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OYSTER SHELL PRODUCTION AND LOSS IN THE CHESAPEAKE BAY

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ABSTRACT Oyster population demographics are used to estimate shell standing stock (g m^{-2}) and rates of shell production (g $m^{-2}y^{-1}$) and loss by oyster, *Crassostrea virginica*, populations in both the Virginia and Maryland portions of the Chesapeake Bay. Source data are from long-term stock assessments whose footprints cover the majority of extant fished reefs in Virginia and a mix of fished and sanctuary reefs in Maryland. Individual longevity in extant fished populations is typically less than or equal to 5 y and truncated when compared with fossil *C. virginica* populations. Shell standing stock and productivity are maximal in year 1 or 2 of the progression of a year class through the population. Maintenance of the underlying reefs structure is dependent on regular shell input from mortality. The combination of truncated population structure and variable recruitment make shell addition temporally unstable. High turnover rates (≥30% y^{-1}) of the shell substrate pool in the oxic region above the sediment water interface are present. Reef accretion rates are generally less than the combination of sedimentation and relative sea level rise in most of the Bay system. Greater individual oyster longevity is required to ensure development of self-sustaining reef structures in the Chesapeake Bay.

KEY WORDS: oysters, *Crassostrea virginica*, Chesapeake Bay, shell production

INTRODUCTION

Oysters, *Crassostrea virginica* (Gmelin, 1791), are the critical live organisms in temperate to tropical coastal and estuarine food webs, as well as the key components of both the physical habitat (hard substrate, see Davies et al. 1989, Gutierrez et al. 2003, Mann & Powell 2007, Powell et al. 2012) and chemical (carbonate and alkalinity, see Waldbusser et al. 2013, Najjar et al. 2020) budgets in those same environments. Management of oyster fisheries requires consideration of two biological reference points, one for the live oysters and one for the shell that results from their death (Powell & Klinck 2007, Mann & Powell 2007, Mann et al. 2009b, Powell et al. 2009, Harding et al. 2010, Southworth et al. 2010). These reference points are not the same, and a general consideration of both the evolution of oysters and the time course of oyster reef formation with rise and fall of sea level over recent geological time indicates that much of the shell accumulation from natural mortality of oysters is required to maintain, and indeed build reef structures. This "shell budget" has generally been ignored over the history of oyster fisheries as demonstrated by the historical overfishing and decimation of reef-associated oyster resources on a global basis (Beck et al. 2011). Managers in the Chesapeake Bay are not alone in historically failing to apply adequate proactive quantitative measures to the reef resource. The emergence of the arguments proffered by Powell and Klinck (2007) and Mann and Powell (2007) has stimulated greater interest in preservation and rebuilding of oyster resources with equal inclusion of management of the shell resource. Indeed, shell budget protocols have recently been adopted in management of the Louisiana oyster resource (Soniat et al. 2012). An extension of this management approach to Chesapeake Bay resources is warranted.

This contribution examines the rates of oyster shell production and loss in both the Virginia (VA) and Maryland (MD) portions of the Chesapeake Bay using long-term data from stock assessments whose footprints cover the majority of extant fished reefs in VA and a mix of fished and sanctuary reefs in MD. The examination is guided by a statement of 10 principles that place the evaluation of rates in the context of targeted repletion (in support of fisheries) and restoration (to develop self-sustaining populations) efforts. These are as follows: (1) in both restoration efforts and fishery management efforts, there must be a goal of no net loss of living oysters or shell substrate; (2) oyster recruitment (R) and growth dictate addition to the living component of a reef; (3) natural mortality (M) and fishing mortality (F), both dictate loss of live oysters; (4) M contributes to the shell substrate on the underlying reef, F does not because oysters (and thus the shell) are removed; (5) high mortality (M) rates result in low shell accumulation because contributing oysters are small—low mortality rates are preferable because oysters survive to larger sizes and contribute much more shell when they die; (6) shell on the reef is lost to burial (B) and biological and chemical degradation (D)—these are termed taphonomic processes; (7) shell loss rates are independent of supply from mortality; (8) stable reefs require equilibrium between shell addition and loss, accreting reefs require shell addition to exceed loss; (9) offsetting inadequate shell supply from mortality (M) through repletion (r) requires continuing addition forever; and (10) a single replenishment action to suitable bottom is not restoration. A graphical depiction is provided in Figure 1.

MATERIALS AND METHODS

Maryland data for the current study originate in the Annual Fall Stock Assessment Survey that employs standard dredge tows. These comprehensive reports are available at https://dnr.maryland.gov/fisheries. Virginia data originate in the Annual Fall Surveys. The VA patent tong survey employs a stratified random survey designed with individual hydraulic patent tong deployments in each strata (Mann et al. 2009b). Summary

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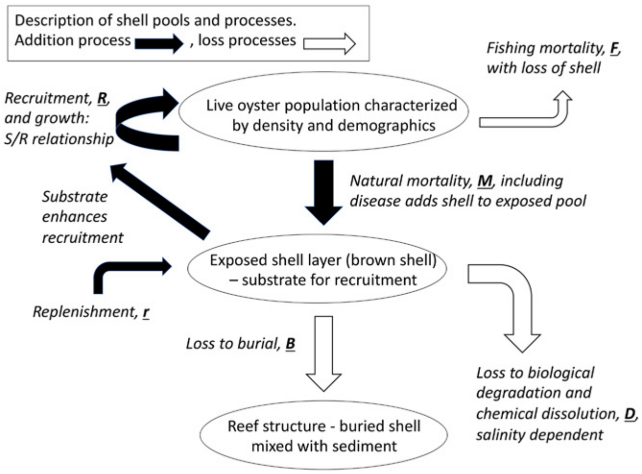

Figure 1. Graphical descriptions of shell pools and processes connecting them in terms of both addition processes and loss processes.

data are reported on the Virginia Oyster Stock Assessment and Replenishment Archive web portal at cmap2.vims.edu/VOSARA/viewer/VOSARA.html.

The stock assessment source databases from both MD and VA provide a multiyear monitoring of oyster density (numbers per unit area) and shell density (weight or volume per unit area) by reef. Additional details of these surveys, including their strengths and weaknesses for the purpose of this report, are addressed later in the text. The live oyster data generate values for both numbers of oysters per m^2, and the demographic of those oysters by length [shell length (SL), longest dimension from the hinge to the growing edge in mm, this should correctly be termed shell height but the commonly accepted convention of length is adopted for this report] intervals at the mm or 2 mm size interval level for both MD data and VA data. From subsamples of the oysters, the length demographics are measured, and shells and meat separated and dried to constant weight. Equations can be generated describing shell length versus dry shell weight [SL (mm) versus DSW (g)], and length versus wet shell weight [SL (mm) versus WSW (g)]. Live shell standing stock can be described as number of oysters per m^2, live DSW per m^{-2}, and wet shell weight per m^2. A time series of annual assessment of shell standing stock values can thus be used in concert with growth and mortality rates to estimate live oyster shell production and loss rates. Note that mortality rates thus generated do not discriminate between natural (M) and fishing (F) mortality, and that a 76-mm minimum SL applies for market oyster harvest in both MD and VA.

The MD dredge survey employs short duration dredge (width 32 inches, 0.81 m) tows on target reefs with examination of both live oyster and shell resources retained in each tow. Tow distances are measured using the odometer function on a Global Positioning System unit and thus swept area per tow is estimated. Catch can be expressed as oysters or shells per unit swept area. Individual oysters are classified as young-of-the-year (YOY, also commonly termed spat), small (<76 mm SL), or market (≥76 mm SL) categories and subsamples are measured for SL. This study used data collected from 2010 to 2015 because data collected during this time frame were available in 2 mm length intervals. Before 2010, data were recorded in 5 mm intervals, which compromised the ability to discriminate year classes within the population. The 2010–2015 interval was more than adequate to provide a base for estimation of growth rate and thus discrimination of year classes. The swept area derived estimates of shell density per unit area are underestimates of total shell presence because the dredge collects from the surface of the reef area, it does not and was not designed to penetrate through to the underlying black shell. Thus, the expected proportions of live oysters (as shell) to brown shell in dredge-based samples will show bias toward the live oyster value and underestimate shell. Thus, both possible overestimate and underestimate errors occur in the source data and calculations. While these compromise the ability to estimate loss of brown shell to taphonomy, the oyster live shell component can still be parsed into production and mortality on an annual basis and the dynamic rate of shell turnover estimated from the survey data. Maryland sampling sites are illustrated in Figure 2.

The VA survey employs a patent tong with a hydraulic closure mechanism that separates the closing mechanism from the retrieval mechanism, these operating in sequence as the sample is collected and retrieved. The tong weighs in excess of 70 kg and samples a one square meter area of bottom. The number of tong deployments per strata is based on a minimum sampling number after the procedure of Bros and Cowell (1987). Retained material is described as live oysters, that is YOY, small, or market oysters, all measured to the nearest mm SL, articulated valves of dead oysters ("boxes," again to nearest mm SL), brown shell (volume in L), and black shell (volume in L). There is a traditional approach to estimating mortality using "box counts." Whereas this is a useful relative approach it is limited as a quantitative measure of mortality rate in that the disarticulation rate of valves is size and probably location dependent and poorly documented (see Mann et al. 2009b, review in Pace et al. 2020). Given that the half-life of a "box" is not well documented for Chesapeake Bay locations, it cannot be used to estimate shell addition to the underlying reef. In this study, shell addition is based on estimates of mortality generated by loss from a cohort over time as described earlier. This approach will overestimate shell addition where shell has been removed by harvest rather than added to the underling reef. Data for this study are from 2006 to 2019. These years have data collected in mm SL intervals and are post the major epizootic of 1999–2002. The current data thus provide a continuation to descriptions for 1993–2006 in the James River (Mann et al. 2009b), 1998–2009 in the Piankatank River (Harding et al. 2010), and 2000–2009 in the Great Wicomico River (Southworth et al. 2010). Virginia sampling sites are illustrated in Figure 3.

