{Cb}$	Estimated index of CPUE at the beginning of the fishery
$\hat{I}_{Ce}$	Estimated index of CPUE at the end of the fishery
L	Negative log-likelihood component
L_{sp}	-Log-likelihood component for abundance of spat
L_{sm}	-Log-likelihood component for abundance of small oysters
L_{mk}	-Log-likelihood component for abundance of market oysters
L_{smb}	-Log-likelihood component for number of small boxes
L_{mkb}	-Log-likelihood component for number of market boxes
L_{abd}	-Log-likelihood component for index of patent tong survey abundance
G_p	Growth parameter penalty
b_p	Box rate of disarticulation penalty
$\check{M}_p$	Mortality deviations penalty
$\check{r}_p$	Recruitment deviations penalty
q_p	Catchability penalty based on Broad Creek model catchability estimates
$-LL$	Negative log-likelihood objective function
	Data and constants
$C_{y,s}$	Harvest of adult oysters by stage
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_{Cb}	Index of catch per unit effort (CPUE) at beginning of fishery
I_{Ce}	Index of catch per unit effort (CPUE) at end of fishery
M_{sp}	Natural mortality of spat
N_a	Added spat on shell
$S_{y,a}$	Survival of added spat on shell (from time of planting to Oct. 1)
$H_{y,a}$	Added habitat
$\sigma_{X,s}$	Log-scale standard deviation for spat, small, market, small box, market box likelihood
$\sigma_{\check{r}}$	Log-scale standard deviation of recruitment deviations
$\sigma_{\check{M}}$	Log-scale standard deviation of natural mortality deviations
σ_b	Log-scale standard deviation of rate of box disarticulation
σ_q	Log-scale standard deviation of catchability
σ_{abd}	Log-scale standard deviation of patent tong survey abundance
σ_G	Log-scale standard deviation of growth probability

adding those to the smalls already in the population that survived natural mortality and harvest, but did not grow to be markets (Eq. (2)),

$$N_{y+1,1} = (N_{y,1} - C_{y,1})(1 - G)e^{-M_y} + N_{y,0}e^{-M_{sp}} \quad (2)$$

Harvest was modeled as a pulse before natural mortality and growth occur. We believe this is 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 and the natural mortality 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 yr^{-1} based on estimates of natural mortality from eastern oysters in the Great Wicomico River, VA (Southworth et al., 2010).

The number of markets each year was calculated as the sum of the number of smalls that survive harvest and natural mortality and grow into markets and the number of markets that survived natural mortality and harvest from the previous year (Eq. (3)),

$$N_{y+1,2} = (N_{y,2} - C_{y,2})e^{-M_y} + (N_{y,1} - C_{y,1})Ge^{-M_y} \quad (3)$$

Natural mortality for smalls and markets was estimated for each year as model parameters. The exploitation rate was calculated as the number of markets harvested divided by the estimated abundance of markets at the beginning of the year (Eq. (4)),

$$u_y = \frac{C_{y,2}}{N_{y,2}} \quad (4)$$

The model also tracked the number of boxes in the small and market size categories to allow estimation of natural mortality for each year. The initial numbers of small and market boxes were estimated as parameters. The number of boxes each year was calculated as the sum of the number of boxes that did not disarticulate and were not broken by fishing activities and the number of adult eastern oysters (small or market) that survived harvest but experienced natural mortality (Eq. (5)),

$$B_{y+1,s} = (N_{y,s} - C_{y,s})(1 - e^{-M_y}) + B_{y,s}e^{-b_{y,s}}(1 - u_y) \quad (5)$$

We assumed that all smalls and markets became boxes after experiencing natural mortality. The abundance of small and market boxes in the first year were estimated as parameters.

Because the fall dredge survey provided an index of density rather than an index of abundance, we estimated the amount of oyster habitat (i.e., bottom habitat with oyster shell or other hard substrate). The area of oyster habitat was estimated for each year using an exponential decline through the estimated amount of habitat in 2010 (Eq. (6a)) with additions for shell planting and habitat restoration (Eq. (6b)),

$$H_{1989} = H_{2010}e^{-d(1989-2010)} \quad (6a)$$

$$H_{y+1} = H_y e^{-d} + H_{y,a} \quad (6b)$$

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 loss of oyster habitat that has been documented (Rothschild et al., 1994; Smith et al., 2005).

2.4.2. Observation model

Catchability was estimated for each of the five stages from the fall dredge survey and for the fishery-dependent indices of density. Estimated catchability was calculated using a mean difference between the observed index and estimated density on the log scale for each stage of the fall dredge survey (Eq. (7)) and CPUE (Eq. (8)),

$$log_e(q_{Xs}) = \frac{\sum_y log_e(I_{X\,y,s}) - log_e\left(\frac{X_{y,s}}{H_y}\right)}{Y} \quad (7)$$

$$log_e(q_g) = \frac{\sum_y log_e(I_{Cb\,y}) - log_e\left(\frac{N_{y,2}}{H_y}\right)}{Y} \quad (8)$$

which is the analytic solution for the maximum likelihood estimate. Catchability for the fishery-dependent indices at the end of the fishing season, required adjusting abundance for the amount of exploitation (Eq. (9)),

$$log_e(q_g) = \frac{\sum_y log_e(I_{Ce\,y}) - log_e\left(\frac{N_{y,2}(1-u_y)}{H_y}\right)}{Y} \quad (9)$$

The model predicted indices of density for the fall dredge survey and fishery CPUE. Predicted indices of density were calculated as the product of catchability and density at the beginning of the season for live oyster stages (Eq. (10)), boxes (Eq. (11)) and fishery CPUE (Eq. (12)) per unit of habitat,

$$\hat{I}_{N\,y,s} = \frac{q_{N,s}\,N_{y,s}}{H_y} \quad (10)$$

$$\hat{I}_{B\,y,s} = \frac{q_{B,s}\,B_{y,s}}{H_y} \quad (11)$$

$$\hat{I}_{Cb\,y,g} = \frac{q_g\,N_{y,2}}{H_y} \quad (12)$$

Predicted fishery CPUE at the end of the season was calculated in a similar manner, but required reducing the abundance by the amount of exploitation (Eq. (13)),

$$\hat{I}_{Ce\,y,g} = \frac{q_g\,N_{y,2}(1-u)}{H_y} \quad (13)$$

2.4.3. Model fitting

Model parameters were estimated by minimizing the objective function, which was the sum of the negative log likelihood components and penalties (Eq. (14)),

$$-LL = L_{sp} + L_{sm} + L_{mk} + L_{smb} + L_{mkb} + L_{abd} + G_p + b_p + \check{M}_p + \check{r}_p + q_p \quad (14)$$

We used a lognormal likelihood function (with additive constants ignored) for all indices in the model (Eq. (15)),

$$L_X = Y_X log_e(\sigma_X) + \sum_y \frac{1}{2}\left(\frac{log_e(X) - log_e(\hat{X})}{\sigma_X}\right)^2 \quad (15)$$

If data were not available for a year, that year was not included in the likelihood function.