Comparison of MD versus VA data require estimation of and correction for dredge efficiency versus patent tong sampling. Patent tong sampling assumes 100% retention efficiency of both live oysters and brown shell elements where penetration to the underlying black shell occurs. This was confirmed in prior, unpublished studies in which the open face of the tong was canvas lined, effectively creating a large grab that enclosed the entire sample, and compared with the unlined "normal" operating mode. Estimates of oyster and brown shell density sampled by tong and dredge were developed as described below to provide corrections to dredge-based data. Prior studies (Chai et al. 1992, Mann et al. 2004) are not in uniform agreement in developing correction functions to effect estimation of density

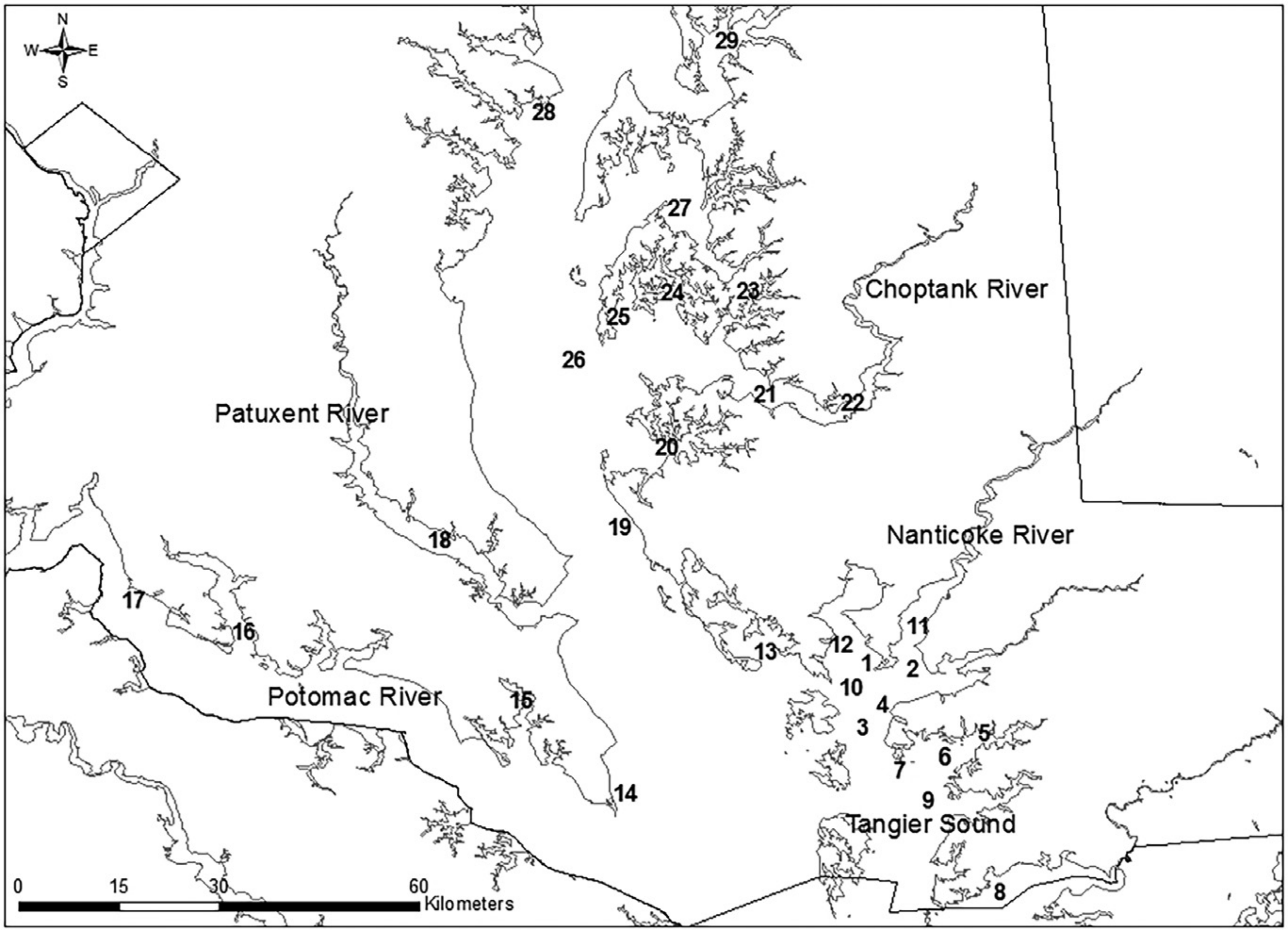

Figure 2. Sampling locations in the Maryland (MD) Chesapeake Bay. (1) Fishing Bay (Clay Island), (2) Upper Tangier Sound (Middle Ground), (3) Tangier Sound (Turtle Egg Island), (4) Tangier Sound (Haines), (5) Manokin River (Georges), (6) Manokin River (Drum Point), (7) Manokin River (Little Deal Island), (8) Pocomoke Sound (Ware Rock), (9) Middle Tangier Sound (Piney Island), (10) Upper Tangier Sound (Sharkfin Shoal), (11) Nanticoke and Wicomico Rivers (Wilson Shoals), (12) Fishing Bay (Goose Creek), (13) Honga (Normans), (14) St. Mary's Shore (Point Lookout Sanctuary), (15) Upper St. Mary's River (Pagan), (16) Wicomico River (Lancaster), (17) Upper Potomac River (Lower Cedar Point), (18) Middle Patuxent River (Broome Island), (19) Dorchester Shore (Punch Island), (20) Little Choptank River (Cason), (21) Choptank River (Sandy Hill), (22) Upper Choptank River (Oyster Shell Point), (23) Tred Avon River (Double Mills), (24) Broad Creek (Deep Neck), (25) Harris Creek (Tilghman Wharf), (26) Talbot Shore (Stone Rock), (27) Eastern Bay North (Turtleback), (28) Lower Anne Arundel Shore (Hacketts), and (29) Upper Chester River (Old Field). Sites 1, 3, 4, 5, and 6 were sampled for the dredge versus tong comparison.

estimates from dredge qualitative data. This is unsurprising given the previously described limitations in dredge design for quantitative sampling, as well as the manner in which dredges may have been towed to capacity before retrieval thus compromising swept area estimates. A dredge versus tong comparison is, however, critical to the current effort. To this end, a series of side-by-side gear comparisons were made of the dredge and hydraulic patent tong operated in survey mode.

In April 2013 (4/16 and 4/17) a 2-day field survey was completed at five sites on the bay side of the Maryland Eastern Shore using both a 32-inch dredge and a patent tong identical to that used in the VA surveys. The five MD locations were Clay Island (Fishing Bay), Drum Point and Georges (Manokin River), Haines and Turtle Egg Island (Tangier Sound). The Manokin River locations are on shell mounds. Georges, in particular, has a softer basal substrate. Tangier Sound sites are on hard sand bottom. At each location, 20 patent tong samples were collected, with station locations being chosen by random numbers applied to a grid overlay on the reef map. Data collection for each sample was as for VA assessment: respective per square meter values for number of YOY, small and market oysters, new and old boxes (articulated valves), brown shell volume in L, and black shell volume in L. All live oysters and boxes were measured to the nearest mm (SL). At each location, four dredge hauls were completed using MD Department of Natural Resources protocols. Tow length was recorded by differential Global Positioning System and swept area estimated. An important prerequisite for an acceptable haul was that the dredge not be full on retrieval. Total volume of material collected was recorded and a subsample (typically 0.5 MD bu or approximately 23 L, note that the MD bushel at 45.9 L differs from the VA bushel at 50 L) taken for further examination. As with the VA protocol, all oysters were measured and categorized as were boxes. Total brown shell volume (blank, devoid of attached oysters) and live oyster volumes (both in L) were examined and recorded.

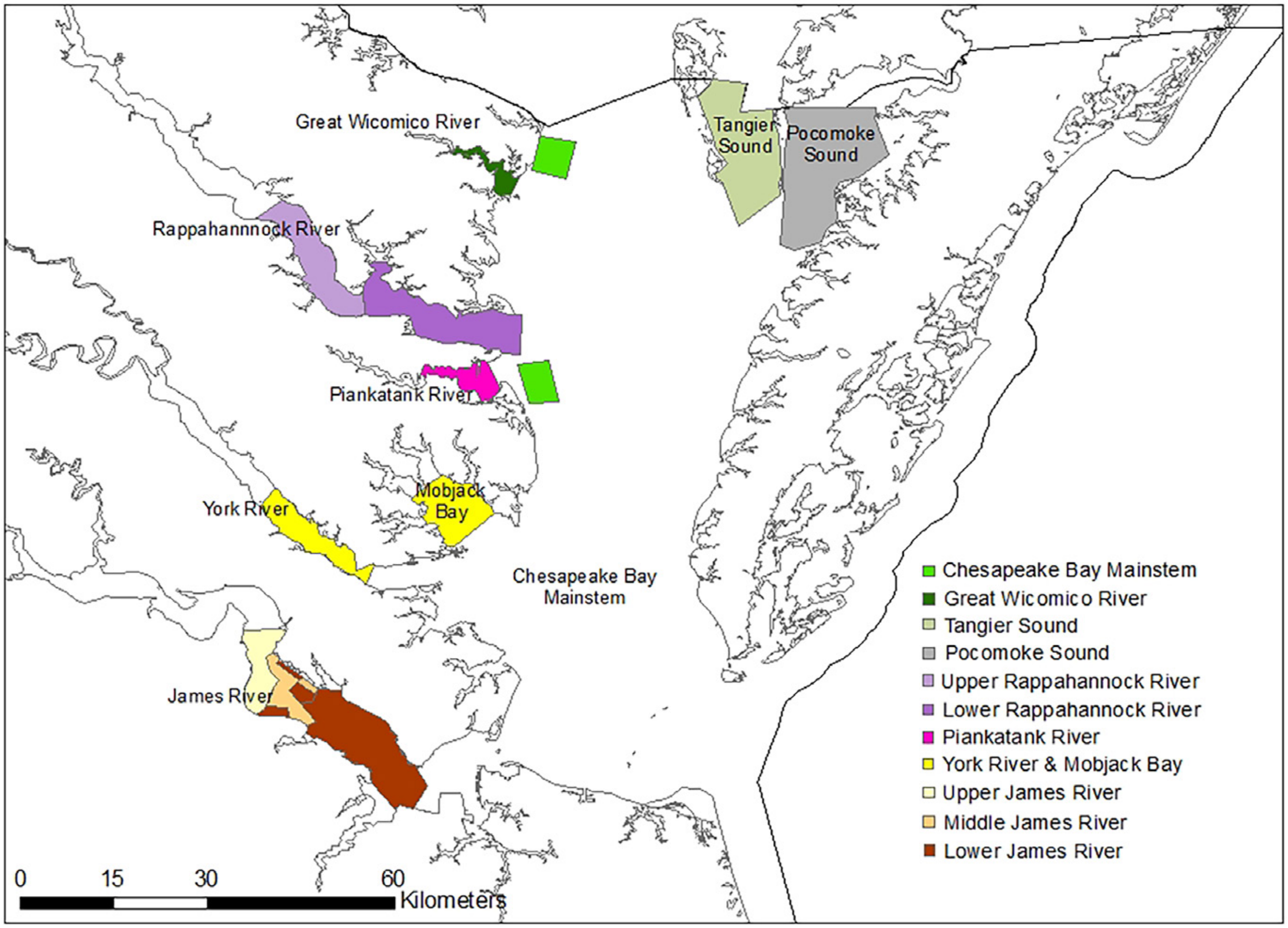

Figure 3. Sampling regions in Virginia (VA). Chesapeake Bay Mainstem includes Deep Rock. Tangier Sound includes California Rock and other reefs. Pocomoke Sound includes reef 13H2 and other reefs. Great Wicomico River includes Shell Bar, Sandy Point, Fleet Point, Haynie, and Cranes Creek. Upper Rappahannock River includes Ross Rock, Bowlers, Long Rock, Smokey Point, and Morattico. Lower Rappahannock River includes Broad Creek, Temple Bay, Drumming Ground, and Parrot. Piankatank River includes Ginny Point, Cape Toon, Burton Point, Bland Point, Heron Rock, and Palace Bar. York River includes Aberdeen, Bell Rock, and Propatank. Mobjack Bay includes Tow Stake and other reefs. Upper James River includes Moon Rock, Lower Horsehead, Upper Horsehead, Middle Horsehead, Triangle Rock, Point of Shoals, V Rock, Upper Deep Water Shoals, and Mulberry. Middle James River includes Lower and Upper Jail Island, Cross Rock, Swash, Dry Lumps, Days Point, Swash Mud, Offshore Swash, Hotel Rock, and Shanty Rock. Lower James River includes Snyders, Wreck Shoal, Thomas Rock, Cruisers, Brown Shoal, and Nansemond Ridge. A comprehensive description of each reef is given at: https://cmap2.vims.edu/VOSARA/viewer/VOSARA.html.

Estimates of growth and mortality were generated as follows. Demographic analysis identifies cohorts. If these are annual, then the chosen demographic provides a description of year class structure. The interannual change in any of the above descriptors provides both a production and a mortality estimate for a chosen year class as it is followed over time. Annual estimates of mortality can be generated as a proportion of the live oysters at the beginning of the year. Cumulative mortality data can be described by a declining exponential function of the form $N_t = N_o \times e^{-Zt}$, wherein Z, total mortality, is a combination of M, natural mortality, and F, fishing mortality. By examination of shell weight at each growth interval, it is tractable to estimate both live shell weight per unit area of the surviving members of the year class and, with mortality, how much shell is added to the inanimate shell pool that forms part of the reef structure/habitat. One challenge in estimating the latter is the unknown point in time between surveys when mortality occurs. This is discussed with example calculations in Mann et al. (2009b) for James River VA oyster populations. A second challenge is to debit the shell addition based on removals with harvest when and where it occurs.

The MD Department of Natural Resources historical database was reformatted to correspond to the VIMS master database to facilitate analysis by common scripts. Not all stations had data sets with individual oyster SL included and a few used pooled samples for SL from more than one dredge tow. These were excluded from the analysis. Final MD analysis was based on 925 stations (141, 162, 156, 146, 140, and 180 in years 2010 through 2015, respectively) from 22 reefs. The VA data included the following number of stations for the 2006 through 2019 continuum: 1,156, 1,261, 1,272, 1,333, 1,350, 1,357, 1,360, 1,364, 1,350, 1,347, 1,340, 1,346, 1,336, and 958, respectively. Having assembled the master databases, options for aggregating data from the many reef systems were examined to categorize data by area or river system.

Drafting the shell budget is a sequential process. The accumulation of shell from mortality is offset by natural processes of burial, mechanical disintegration, and dissolution (taphonomic processes, Davies et al. 1989), and removal associated with harvest. Importantly, taphonomic processes continue independent of shell production. Long-term taphonomic loss continues in the absence of oyster recruitment, growth, and mortality, and can result in loss of reef structure (Powell et al. 2012). The survey database in MD focuses on brown shell because the dredge sampling removes material from the reef surface rather than attempting to penetrate through to the underlying black shell. Taphonomic loss is estimated as the difference between estimated cumulative shell and observed shell volume in the survey database. Note there is a change in units herein—production is estimated in weight whereas shell presence is in volume. This is a historic artifact of survey protocols in that these parameters were set in place before any construct for developing fine estimates of shell budgets. Shell planting and management was and is in volumetric units—bushels. The implementation of a weight to volume conversion function is described in Mann et al. (2009a, 2009b). The survey database in VA includes standing estimates of shell volume in units of liters (L) per m^2 as both brown shell (volume of live shell plus shell from mortality above the sediment water interface in oxic water) and black shell (volume below the sediment water interface in anoxic sediment) from patent tong sampling (details below). The presence of both brown and black shell in a sample indicate complete penetration of the sampling tong through the overlaying brown layer; however, the black underlying layer is incompletely sampled because the reef base extends well into the basal sediment. For this reason, black shell data have not been included in the current analyses.

A draft of a shell budget based on time series measures of shell in live oysters and brown shell can thus be developed. When brown shell values are considered in combination with that added annually through mortality, there is an expectancy that this sum will steadily increase. The measured brown shell is typically less than this expected sum with the difference being the loss to taphonomy and harvest. Thus, a loss rate that can be expressed as an absolute rate per unit area, a rate related to standing stock and/or production of live oysters on that unit area (so, providing stock and production rate estimates that are required to balance loss and retain environmental integrity), a rate related to local environmental conditions of salinity, turbidity, food and/or other considerations, and more as desired. Shell production is not a constant rate for all situations, and its balance against loss will vary between locations as well as over time. The series of estimations outlined above is only as good as the data contributing to those estimations. Neither the MD nor VA surveys were originally designed with shell budget estimation in mind. Thus, the described estimations are accompanied by a discussion of the limitations of the data where they arise.

The above described databases include comprehensive length demographics plus additional subsampling for individual descriptors including whole animal SL (as mentioned), shell width, shell height, wet and DSW, wet and dry meat (tissue) weight, and ash (inorganic fraction) tissue weight. Only shell data were used for the current report. To develop a shell budget, the priority data are SL and DSW—shell volumes can be generated from weight if the desire is to work in volume rather than weight, although both are equally tractable herein. Corresponding data streams for both SL and DSW parameters were generated for 22 reefs in MD for 2011–2013 (n = 25 for each reef for each year, total n = 75 per reef) and for 53 reefs in VA for 2010 and 18–20 reefs for 2011–2016 (n = 25 for each reef for each year).