The models for Broad Creek, the Little Choptank River Closed, and Harris Creek Closed were fitted to estimates of abundance from patent tong monitoring in 2011 for Harris Creek and the Little Choptank, and in 2013 for Broad Creek (Eq. (16)),

$$L_{abd} = \frac{1}{2}\left(\frac{log_e(N_{yr,abs}) - log_e(N_{sum} - C_{sum})e^{-\frac{2}{3}M}}{\sigma_{abd}}\right)^2 \quad (16)$$

The log-scale standard deviation was specified as 0.13 (the estimated standard error of abundance estimates from bootstrapping). Models assumed that 2/3 of the natural mortality occurred between the end of the fishery and data collection. Accounting for the fraction of mortality was necessary because the majority of patent tong monitoring data were from late August.

We incorporated penalties on some of the parameters to stabilize the estimates and to include outside information in the parameter estimation (Maunder, 2003). The initial number of smalls, markets, small boxes and market boxes in the first year were penalized in the likelihood function if they deviated from the equilibrium solution for a stable age distribution assuming a normal distribution on the log scale with a standard deviation of 0.4. The stable age distribution was calculated assuming that recruitment, natural mortality, and fishing mortality were constant prior to the first year of the model. This constraint on the initial abundances by stage was included because some areas had difficulty estimating initial abundance due to sparse data. The probability of growth was constrained using a normal penalty (on the log scale) with a median of 0.45 (Eq. (17)) based on growth of known age eastern oysters in Maryland oyster sanctuaries (Paynter et al., 2010; Wilberg et al., 2011),

$$G_p = \frac{1}{2}\left(\frac{\log_e(\bar{G}) - \log_e(G)}{\sigma_G}\right)^2 \tag{17}$$

The log-scale standard deviations (SDs) for each penalty were assumed to be known. The log-scale SD for growth was assumed to be 0.3 following Wilberg et al. (2011).

Normal penalties on the log scale were also applied to the disarticulation rate of boxes based on field-based estimates from Maryland (Eq. (18); (Christmas et al., 1997)).,

$$b_p = \frac{1}{2}\left(\frac{\log_e(\bar{b}) - \log_e(b)}{\sigma_b}\right)^2 \tag{18}$$

The log-scale SDs for the disarticulation rate of boxes were assumed to be 0.7.

Log-scale deviations from mean natural mortality (Eq. (19)) and recruitment (Eq. (20)) were penalized assuming a normal distribution,

$$\check{M}_p = \sum_y \frac{1}{2}\left(\frac{log_e\check{M}_y}{\sigma_{\check{M}}}\right)^2 \tag{19}$$

$$\check{r}_p = \sum_y \frac{1}{2}\left(\frac{log_e\check{r}_y}{\sigma_{\check{r}}}\right)^2 \tag{20}$$

The log-scale SDs for the natural mortality deviations was assumed to be 0.5 (Shumway, 1996). The log-scale SD for deviations in recruitment was assumed to be 2.0 due to the highly variable nature of the recruitment process (North et al., 2008; Southworth et al., 2010).

Catchability coefficients for each stage of the fall dredge survey were penalized with normal distributions on the log-scale using the Broad Creek model estimates of catchability (Eq. (21)),

$$q_p = \frac{1}{2}\left(\frac{\log_e(q) - \log_e(q_{BC})}{\sigma_q}\right)^2 \tag{21}$$

because the unconstrained models in some regions estimated rates of exploitation that were inconsistent (near zero) with the substantial reduction in fishery dependent CPUE observed during the fishing season.

2.5. Sensitivity analyses

We performed sensitivity analyses to determine how assumed input values affected model estimates. We used values near plausible limits in the sensitivity analyses to determine the maximum potential for change in the model estimates. To assess the sensitivity of the model to the fraction of small eastern oysters in the harvest, we ran the model with 2%, and 10% of harvest consisting of smalls, which were identified as plausible lower and upper bounds in conversations with commercial fishers. We also ran the model using different average sizes for smalls, 56 mm and 71 mm (minimum and maximum plausible average shell heights for undersized oysters), that changed the number of smalls per bushel to 410 and 313, respectively. Additionally, we conducted two sensitivity runs with spat mortality at 0.5 and 0.9 yr^{-1} based on the range of estimated spat mortality in the Great Wicomico River (Southwerth et al., 2010). Lastly, we conducted several sensitivity analyses to determine the effects of the penalties on our estimates; these included doubling the log-scale SDs for growth, natural mortality deviations, and recruitment deviations. We ran sensitivity analyses using the Broad Creek model to avoid excessive model runs and because the Broad Creek model results were the most stable. We characterized the sensitivity of estimates of the probability of growth, the mean annual rate of natural mortality, the rate of habitat decline, mean recruitment, and the mean abundance of adults.

3. Results

3.1. Model fits

The model fit the pattern of the fall dredge survey and CPUE indices well across stages, gear and regions (Figs. S1-S8). Estimated relative density of spat followed the pattern of higher values at the beginning and ending periods of the time series, but were somewhat less variable than the observed values (Fig. S1). Estimated relative density of both adult stages (live small and market sized oysters) showed a large decline in the early or mid-2000s and generally increased after 2005, which matched the trends in the data (Figs. S2 and S3). The observed indices of small and market boxes were highest in the early 1990s and early 2000s (Figs. S4 and S5) and were generally lower after 2004. Model estimates generally tracked the small and market box relative densities well, but the fit to small boxes was better than for market boxes. The trend in hand tong CPUE at the beginning and end of the fishing season (Figs. S6 and S7) tracked with the trend in small and market relative density for each of the nine regions. Trends in the observed hand tong CPUE were similar for the beginning and end of the fishery, but the CPUE tended to be higher at the beginning than at the end. Power dredge CPUE was substantially greater at the beginning of the season (Fig. S8) than at the end (Fig. S9) in regions where this gear was allowed.