A critical analytical step in the shell budget as presented is the ability to generate a year class structure from the demographic plot. Bhattacharya (1967) provides a simple method for "resolution of a distribution into Gaussian components"—that is, year classes in the distributions presented in these databases. The current analysis used TropFish R, an R script based on the works of Bhattacharya (1967).

RESULTS

A summary of the dredge (D) versus patent tong (P) comparisons is given in Table 1. The challenge in developing a dredge to tong conversion function is 2-fold: What are the overall relative efficiencies of the gear types, and is there gear dependent size-based selectivity such that at defined size intervals there are deviations from the overall relationship? In a relationship devoid of size selectivity and equal efficiency, a 1:1 slope would be obtained when plotting density estimates by dredge (ordinate) versus density estimates by tong (abscissa). Where estimates by

TABLE 1.

Summary of dredge (D) versus patent tong (P) comparisons at five locations in Maryland waters: Clay Island (Fishing Bay), Drum Point and Georges (Manokin River), Haines and Turtle Egg Island (Tangier Sound).

Location Name	Gear Type	Area sampled (m^2)	Shell volume collected (L)	Shell volume (L m^{-2})	YOY (# m^{-2})	Small + market (# m^{-2})
Drum Point (6)	D	26.0 ± 1.3	43.8 ± 13.1	1.7 ± 0.5	4.3 ± 2.0	16.3 ± 5.2
Drum Point (6)	P	–	6.2 ± 3.9	6.2 ± 3.9	12.4 ± 9.7	46.7 ± 33.8
Georges (5)	D	14.6 ± 0.5	76.3 ± 6.0	5.2 ± 0.4	8.6 ± 2.3	58.8 ± 6.0
Georges (5)	P	–	13.6 ± 5.7	13.6 ± 5.7	24.4 ± 19.3	99.5 ± 60.0
Clay Island (1)	D	19.9 ± 0.9	35.0 ± 8.2	1.8 ± 0.4	0.7 ± 0.3	7.7 ± 3.0
Clay Island (1)	P	–	3.6 ± 2.0	3.6 ± 2.0	2.1 ± 1.9	14.3 ± 7.1
Turtle Egg Island (3)	D	41.6 ± 5.5	37.5 ± 13.4	0.9 ± 0.2	0.7 ± 0.3	4.1 ± 0.8
Turtle Egg Island (3)	P	–	4.1 ± 1.5	4.1 ± 1.5	7.0 ± 4.3	15.5 ± 6.5
Haines (4)	D	43.4 ± 4.1	29.4 ± 5.2	0.7 ± 0.7	0.5 ± 0.2	1.9 ± 0.2
Haines (4)	P	–	5.3 ± 1.8	5.3 ± 1.8	4.3 ± 2.0	7.0 ± 3.9

At each location, n = 4 for dredge samples, n = 10 for patent tong samples. All values are mean ± SD. Locations and reef numbers are given on Figure 2. YOY, young-of-the-year.

tong exceed that by dredge the slope decreases but the straight line remains. Where selectivity at defined size ranges is present, a deviation will be observed from the straight line plot. In the current data sets, there is an expected decrease in density with increasing size. Data from comparison studies were explored as follows. Data for YOY and >YOY (small + market) oysters were examined separately. For plotting, data were initially aggregated within each sample into 5 mm length bins to examine bias. At each site, descriptors of mean, SD, and range were generated for each of the dredge (n = 4) and tong (n = 20) samples. Scatter plots were made for mean values for each site. Small numbers of total oysters in any one size bin in combination with small variation in a length demographic between dredge and tong sample, result in any such plots showing considerable variation around a descriptive line. For example, if two sequential size categories, such as 20–24 mm and 25–29 mm SL, contain a total of four oysters with the dredge sample length being 22, 23, 24, and 27 mm and the tong sample being 23, 24, 25, and 26 mm, the arbitrary choice of bin size depicts a 3:1 ratio by number for the dredge sample versus a 1:1 ratio for the tong sample. Thus, scatter plots were made of cumulative length data for each site to combat the effect of small sample sizes within bins. A general lack of size-based selectivity was notable. A 1:1 slope throughout the size range was not observed; however, linear fits to location data provide high r^2 values in all cases indicating that consistent relationships existed between density estimates generated by the two gear types. The individual data series, numbers in parentheses correspond to locations on Figure 2, are described by the following where x = density estimated by dredge and y = density estimated by patent tong:

	YOY	>YOY
Drum Point (6)	$y = 2.69x$, $r^2 = 0.91$	$y = 2.74x$, $r^2 = 0.94$
Georges (5)	$y = 2.92x$, $r^2 = 0.97$	$y = 1.73x$, $r^2 = 0.98$
Clay Island (1)	$y = 3.27x$, $r^2 = 0.91$	$y = 1.62x$, $r^2 = 0.95$
Turtle Egg Island (3)	$y = 9.10x$, $r^2 = 0.97$	$y = 3.48x$, $r^2 = 0.90$
Haines (4)	$y = 8.95x$, $r^2 = 0.97$	$y = 3.31x$, $r^2 = 0.89$
All locations	$y = 2.93x$, $r^2 = 0.93$	$y = 1.80x$, $r^2 = 0.95$

The range of values observed at each location varied, being lowest at Haines and Turtle Egg Island, higher at Drum Point and Clay Island, and highest at Georges (see Table 1). When all locations are considered on a single plot, a communal descriptor of $y = 2.93x$ is observed with $r^2 = 0.93$ for YOY, and $y = 1.80x$ with $r^2 = 0.95$ for >YOY. These communal descriptors were used to correct dredge density estimates to equivalent patent tong estimates for oysters density.

The SL versus DSW relationships for the 22 reefs sampled in MD (2011–2013) and for the 53 reefs sampled in VA (2010–2016) were explored using power relationships where y (DSW) $= a \times SL^b$ (Table 2). The exponent b incorporates the variation in shape of the oyster, where the shape is a tube when $b = 2$, and a sphere when $b = 3$ (see Powell et al. (2015) for a comprehensive review of b exponents in oysters). The constant "a" in the power function, although a small value, explores shell thickness. The shell thickness is also incorporated in the exponent b value in that shell thickness increases with size. Thus, a spherical shape with increasing shell thickness can generate b values in excess of 3. For each data set in both MD and VA samples, the SL and DSW data were plotted by individual year and reef, then aggregated by year for each reef. In several instances, small

TABLE 2.

Reef-specific allometric descriptors for the relationships between SL (mm) and DSW (g), for MD Chesapeake Bay reef systems 2011–2013.

Reef #	Reef Name	a	b	r^2
15	Lancaster	6.70E-03	2.18	0.65
28	Old Field	2.30E-03	2.39	0.8
7	Ware Rock	2.00E-03	2.41	0.81
10	Wilson Shoals	2.00E-03	2.42	0.85
18	Punch Island	1.40E-03	2.52	0.79
19	Cason	1.20E-03	2.52	0.85
14	Pagan	1.10E-03	2.53	0.86
23	Deep Neck	1.20E-03	2.55	0.81
16	Lower Cedar Point	1.20E-03	2.57	0.92
21	Oyster Shell Point	1.20E-03	2.58	0.89
22	Double Mills	1.10E-03	2.58	0.89
13	Point Lookout Sanctuary	9.00E-04	2.58	0.81
24	Tilghman Wharf	6.00E-04	2.71	0.86
20	Sandy Hill	5.00E-04	2.73	0.94
8	Piney Island	5.00E-04	2.73	0.88
9	Sharkfin Shoal	5.00E-04	2.75	0.84
11	Goose Creek	5.00E-04	2.75	0.85
17	Broomes Island	5.00E-04	2.76	0.91
25	Stone Rock	4.00E-04	2.82	0.88
12	Normans	3.00E-04	2.91	0.85
26	Turtleback	2.00E-04	2.93	0.94
27	Hacketts	2.00E-04	2.95	0.91

n = 25 for each reef for each year, total n = 75 per reef. Data are ranked by reef with increasing b value. Locations are on Figure 2. DSW, dry shell weight; MD, Maryland; SL, shell length.

reefs in immediate proximity to one another in the VA data set have been pooled (e.g., Mobjack "All" and Tangier "All") so the number in the summary table is less than the number given in the previous paragraph. The fitted allometric relationships are described in Table 2 for MD and in Table 3 for VA.

The 22 MD reefs (Table 2, Figure 2) present a general continuum of decreasing values of the constant "a," with increasing values of b (from elongate to more rounded shape), the latter gradually increasing from 2.18 (all years included) at Lancaster to 2.95 at Hacketts. The growth forms and condition of oysters are expected to be influenced by local conditions (Mann 1978). The Chesapeake Bay and its subestuaries represent salinity clines that are included in the current database. In MD, streamflows were close to normal during 2010, whereas 2011 had spring freshets, a tropical storm, and a hurricane, resulting in large-scale mortalities in the upper bay. Streamflow returned to more typical values in 2012 and 2013 (waterdata.usgs.gov). The current MD oyster data thus include a wide range of flow conditions. A shell budget was developed for each MD reef using the unique b value. Growth analysis, described later in the text, dictated employment of a single age versus length curve for all reefs.

Table 3 describes a and b values for 53 VA reefs sampled over the 2010–2016 period, arranged by region (Fig. 3). Pocomoke and Tangier b values are between 2.79 and 3.12. For the Great Wicomico, there is general agreement between 2010 and combined values, with long-term b values in the middle of a range from 2.73 to 3.28. A comparison of Upper and Lower Rappahannock River b values illustrate a general increase in a downstream direction with most values being in the range

TABLE 3.

Reef-specific allometric descriptors for the relationships between SL (mm) and DSW (g) for VA Chesapeake Bay reef systems for 2010 (*n* = 25) and 2011–2016 (italics, *n* = 25 for each reef for each year, total *n* = 150 per reef).

Region name	Reef name	a	b	r^2	Region name	Reef name	a	b	r^2
Tangier Sound	*California*	*2.00E-04*	*2.95*	*0.93*	York River	Bell Rock	1.00E-04	2.98	0.91
	All	1.00E-04	3.04	0.95		Propatank	5.00E-05	3.25	0.98
Pocomoke Sound	*13H2*	*4.00E-04*	*2.79*	*0.84*	Mobjack Bay	*Tow Stake*	*5.00E-04*	*2.73*	*0.92*
	All	9.00E-05	3.12	0.96		All	2.00E-05	3.49	0.93
Great Wicomico River	Shell Bar	1.00E-03	2.46	0.76	Upper James River	Moon Rock	7.30E-03	1.85	0.84
	Sandy Point	4.00E-04	2.73	0.94		Middle Horsehead	6.00E-03	1.87	0.91
	Shell Bar	*2.00E-04*	*2.83*	*0.87*		Triangle Rock	3.30E-03	2.00	0.89
	Cranes Creek	*3.00E-04*	*2.83*	*0.85*		Point of Shoals	3.40E-03	2.02	0.68
	Fleet Point	1.00E-04	3.09	0.94		Upper Horsehead	3.30E-03	2.02	0.85
	Haynie	8.00E-05	3.11	0.95		*Middle Horsehead*	*1.80E-03*	*2.15*	*0.88*
	Cranes Creek	4.00E-05	3.28	0.91		*Point of Shoals*	*1.80E-03*	*2.16*	*0.84*
Upper Rappahannock River	Ross Rock	3.60E-03	2.24	0.94		Lower Horsehead	1.60E-03	2.23	0.85
	Bowlers	8.00E-04	2.67	0.88		V Rock	1.20E-03	2.27	0.86
	Ross Rock	*8.00E-04*	*2.67*	*0.93*		*Upper Deep Water Shoals*	*8.00E-04*	*2.37*	*0.76*
	Long Rock	3.00E-04	2.86	0.90		Mulberry	2.00E-04	2.76	0.94
	Morattico	*1.00E-04*	*3.08*	*0.94*		Upper Deep Water Shoals	7.00E-05	2.98	0.68
	Smokey Point	1.00E-05	3.56	0.92	Middle James River	Lower Jail Island	1.80E-03	2.36	0.92
	Morattico	8.00E-06	3.74	0.94		Cross Rock	1.00E-03	2.42	0.88
Lower Rappahannock River	Broad Creek	6.00E-04	2.65	0.89		Swash	1.00E-03	2.44	0.86
	Broad Creek	*2.00E-04*	*2.87*	*0.91*		Dry Lumps	8.00E-04	2.53	0.87
	Temple Bay	2.00E-04	2.9	0.92		Days Point	5.00E-04	2.67	0.93
	Parrot	2.00E-04	2.93	0.89		Swash Mud	2.00E-04	2.72	0.90
	Drumming Ground	2.00E-04	2.98	0.87		Offshore Swash	5.00E-04	2.72	0.91
	Drumming Ground	*1.00E-04*	*3.04*	*0.85*		Hotel Rock	3.00E-04	2.76	0.77
	Parrot	4.00E-05	3.28	0.90		Shanty Rock	3.00E-04	2.82	0.95
Chesapeake Bay Mainstem	Deep Rock	1.00E-04	3.03	0.84		Upper Jail Island	1.00E-04	3.05	0.92
Piankatank River	*Ginny Point*	*2.00E-04*	*2.97*	*0.94*		Offshore Jail Island	3.00E-05	3.27	0.92
	Palace Bar	*1.00E-04*	*3.05*	*0.91*	Lower James River	Wreck Shoal	2.00E-03	2.29	0.69
	Cape Toon	1.00E-04	3.06	0.95		*Wreck Shoal*	*2.00E-04*	*2.92*	*0.89*
	Burton Point	6.00E-05	3.19	0.96		Cruisers	2.00E-04	2.92	0.95
	Bland Point	3.00E-05	3.27	0.94		*Thomas Rock*	*2.00E-04*	*2.93*	*0.93*
	Heron Rock	3.00E-05	3.27	0.94		*Nansemond Ridge*	*1.00E-04*	*3.00*	*0.92*
	Palace Bar	1.00E-05	3.56	0.98		Thomas Rock	5.00E-05	3.22	0.96
York River	*Bell Rock*	*5.00E-04*	*2.75*	*0.90*		Brown Shoal	3.00E-05	3.31	0.96
	Aberdeen	4.00E-04	2.78	0.85		Snyders	3.00E-05	3.39	0.96
	Aberdeen	*3.00E-04*	*2.85*	*0.89*		–	–	–	–

Individual reef data are ranked within each region (see region locations in Figure 3) by increasing b value. DSW, dry shell weight; VA, Virginia; SL, shell length.

2.88–3.28. Long-term *b* values for the Piankatank are in the 2.96–3.26 range with one exceptional year (2010) for Palace Bar, where *b* is driven by three high points in the data set. York River *b* values are between 2.75 and 3.25. While in 2010 flow in the MD Bay was normal, streamflow in the James River in VA was unusually high in 2010 compared with the 2011–2016 period (waterdata.usgs.gov). Thus, the ranked order of the James River reefs observed for 2010 should be representative of a multiyear data set, the absolute *b* values may not be near the means for the 2011–2016 period. The James River *b* values suggest similarity within each region. In 2010, the *b* value for Upper Deep Water Shoals was lower than in the multiyear estimator. Mulberry is also a 2010 outlier having a higher value (*b* = 2.76). In both instances, these are driven by a small number of individual oyster data points. The 2010 *b* values for both Upper Jail Island and Offshore Jail Island provide single year high *b* values driven by 2 or 3 data points.

The r^2 values for individual year-reef plots regularly exceed 0.80, often 0.90, providing confidence in the utility of the approach. The large *n* values (75–150) provided by multiyear observations also provide high r^2 values indicating general consistency between years. Any such plots are limited by the data ranges, and those examined herein include oysters with SL greater than 30 mm. Oysters with SL greater than 130 mm are not abundant in this data set, thus consideration of disparities in predicted weights from SL should be limited by the length range included.

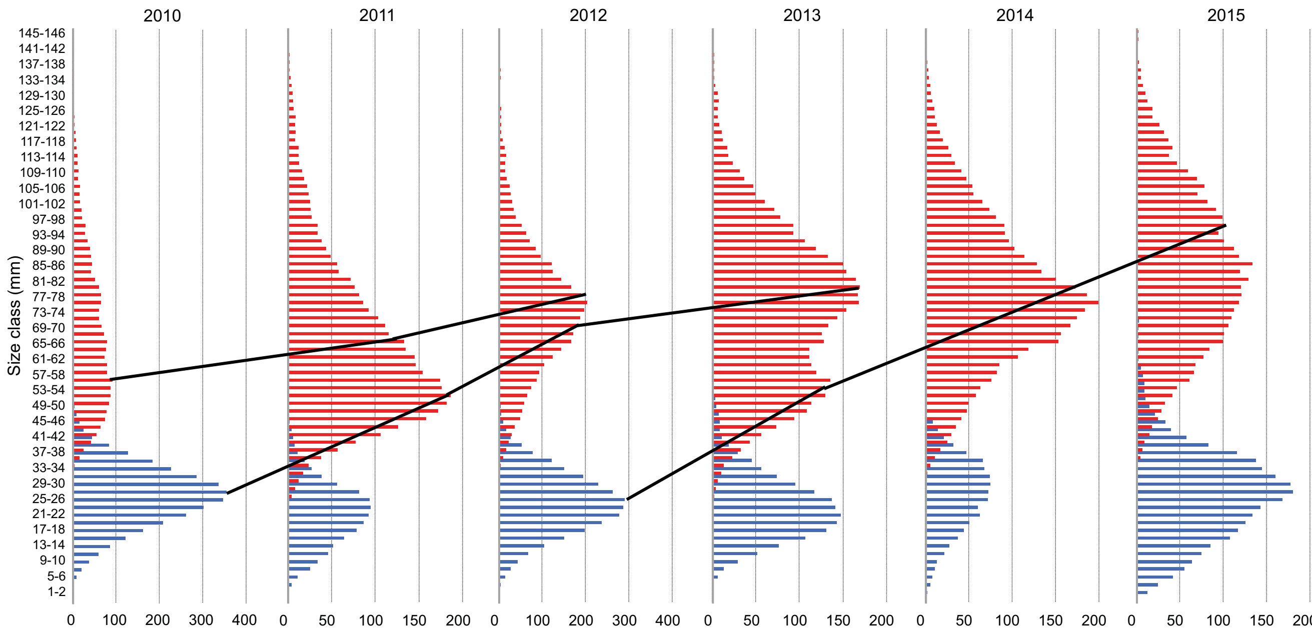

Figure 4. Shell length frequency by 2 mm intervals with a 6 mm smoothing of all Maryland (MD) reefs from 2010 to 2015. The smallest cohort is YOY Lines joining peaks represent growth curve estimates.