3.2. Mortality

The estimated natural mortality rates showed a consistent pattern over time across regions with mortality rates highest (50%–90% yr^{-1}) during the early 1990s and early 2000s (Fig. 2). Estimated natural mortality was lower during 2004–2015 and varied among regions from 7% to 32% yr^{-1}. The Harris Creek Closed region had the highest average annual rate of natural mortality at 57% yr^{-1}, and the Little Choptank Open model estimated the lowest average rate of natural mortality at 16% yr^{-1}.

3.3. Recruitment

Estimated recruitment decreased from an average of 88 million spat in 1989 to 27 million spat in 2015, a 69% reduction (Fig. 3). The Broad Creek and Harris Creek Closed regions had the highest average recruitment of 123 million and 81 million spat, respectively, across the time series. The Tred Avon (12 million) and Upper Choptank (23 million) had the lowest average recruitment. In most regions, the highest estimated recruitment occurred during 1990-1995. Broad Creek and the Lower Choptank River had their peak recruitment during 1997 and 1998, respectively. Estimated recruitment was generally low during 2000–2010, after which a small increase occurred. For Broad Creek, the Lower Choptank, the Middle Choptank, the Upper Choptank, Little Choptank Closed, Harris Creek Open and Harris Creek Closed regions, recruitment increased in 2012.

3.4. Abundance

Estimated adult abundance, consisting of small and market oysters, was highest in the late 1980s or early 1990s for all regions except Broad Creek; the peak abundance occurred in the late 1990s in Broad Creek (Fig. 4). Total estimated adult abundance declined in the CRC by 44%

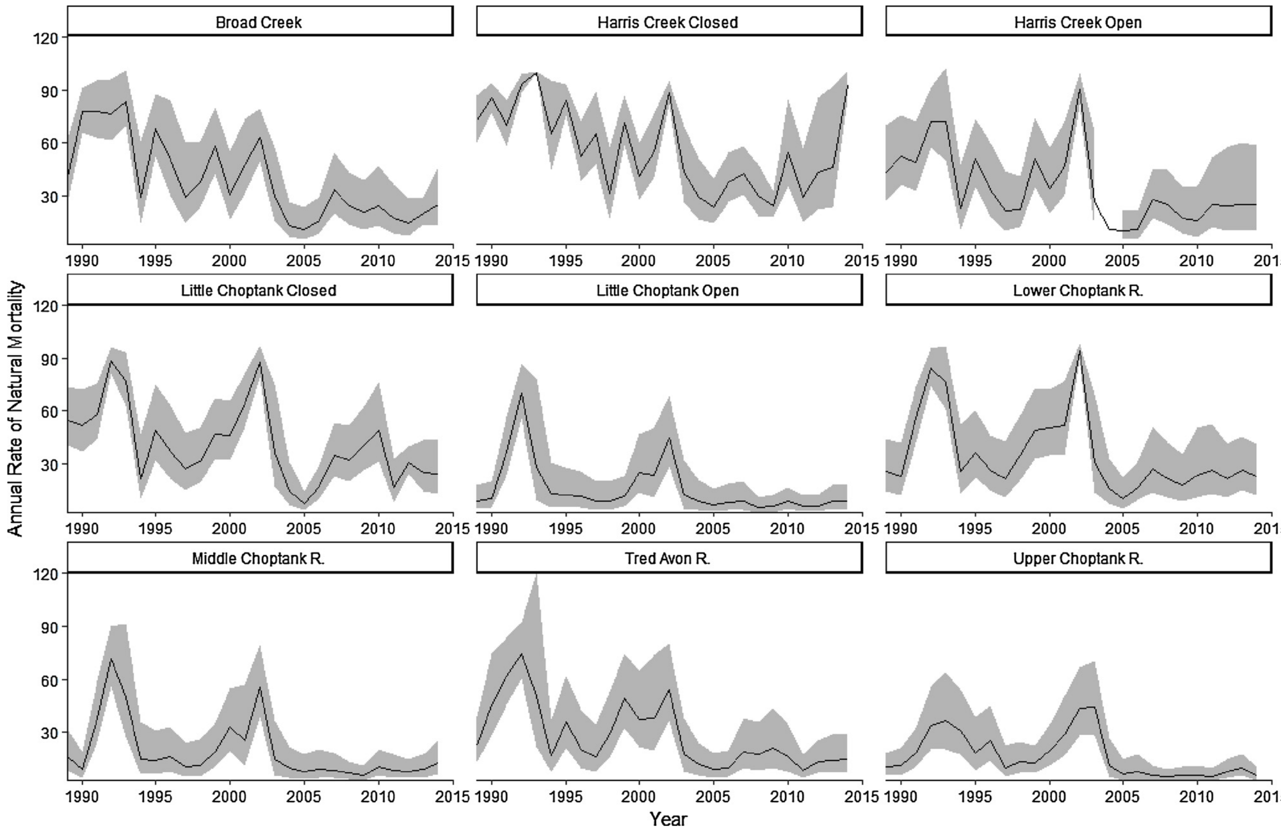

Fig. 2. Estimated natural mortality (% yr^{-1}) for small and market adult oysters and 95% confidence intervals (shaded) in each region of the Choptank River Complex during.1989–2015.