The year class structure in VA data was examined by the area aggregations described above and found to produce reasoned year classes. The MD data were also examined on an individual reef basis, but was compromised by variability in year class strength within the 2010–2015 time frame and/or inclusion/exclusion criteria for data sets in the analysis as described earlier. Thus, all MD data were then aggregated on a single plot (Fig. 4). The continuous lines between the year plots join the peaks of identified year classes. The expected decrease associated with mortality is not always present when following a single year class across the time frame because this is an aggregated demographic and there is not equal representation of all reefs with respect to *n* values of included oysters, again partially driven by station exclusion criteria; however, the large number of oysters included represents the size distribution well, so generation of a growth curve is considered tractable.

For the analysis in TropFish R, the demographic data were presented as 2 mm intervals from 2 through 200 mm SL for the aggregated MD reefs and the VA aggregated reefs as per the previous description. TropFish R allows the identification of year classes in a simple, sequential high through low point discrimination on the output plots. The sequence of plots identifies peaks in the demographic that correspond to year classes. For the MD data plot, these peaks are at SL values of 28 mm, 58 mm, 82 mm, 106 mm, 122 mm, 138 mm, 152 mm, and 158 mm. Given that surveys are completed in November of each year these peaks correspond to year classes YOY and ages 1 through 7, respectively. Assuming a recruitment in the midsummer (June–July) period, actual age is approximately 0.5 y for YOY with +1 y increment for each year class (1.5 y, 2.5 y, etc.). This provides a length (SL, mm) at actual age (x, y) plot that is described by the polynomial:

$$\text{SL(mm)} = -1.714x^2 + 32.33x + 12.59,\ r^2 = 0.999$$

There is general concordance of the TropFish peaks with Figure 4. The value of the TropFish generated plot is the discrimination of year classes in lengths greater than 100 mm SL that are not immediately evident in Figure 4. The numbers in each year class were separated by the midpoint between the identified peaks at 43 mm, 70 mm, 94 mm, 114 mm, 130 mm, 145 mm, and 155 mm. For simplicity, we assume no overlap in year class lengths. Thus, all less than 43 mm SL = year class 1, 44 mm through 70 mm SL = year class 2, and so forth.

Time series demographic plots were made for each of the MD stations and the progression of year classes noted based on procedures of Bhattacharya (1967) and TropFish R. The growth curve was overlain on the identified year classes to estimate mortality rates. This approach was compromised by a high proportion of the plots having low initial population densities with resulting challenges to generation of a declining density curve. Thus, analysis was refocused on 12 individual year classes: Broad Creek in 2009 and 2012, Fishing Bay in 2010 and 2012, Middle Tangier Sound in 2010, Upper St. Mary's River in 2009 through 2013, and Upper Tangier Sound in 2010 and 2012. All exhibited initial densities at year 1 between 232 and 55 oysters per m^2. All estimates set survival to 100% at age 1 year. A common mortality curve of the form $N_t = N_o \times e^{-Zt}$, wherein Z is a combination of M and F. The resulting estimate gave Z = 1.02, $r^2 = 0.85$, $n = 12$.

The above described procedure was repeated for each of the regional aggregations in the VA data sets. The data sets are substantial. For example, that for the Piankatank River includes 84,492 oysters from 1,026 stations over the 14-y study period. The following length (SL, mm) at actual age (*x*, *y*) descriptors were generated. Effectively all have $r^2 = 1$. Note that von Bertalanffy (1938) fits, with estimation of K and L_{inf} values, were not attempted because the populations are drastically age truncated resulting in minimal or no representation in older age class.

Chesapeake Bay (mainstem)	SL (mm) = $-1.93x^2 + 32.09x + 2.11$
Great Wicomico	SL (mm) = $-1.15x^2 + 25.2x + 7.87$
Tangier Sound	SL (mm) = $-2.84x^2 + 36.36x + 0.22$
Pocomoke Sound	SL (mm) = $-2.3x^2 + 36.42x + 2.14$
Upper Rappahannock	SL (mm) = $-2.43x^2 + 33.36x + 6.42$
Lower Rappahannock	SL (mm) = $-2.84x^2 + 36.36x + 0.22$
Piankatank	SL (mm) = $-1.93x^2 + 28.28x + 4.88$
York & Mobjack	SL (mm) = $-1.68x^2 + 30.48x + 1.04$
Upper James River	SL (mm) = $-1.7x^2 + 28.6x - 0.64$
Middle James river	SL (mm) = $-1.5x^2 + 30.3x - 0.98$
Lower James River	SL (mm) = $-1.37x^2 + 26.93x + 1.74$

These growth rates are difficult to compare with prior reports for the James, Piankatank, and Great Wicomico Rivers (Mann et al. 2009b, Harding et al. 2010, Southworth et al. 2010) given the forms of fit applied, the limited size range used herein, and the fact that earlier data were fitted to data recorded in 5 mm SL bins.

Time series demographic plots were made for each of the VA regions and the progression of year classes noted based on procedures of Bhattacharya (1967) and TropFish R. The growth curve was overlain on the demographic data, the year classes identified and a mortality curve for each year class estimated. The mortality curve was again described by a declining exponential of the form $N_t = N_o \times e^{-Zt}$ with survival set to 100% at age 1 y. This is an age truncated population—all of the above values reflect some impact of included fishing mortality, F, on harvest in the demographic. Area-specific harvest data are, however, unavailable and thus M cannot be reliably estimated in isolation. In some instances, singular intense harvest events occur in the 2006–2016 period and limited years are excluded from the analysis (see summary below). The impacts of seed harvest in particular in the Great Wicomico and Piankatank Rivers contribute to high Z values. The Z estimates are given below for the period 2006–2016 (n = 11, unless otherwise stated). Note that data estimation requires data for a 4-y period, thus 2016 estimates include data through 2019.

Chesapeake Bay	$Z = 0.95$, $r^2 = 0.93$, $n = 10$
Great Wicomico	$Z = 1.15$, $r^2 = 0.91$, $n = 8$, seed harvest include atypical values
Tangier Sound	$Z = 0.81$, $r^2 = 0.88$, $n = 8$, alternating years of rotational harvest include atypical values
Pocomoke Sound	$Z = 1.09$, $r^2 = 0.85$, $n = 9$, alternating years of rotational harvest include atypical values
Upper Rappahannock	$Z = 1.11$, $r^2 = 0.96$, $n = 11$, staggered 3 y rotational harvest.
Lower Rappahannock	No value—all years' low density
Piankatank	$Z = 1.87$, $r^2 = 0.94$, $n = 8$, significant seed harvest 2008 onwards
York & Mobjack	$Z = 1.21$, $r^2 = 0.97$, $n = 9$, harvest years include atypical values
Upper James River	$Z = 0.89$, $r^2 = 0.96$, $n = 8$, most reefs open to seed harvest every year
Middle James river	$Z = 1.06$, $r^2 = 0.95$, $n = 7$, most reefs open to seed harvest every year
Lower James River	$Z = 1.026$, $r^2 = 0.99$, $n = 11$

The demographics from the TropFish output were used to delineate year classes by SL intervals for all of the MD reefs and the VA aggregations. The length to shell weight allometric relationships were then used to estimate shell weight per unit area for each year class within a sample for each reef/year combination. An example for the Piankatank River is as follows: a single allometric relationship for DSW versus SL for the entire Piankatank data were developed from the reef level entries (Table 3) and is described thus: DSW (g) = $2E\text{-}04x^{2.95}$, $r^2 = 0.92$, $n = 297$, where x = SL (mm). The distribution of DSW by length for the Piankatank River for the entirety of the 2006–2019 period is illustrated in Figure 5. Note how the values for greater than 80 mm SL oysters decreases despite the increase in weight per shell. The mortality of animals in this size range (>3-y-old) underscores the importance of even marginal increases in survival to 4- or even 5-y-olds to the shell resource. The Piankatank oyster resource is not open to public market oyster harvest but is periodically managed as a source of "seed" or submarket size oysters that are harvested for transfer to other sites and subsequent grow out to market size at the recipient sites. Seed oyster harvest is thus included in mortality for this site.

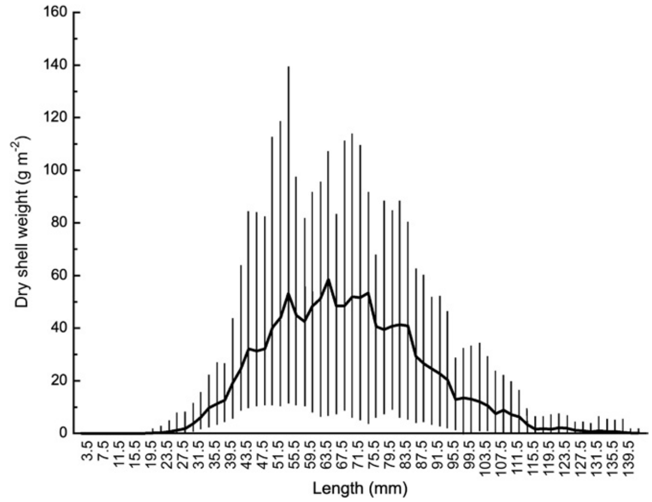

Figure 5. Dry shell weight (DSW, g m^{-2}) demographic from 2006 to 2019 for Piankatank River oysters (n = 84,492). Mean value is given with range. See text for additional details.