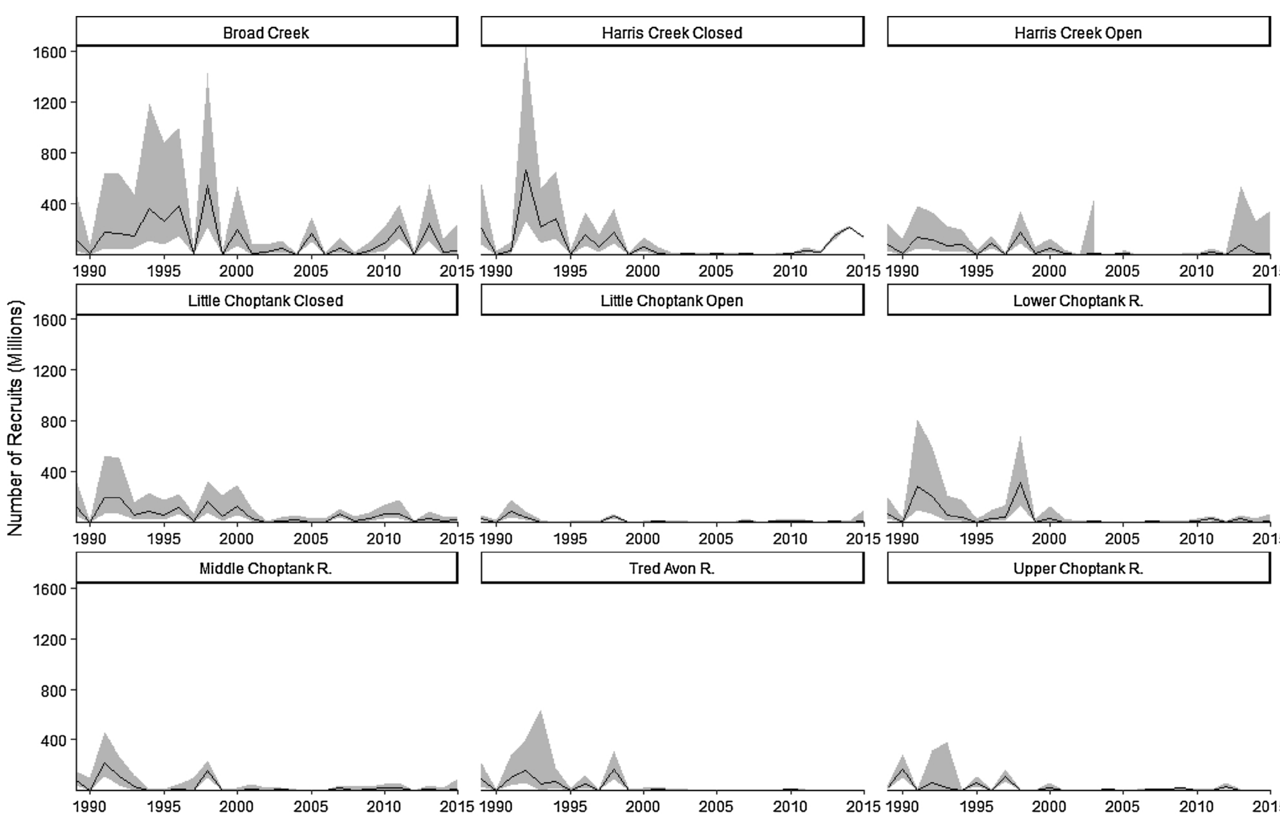

Fig. 3. Estimated recruitment with 95% confidence intervals (shaded) in each region of the Choptank River Complex during 1989–2015.

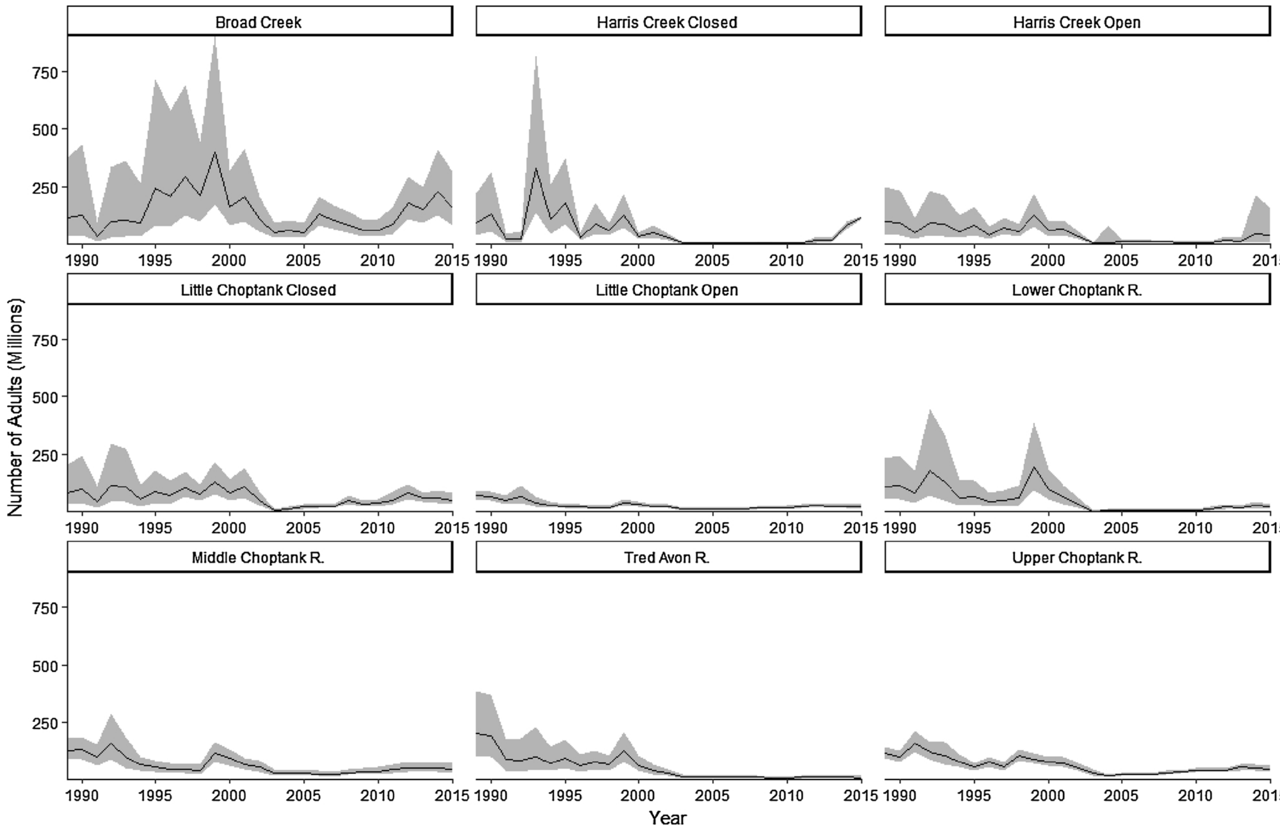

Fig. 4. Estimated adult (small and market) eastern oyster abundance with 95% confidence intervals (shaded) in each region of the Choptank River Complex during 1989–2015.

during 1989-2015. Broad Creek and the Little Choptank Closed regions had the highest average abundance at 140 million and 65 million adults, respectively, during 1989-2015. The Tred Avon and Harris Creek Open regions both had the lowest average adult abundance at 29 million and 44 million, respectively. Abundance increased in all regions in the late 1990s and then declined substantially thereafter with abundance in most regions being below their average at the end of the time series. The main exception was Broad Creek, which experienced an increase in abundance starting in 2005. The other exception was the Harris Creek Closed region that increased by 110 million adult oysters after 2010. The increases in estimated adult abundance in these regions were preceded by high recruitment in the previous year.

3.5. Habitat

Estimated patterns in habitat change differed among regions (Fig. 5), with some regions suffering substantial amounts of habitat loss and others experiencing low amounts. On average, the amount of available oyster habitat in the CRC declined by an estimated 66% during 1989-2015. Estimated habitat declined the least in the Upper Choptank, Broad Creek, and the Middle Choptank. The steepest rates of habitat loss were in the Tred Avon (9% yr^{-1}), Lower Choptank (7% yr^{-1}), and both Harris Creek models (5–6% yr^{-1}).

3.6. Exploitation

The average estimated exploitation rate for the CRC in aggregate decreased 19.1% yr^{-1}during 1989–2015, and the average exploitation rate among all regions of the CRC during 1989–2015 was 9.1% yr^{-1}. Estimated exploitation rates were highest during the same periods when adult abundance was highest for most regions (Fig. 6). During 1989–2010 Harris Creek Closed experienced the highest average exploitation rate (14.9% yr^{-1}) prior to becoming an oyster sanctuary, and the Tred Avon region experienced the lowest average exploitation rate (4.2% yr^{-1}). Estimated exploitation rates were relatively high (between 40% and 50% yr^{-1}) in the early 1990s. Exploitation increased from low levels to between 10% and 50% yr^{-1}during 1995–2000. Exploitation rates were below 10% yr^{-1} during 2000–2010 followed by another sharp increase after 2010 in most regions. Notable exceptions to this pattern included Broad Creek, where estimated exploitation rate was higher during 2005–2010 and 2012–2015 (20–45% yr^{-1}), Harris Creek Closed, where the exploitation was highest during 1995–2000 and 2005–2010 (50–60% yr^{-1}), and the Lower Choptank and Harris Creek Open, where the exploitation rate increased substantially after 2010. The estimated exploitation rate remained low in the Middle and Upper Choptank, Tred Avon, and Little Choptank Closed.

3.7. Parameter estimates

We compared estimates of the values of several parameters among regions, and they were similar for most parameters (Table 2). The probability of growth from the small to market stage was consistently between 0.30 and 0.50 yr^{-1} for all regions except for the Lower Choptank, which had the lowest value (0.26 yr^{-1}). The catchability for live small and market stages was generally 2–3 times higher than the catchability of boxes or spat. Estimates of catchability for the Lower Choptank model were higher than the other regions. Instantaneous rates of disarticulation were consistently between 0.8 and 1.5 yr^{-1} and were greater for small boxes than market boxes. The highest rates of disarticulation were estimated in the Lower Choptank model at 1.6 yr^{-1} for small boxes, and 1.3 yr^{-1} for market boxes.

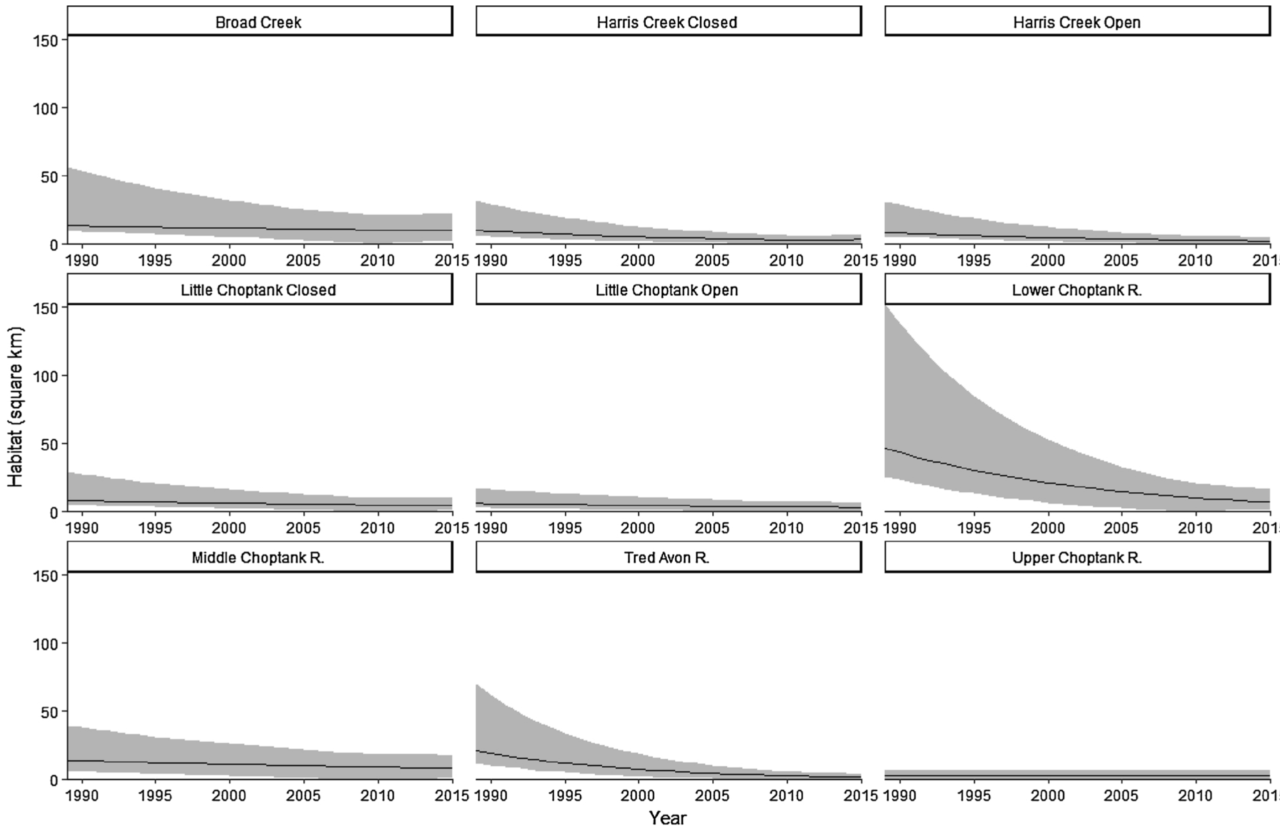

Fig. 5. Estimated change in the area of hard bottom oyster habitat and 95% confidence intervals for each region of the Choptank River Complex during.1989–2015.