Data for DSW per unit area on MD and VA reefs by age class are summarized as median, quartiles, and ranges for age classes 1 through 5 in Figure 6 for MD (sampling years 2010–2015) and VA (2006–2019). YOY data are omitted given that these contributions are minimal. Note that 2010 MD source data include YOY through age 4 oysters, thus this sample includes data on year classes 2006 through 2010 (the 2010 4-y-olds were YOY in 2006). Thus, a 2010–2015 time series can be reconstituted as year classes 2006 through 2015. Similarly, VA data from sampling in years 2006–2019 can be reconstituted as year classes 2002 through 2019. Very few oysters survive to 5 or more years of age. In MD, the major contributions to the live shell pool is generally from 2-y-olds with 3 and, to a lesser extent 4-y-olds contributing at sites in St. Mary's shore, Nanticoke and Wicomico Rivers, Tred Avon River, Upper Chester, Upper Choptank, and Upper Potomac Rivers. These include areas where sanctuary status has been in place for over 5 y and where disease-related mortality has been low in recent years. In VA, the populations are more age truncated than in MD with only the low salinity sanctuary in the upper James River showing substantial survival into year classes 3 and 4. Recall that the minimum harvest size is 76 mm SL and, depending on area, approximately corresponds to this age group transition. The entire Bay wide system is one in which shell in the live pool

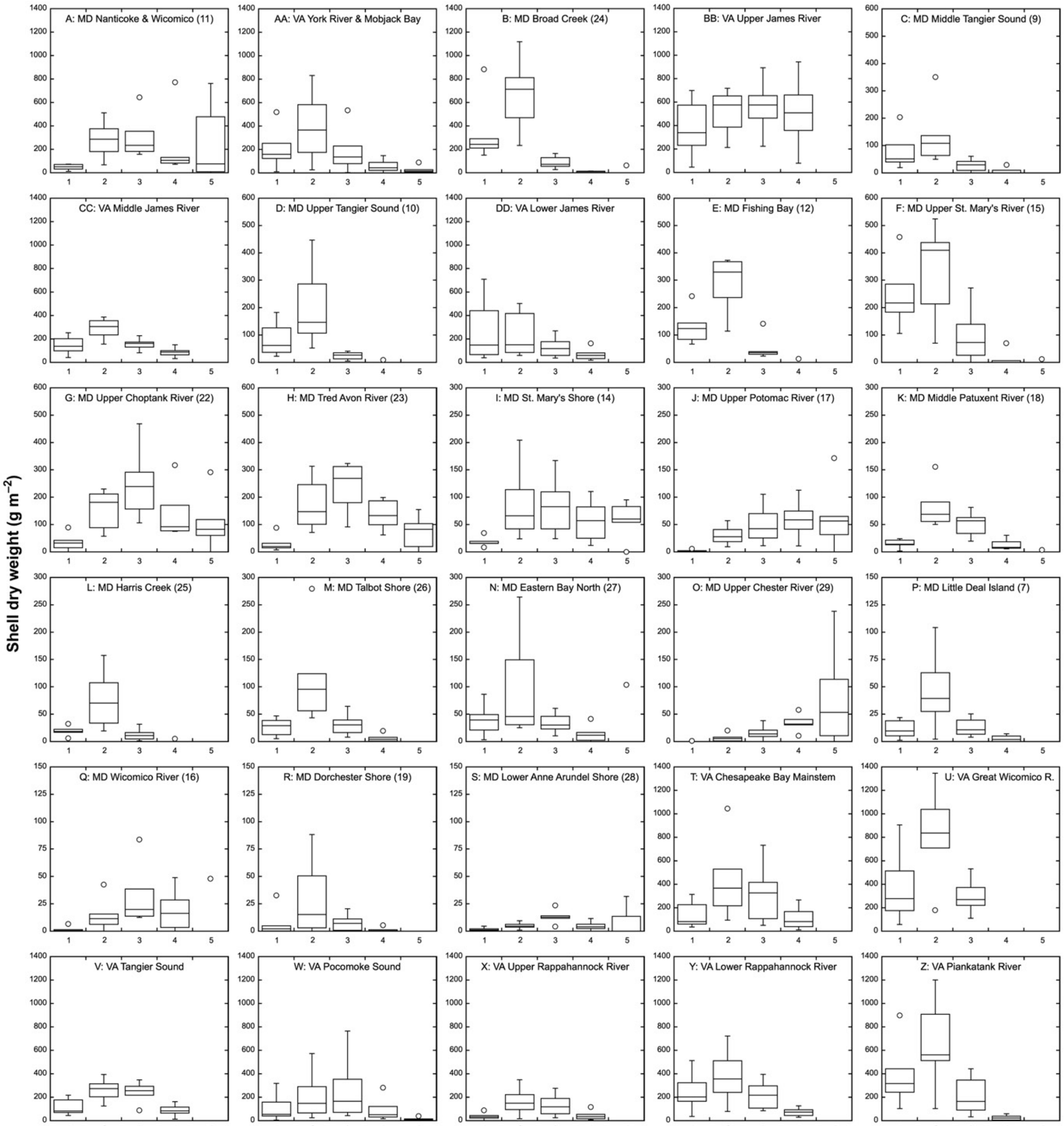

Figure 6. Demographic profile of dry shell weight per unit area on Maryland (MD) (panels A through S) and Virginia (VA) (panels T through DD) reefs by age class for year classes originating in 2010 through 2015 for MD and 2009 through 2019 for VA. Values are median, quartile, and range across all plots. Note that the plot ordinates have one of four scales (0–1,400, 0–600, 0–300, and 0–150 g m^{-2}) to accommodate spatial differences.

turns over quite rapidly; the contribution of a single year class peaks in 2–3 y and is gone by 4–5 y.

The values encompassed by the ordinates in Figure 6 covers median values in the range 0–800 g m^{-2} with quartiles less than 1,000 g m^{-2} and maximum values at less than 1,400 g m^{-2}. Year class 2 or 3 median VA values range between 150 and 600 g m^{-2} with highest values in the Great Wicomico, Piankatank, and upper James River. The lowest values were observed in Tangier and Pocomoke Sounds, Upper Rappahannock and the Middle James River. With the exception of Broad Creek, Upper St. Mary's River, and Fishing Bay in MD, where year 2 median values were 700, 400, and 350 g m^{-2}, respectively, all MD median values were less than 300 g m^{-2} with most in the 0–200 g m^{-2} range. The observed ranges in Figure 6 illustrate the comparatively robust status of most of the VA reefs in comparison with the MD reefs; however, all plots should be cause for concern in that they reflect both low live standing stock, and thus low potential for annual addition to the underlying reef structure.

DISCUSSION

An extensive data set is presented on both oyster vital rates and shell standing stock. From these rates of shell production and loss, and thus reef accretion rates can be estimated. The entire Chesapeake Bay wide system is one in which shell in the live pool turns over quite rapidly; the contribution of a single year class peaks in 2–3 y and is gone by 4–5 y. This is in stark contrast to fossil populations in the Bay where individuals in the 10–15 y range were present (Lockwood & Mann 2019). The extant, apparently stable system is not stable—it is dynamic and arguably unstable. The implications of dynamic turnover are 2-fold. First, lack of longevity limits shell contribution per individual and can be locally exacerbated by harvest. Second, one or more recruitment failures can place the underlying structure in jeopardy. The observed balance is the end product of these dynamic components, and should not be viewed as indicative of long term stability, but one of rapid substrate turnover that is vulnerable to minor perturbation.

The importance of survival to old age cannot be understated in maintaining reef structure. The general paucity of oysters greater than 130 mm SL in extant populations is noted; however, a few oysters greater than 150 mm SL were caught in both the MD and VA surveys. What would be the impact on shell production if these large oysters, representing older year classes, were present in even modest abundance? This question has two components: Would the regional impact be uniform and what would be the overall shell production? Consider again the allometric relationships and the demographics of both MD and VA populations. The allometric relationships of SL versus DSW are displayed in Figure 7 for the four sites representing the lowest and highest DSW versus SL relationships for MD and VA, respectively, from Tables 3 (MD) and 4 (VA). These are Pagan and Normans in MD, and Middle Horsehead and Ross Rock in VA. Shell length is plotted on the abscissa axis in mm, truncated between 30 and 140 mm SL, versus DSW in gram on the ordinate axis. When Figure 7 and Table 2 are considered together, it is evident that MD data show strong coherence among all 22 sites examined. For example, the spread in SL for a DSW of approximately 200 g is 100–125 mm. A corresponding consideration of the VA sites in Figure 7 and Table 3 shows a greater spread among the plots. Whereas Ross Rock has a DSW value of approximately 200 g corresponding to an SL value of approximately 110 mm, several VA data sets and notably Middle Horsehead never exceed DSW values of 100 g even when SL is extrapolated to 140 mm. The MD oysters are consistently either more rounded per unit length or have thicker shells or both. James River oysters, particularly those from upriver stations, are both unusually elongate and thin shelled. Despite these morphometric variations, the plots underscore the substantial increase in individual shell weight, generally a 5–6 fold increase with the exception of some James River stations, with increasing shell weight from 76 mm SL (market size) to 140 mm SL. The demographic in Figure 5 would be substantially changed by increased longevity at all stations.