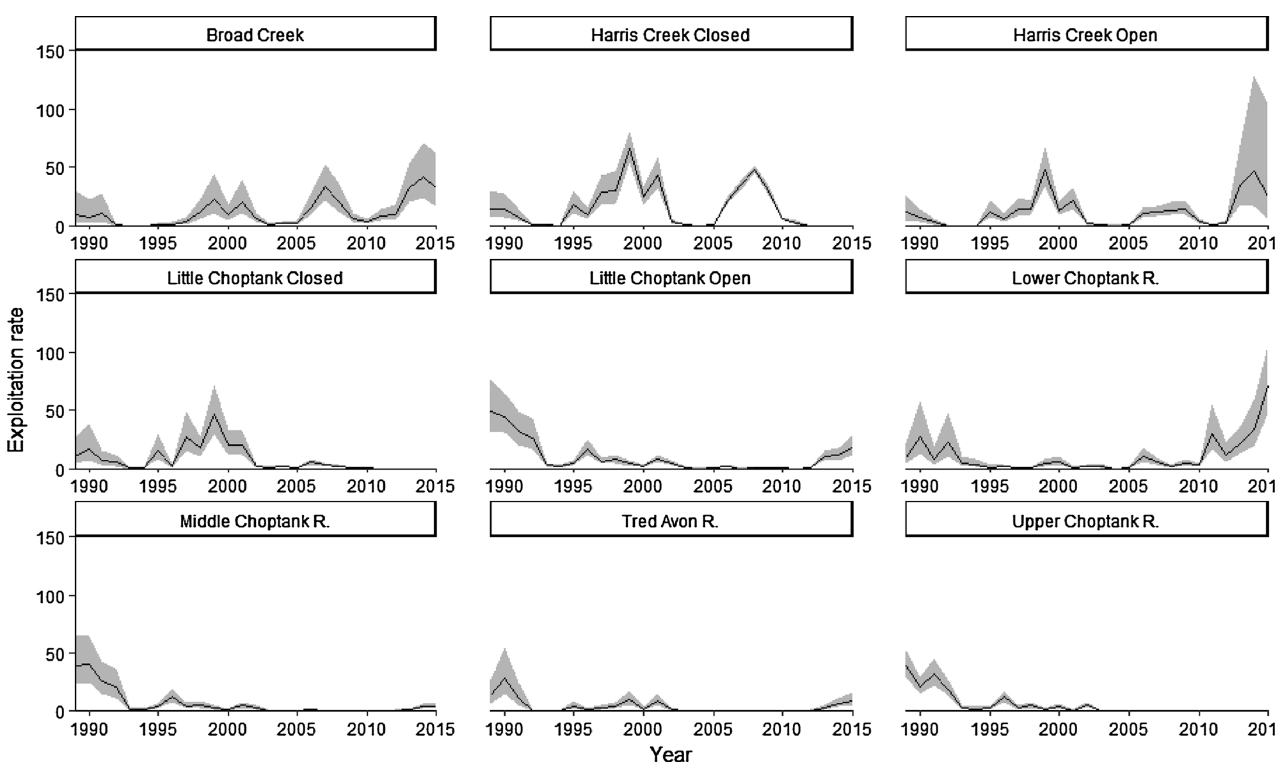

Fig. 6. Estimated exploitation rate (% yr^{-1}) of market-sized eastern oysters with 95% confidence intervals (shaded) for all regions of the Choptank River Complex during.1989–2015.

Table 2
Estimated values of parameters that were assumed constant in the model. G represents the probability of an oyster growing from the small to market stage (yr^{-1}), h the rate of habitat loss (% yr^{-1}), d the instantaneous rate of box disarticulation (yr^{-1}), and q the catchability coefficient. The subscripts for d and q indicate the stage: spat (sp), small (sm), market (mk), small box (smb), and market box (mkb). Regions are identified using the following abbreviations: Broad Creek (BC), Lower Choptank River (LC), Middle Choptank River (MC), Upper Choptank River (UC), Tred Avon River (TA), Little Choptank Open (LCO), Little Choptank Closed (LCC), Harris Creek Open (HCO), and Harris Creek Closed (HCC).

	G	h (%)	d_{sm}	d_{mk}	q_{sp}	q_{sm}	q_{mk}	q_{smb}	q_{mkb}
BC	0.30	1.25	1.03	0.85	5.30	15.05	10.94	3.84	4.48
LC	0.26	7.14	1.59	1.25	13.92	26.01	42.49	7.53	21.02
MC	0.50	2.01	0.87	0.83	3.31	13.52	9.79	4.26	7.73
UC	0.28	0.00	1.24	1.31	2.40	4.78	4.06	1.47	2.88
TA	0.48	9.24	0.98	0.85	3.14	14.61	10.37	4.59	5.35
LCO	0.48	2.53	0.85	0.74	3.28	13.30	9.40	4.61	8.28
LCC	0.38	2.36	1.35	1.37	3.08	13.17	11.65	3.83	6.88
HCO	0.35	5.26	1.27	1.00	4.13	16.69	13.76	3.45	4.38
HCC	0.32	5.67	0.98	1.35	2.95	17.45	40.74	3.61	12.34

Table 3
Sensitivity analyses results for the Broad Creek estimation model. Broad Creek model results are provided in the first row. Values below indicate the relative differences (%) from the parameter values obtained from the base model. Parameter values are from left to right: growth (G), average annual rate of natural mortality (M), average annual recruitment (r), and average annual adult abundance (N), and rate of habitat loss per year (h). Refer to the methods section for scenario descriptions.

Scenario	G	M	r	N	h
Broad Creek model constants	0.30	0.41	123	140	1.25
2% smalls	0.41	0.22	2.55	2.54	2.82
10% smalls	−0.81	−0.66	−4.19	−4.18	−4.97
56 mm smalls	−0.13	−0.10	0.26	0.21	0.30
71 mm smalls	0.05	−0.11	−0.20	−0.16	−0.21
$M_{sp} = 0.5$	−0.39	−1.56	−19.28	−0.49	−16.75
$M_{sp} = 0.9$	0.28	1.38	24.16	0.72	15.86
$\sigma_{\tilde{M}}$ (2x)	14.00	−42.28	−47.92	−36.08	−99.64
$\sigma_{\tilde{r}}$ (2x)	−3.50	5.51	25.96	21.03	183.55
σ_{G} (2x)	−24.49	7.19	32.41	26.82	11.18

3.8. Sensitivity analyses

The Broad Creek model was not sensitive to alternative assumptions about the fraction of small oysters in the harvest, the average size of small oysters in the harvest, the natural mortality rate for spat, or the standard deviations for natural mortality, recruitment variability, or growth (Table 3). The parameter estimates from the sensitivity scenarios were almost always within 30% of the estimates for the base model. Model estimates were moderately sensitive in the scenario with higher variability of natural mortality; the average natural mortality rate, average recruitment, and average abundance decreased by approximately 30%. Generally, mean recruitment and adult abundance were the most sensitive estimates. The estimate of habitat loss for Broad Creek was relatively low (1.25% yr^{-1}), so even large percentage-wise changes in the estimated rate of habitat loss were on the order of +/- 2% yr^{-1} differences.

4. Discussion

Abundance of eastern oyster in the CRC has increased since 2004 because of relatively low natural mortality rates and increased recruitment in recent years. Natural mortality rates of eastern oysters have been stable near or below 30% yr^{-1} in almost all regions of the CRC since 2004, the longest period of low mortality in 27 years (Tarnowski, 2016). This period of low natural mortality was potentially due to a confluence of advantageous environmental conditions for recruitment and low levels of diseases and potentially increased resistance to Dermo (Yu et al., 2011; Zhang et al., 2014). The high recruitment events caused increased abundance during 2010–2015 in regions of the CRC open to harvest. Recruitment events may have been influenced by salinity (Kimmel and Newell, 2007; North et al., 2008) and freshwater flow (Tarnowski, 2016), with recruitment higher in low salinity years.

The pattern of natural mortality rates over time matched closely with mortality rate estimates for the Chesapeake Bay, Maryland, from Jordan and Coakley (2004); Vølstad et al. (2008), and Wilberg et al. (2011). Previous studies estimated a lower natural mortality rate, 50% yr^{-1}, during 2000–2002 (Jordan and Coakley, 2004; Vølstad et al., 2008; Wilberg et al., 2011), whereas we estimated rates between 50 and 90% yr^{-1} during that same period. Additionally, Vølstad et al. (2008) and Wilberg et al. (2011) estimated consistent, lower rates of natural mortality around 25% yr^{-1} after 2004; our results showed that low natural mortality rates have persisted with an average rate of annual mortality between 6–32% yr^{-1} during 2004–2015 for the CRC. The previous studies that estimated natural mortality rates had larger spatial scales than we used. It is possible that the natural mortality rates are higher in the CRC than in other portions of the Chesapeake Bay, Maryland. There was a small increase in mortality at the tail of the time series visible in all regions; although the drivers are not clear.

Our estimates of abundance in the CRC were consistent with previous Maryland-wide estimates of abundance and the fraction of harvest that came from the CRC (Tarnowski, 2016). Wilberg et al. (2011) estimated the abundance of adult (small and market stages) eastern oysters in the Maryland portion of Chesapeake Bay to be 851 million in 2009; our models estimated abundance in 2009 to be between 30%–40% of that value, which was close to the average fraction of harvest from the CRC (28%; Tarnowski, 2016). Most of the abundance in the CRC was in Broad Creek with an average of 160 million adults after 2010, which has supported the highest level of eastern oyster harvest (19%) in the Maryland portion of the Chesapeake Bay (Tarnowski, 2016).

Patterns in exploitation have changed most over 2010–2015, and changes were likely due to a combination of factors including implementation of large oyster sanctuaries, increased power dredging effort, and strong recruitment events in 2010 and 2012. The average exploitation rate was 9.1% yr^{-1}among regions for the time series, but patterns over time differed among regions. The exploitation rate in Broad Creek increased from 2.9% to 31.6% yr^{-1}, the Lower Choptank increased from 2.7% to 71% yr^{-1}, and Harris Creek Open increased from 3.2% to 25.2% yr^{-1} during 2010 - 2015. These increased rates were associated with substantial increases in effort. During 2010–2015, power dredging effort in the Lower Choptank and Harris Creek Open increased ten-fold, and four-fold, respectively. Broad Creek appears to have experienced a higher rate of exploitation than other CRC regions during 2010–2015. The rates of exploitation in the CRC during 2010–2015 were generally 20% yr^{-1} or higher during years of high abundance, which was about twice the upper limit of the exploitation rate that would produce maximum sustainable yield (MSY; ˜10%; Wilberg et al., 2013), and much higher than is allowed in Delaware Bay, New Jersey, 2–9% yr^{-1} (Bushek and Ashton-Alcox, 2013). Thus, exploitation rates in recent years may have been above sustainable levels in some regions. However, the reduction in natural mortality rates in recent years allowed population growth despite periods of high fishing pressure; this may be especially true for Broad Creek. Increases in abundance with fishing mortality rates above those that are expected to produce MSY are possible over the short term. However, if high levels of fishing mortality continue over the longer term, we would expect abundance to decline. Additionally, the fishing mortality rates that produce MSY may vary across Chesapeake Bay, and some areas of the CRC may be able to support higher levels of fishing than others.

The rate at which habitat declined was region-specific and showed the most uncertainty of estimated quantities. Estimates of the annual rate of habitat decline were highest in Tred Avon (9% yr^{-1}) and Lower Choptank (7% yr^{-1}) regions. The rates from these regions are consistent with the amount of habitat degradation reported by Smith et al. (2005) in the Lower Choptank, Middle Choptank, and Tred Avon during 1999 - 2001. Estimates from regions that were predominantly fished with hand tongs, like the Middle Choptank and Upper Choptank, and Broad Creek, had lower estimated habitat loss (1–3% yr^{-1}) over the 27-year time series. Although Harris Creek Closed had an estimated rate of 5.7% habitat loss yr^{-1}, this trend abated during 2012–2014 due to extensive habitat restoration efforts made to the region (Westby et al., 2016; Tarnowski, 2016). Wilberg et al. (2011) estimated 4.1% yr^{-1} habitat loss for the Maryland portion of Chesapeake Bay during 1980–2008, which was consistent with the average rate in the CRC, 4.0% yr^{-1}.

Our models incorporated more data sources than previous stock assessments on eastern oysters in Chesapeake Bay (Wilberg et al., 2011) and were conducted at a finer spatial scale. We included fishery CPUE, estimates of habitat data, amount of habitat added by restoration activities, estimates of abundance from patent tong monitoring, and the number of eastern oysters planted. For stock assessments at a finer spatial scale, these data provided models with vital information to accurately estimate quantities of interest, as models with less data often had difficulty estimating the parameters. Furthermore, we used an updated estimate of the number of eastern oysters per bushel and incorporated harvest of smalls into the model. Fitting the models to fishery CPUE provided important information about how much eastern oyster abundance was depleted during the fishing season. Our models used two rates of underreporting as well, which are likely to be more accurate than the assumed rate of 50% from Wilberg et al. (2011). These rates did not affect trends in population dynamics but helped provide estimates on a more realistic scale given conversations with commercial fishers and oyster buyers. We also believe that including the harvest of smalls and updating the number of eastern oysters per bushel to scale harvest resulted in more realistic estimates of exploitation and abundance. There was potential for density dependence in the capture efficiency of the fall dredge survey gear that may have led to hyperstability in the indices of density (Morson et al., 2018). However, the differences in density among sites and years in the CRC is lower than in Delaware Bay, so we do not believe density dependent catchability in the fall dredge survey is likely a large issue. We Fishery-dependent CPUE often is density dependent (Wilberg et al., 2010). If our fishery-independent CPUE indices are hyperstable, then we expect that the models would overestimate abundance and underestimate the exploitation rate.

Our study represents the first eastern oyster stock assessments for Maryland's three largest oyster sanctuaries. Stock assessments that include no-take areas without consideration of spatial structure often result in biased estimates because the closed areas mean the whole population is not subject to the same fishing mortality (Punt and Methot, 2004; Field et al., 2006; Pincin and Wilberg, 2012). To address this problem, we developed separate models for regions containing sanctuaries. Our models for the Little Choptank and Harris Creek tributaries account for the spatial differences in harvest activity by assuming zero harvest after 2010 for the closed portions. Spatial disaggregation at a fine spatial scale can be difficult when the data are insufficient (Fulton et al., 2015). For example, the Middle Choptank, Upper Choptank, and Tred Avon regions also contain oyster sanctuaries, but disaggregated models could not converge on a solution for multiple parameters. Harvest has been low in these regions for most of the 27 years modeled, and the models used in this study rely on robust fishing data to characterize the population dynamics of eastern oysters (Wilberg et al., 2011).

Spatially disaggregating the Little Choptank and Harris Creek models allowed us to compare population dynamics in the sanctuaries with the adjacent areas that were open to fishing. Sanctuary models for both regions estimated higher adult abundance and recruitment than areas open to fishing both before and after the sanctuaries were established in 2010. Estimated recruitment and abundance in the Harris Creek sanctuary model were markedly higher during 2013–2015, likely due to large-scale seeding and habitat restoration efforts (Table S1). This increase was also visible, albeit more modestly, in estimates of abundance and recruitment for the open model and is potentially indicative of a spillover effect of larvae advected from the sanctuary (Pincin and Wilberg, 2012). The same pattern appears in the Little Choptank models, but at a smaller scale as restoration activity in this area was not as intensive as in Harris Creek during our study period. Despite being modeled independently, we expected similar patterns in the results of each disaggregated region due to their close spatial proximity and shared histories of fishing activity. These similarities were even more pronounced in certain parameter estimates among the disaggregated regions than among all regions in the CRC (Table 2). Spatially explicit stock assessment models have the potential to provide fishery managers with tools to make finer scale management decisions with respect to harvest and restoration efforts.

We did not include linkages between oyster habitat and population dynamics in our models. For example, the habitat function did not include a linkage to the number of new live oysters or boxes that entered the populations each year. Although both may constitute habitat, converting the number of estimated adults and boxes into habitat remains a challenge because the amount of habitat created by each oyster depends on their orientation in three dimensions as well as the habitat on which they settled and grew. Other approaches have been developed to consider oyster habitat-population dynamics models (e.g., Wilberg et al., 2013; Jordan-Cooley et al., 2011; Moore et al., 2018), but these examples were not statistical models. To estimate parameters of more complicated habitat-population dynamics models, we would need more habitat data than were available for our region. Similarly, we did not include effects of oyster habitat on recruitment and rather estimated recruitment in each year and region as independent parameters. Mechanistic modeling of recruitment would require detailed information about egg production within each region, larval transport, larval mortality, settlement, and post settlement mortality. We did not have data on these stages of the oyster life cycle to include more specific details within our model.

The eastern oyster populations within the CRC have experienced heavy fishing pressure during 1988–2015, and the autogenic nature of eastern oysters make them particularly vulnerable to overfishing (Wilberg et al., 2013). Habitat, recruitment, and abundance declined by 50–70% in the CRC during the last 27 years, despite increases in abundance in recent years. Rates of exploitation increased beyond sustainable rates during years of high abundance, particularly in regions where power dredging is the dominant gear type for fishing. The rates of habitat decline generally agree with the Beck et al. (2011) estimate of an 85% loss of oyster reefs worldwide. The fishery in the CRC appears to depend on high recruitment events, such that increases in abundance seem to lead to an increase in the exploitation rate. This type of fishery response may prevent the population from increasing substantially in regions that are open to harvest.

Funding

This work was supported by the National Science Foundation [OCE-1427019].

Acknowledgements

We thank two anonymous reviewers for helpful comments that improved this manuscript. We thank the Maryland Department of Natural Resources, the National Oceanic and Atmosphere Administration, the Oyster Recovery Partnership, and the University of

Maryland Center for Environmental Science Paynter Lab for providing data. We thank the OysterFutures stakeholder group for their input that helped improve the assumptions of the models. Dr. D. Liang and Dr. E. North provided helpful comments on an earlier version of this manuscript. Support was provided by the National Science Foundation under grant number OCE-1427019.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.fishres.2018.12.023.

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