Figure 8 is a suite of region-specific plots of time series observations of brown shell (x, L m^{-2}) versus live shell (y, L m^{-2}) that illustrate, despite variation between regions, the apparent stability of the shell budget components along a fixed relationship when considered as a whole over the 2006–2019 period. Diversions from this relationship, driven by repletion or unusually high recruitment, return in a hysteresis-like manner as subsequent shell loss rates from the brown pool exceed the ability of recruitment, growth and mortality to maintain an expanded shell base. The large shell planting and repletion efforts in the York/Mobjack region from 2008 onwards illustrate this temporal variability. Where repletion is minimal or not active, for example parts of the James River, the plot shows compliance to this relationship over time, often despite harvest related removals.

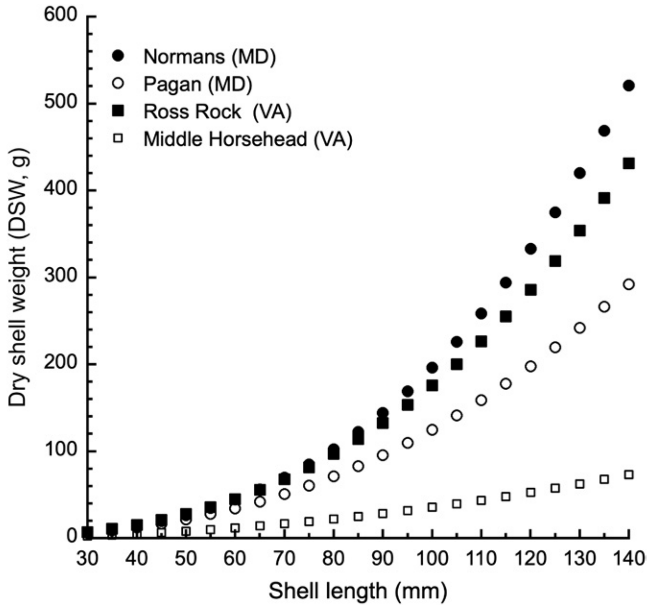

Figure 7. Allometric relationships of shell length (SL) (mm) versus dry shell weight (DSW) (g) for two reefs in MD (Normans and Pagans) and two reefs in VA (Ross Rock and Middle Horsehead). All plots are SL truncated between 30 and 140 mm SL on the *X* axis.

Two subtle points emerge from Figure 8. Within the range portrayed, the addition rates to the brown shell pool from mortality generally match the loss rates to taphonomy and burial, and the intercept of the plot on the *X* axis suggest a base brown shell value of approximately 4 L m^{-2} that corresponds to no live shell component. At brown shell values above this base, live shell increases along a linear relationship; each unit increase in live shell is accompanied by an approximate doubling of brown shell. That is, there is a residual brown shell value that agrees with the preservation "boundaries" described by Powell et al. (2012).

Previously, Mann et al. (2009b) presented the relationship between live shell weight and total (live plus brown) shell weight at eight reefs in the James River for the 1998–2006 period, and described each plot in four quartiles or scenarios: low shell plus low live, low shell plus high live, high shell plus low live, and high shell plus high live. Mann et al. (2009b) noted that only the first (low shell plus low live) and last (high shell plus high live) were stable and that transitions into the second and third scenarios were temporally unstable as populations reverted to the first or fourth scenario. Figure 8 is in general agreement with the concept of a structured relationship between live shell and brown shell abundance as described by Mann et al. (2009b). Note that Figure 8 describes an equilibrium but does not give

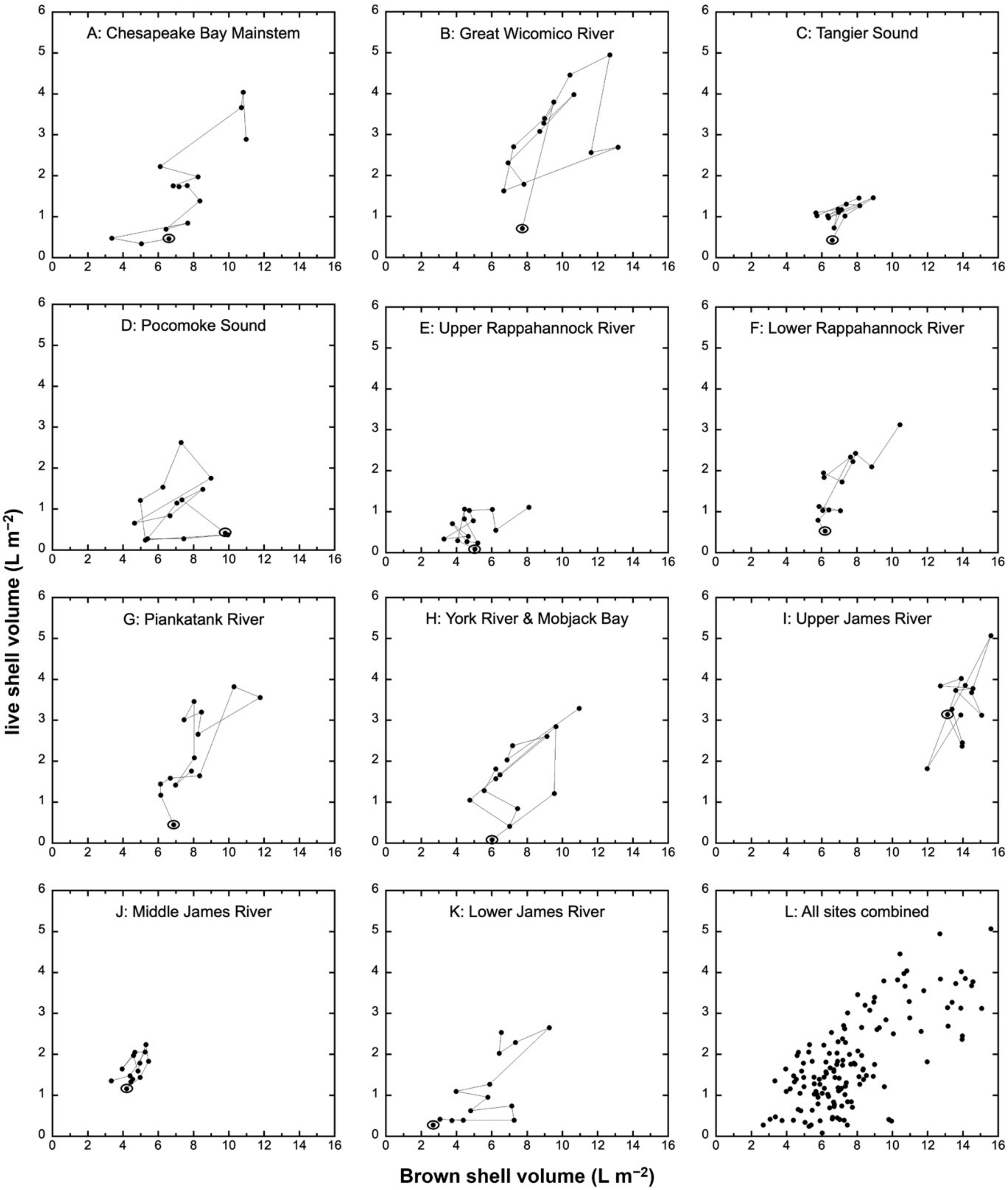

Figure 8. Virginia Chesapeake Bay, 2006–2019: Time series observations from 2006 to 2019 of brown shell volume (L m^{-2}) versus live shell volume (L m^{-2}) for the 11 regions in Virginia (VA). Panels A though K describe individual areas as in text and Figure 3. Each plot line traces the time progression for the individual area with starting (2006) point marked with a larger symbol. Panel L is all years, all locations, and describes the increase in live shell weight with brown shell weight. See text for additional details.

the rates of transfer of components in that equilibrium—this is addressed later in this text.

Having examined demographics and age structure, it is relevant to examine rates of addition and loss to the live and brown shell pools described in Figures 5, 6, and 8. Consider a typical demographic from Figure 6 with a maximum dry shell density in the range 800–1400 g m^{-2}. Figure 9 provides simulations of a single year class over a 10-y period. Initial oyster density as YOY is set at 100 m^{-2}, a value typical of the range in the data reported in Figure 6. Panel A describes survival as a declining function wherein instantaneous mortality, M, varies between 0.85 and 1.25, values commensurate with those reported earlier for VA regions. Note that in this simulation Z = M, that is, no fishing mortality; all dying oysters contribute to the underlying shell mass and no shell is lost to harvest. These are thus generous estimates compared with field situations where shell loss occurs with harvest. Survival is less than 20% by year 2 and mortality is essentially completed by year 5. Using the MD composite growth curve generated from Figure 4 and the SL versus DSW allometry of oysters from the Piankatank River, a standing stock of shell (DSW g m^{-2}) is given in Panel B. Note both the shape and associated values of the curves in Panel B. At the highest M value, the inflection point in the curve occurs at 913 g m^{-2} and year 1 at M = 1.25, before any fishing mortality

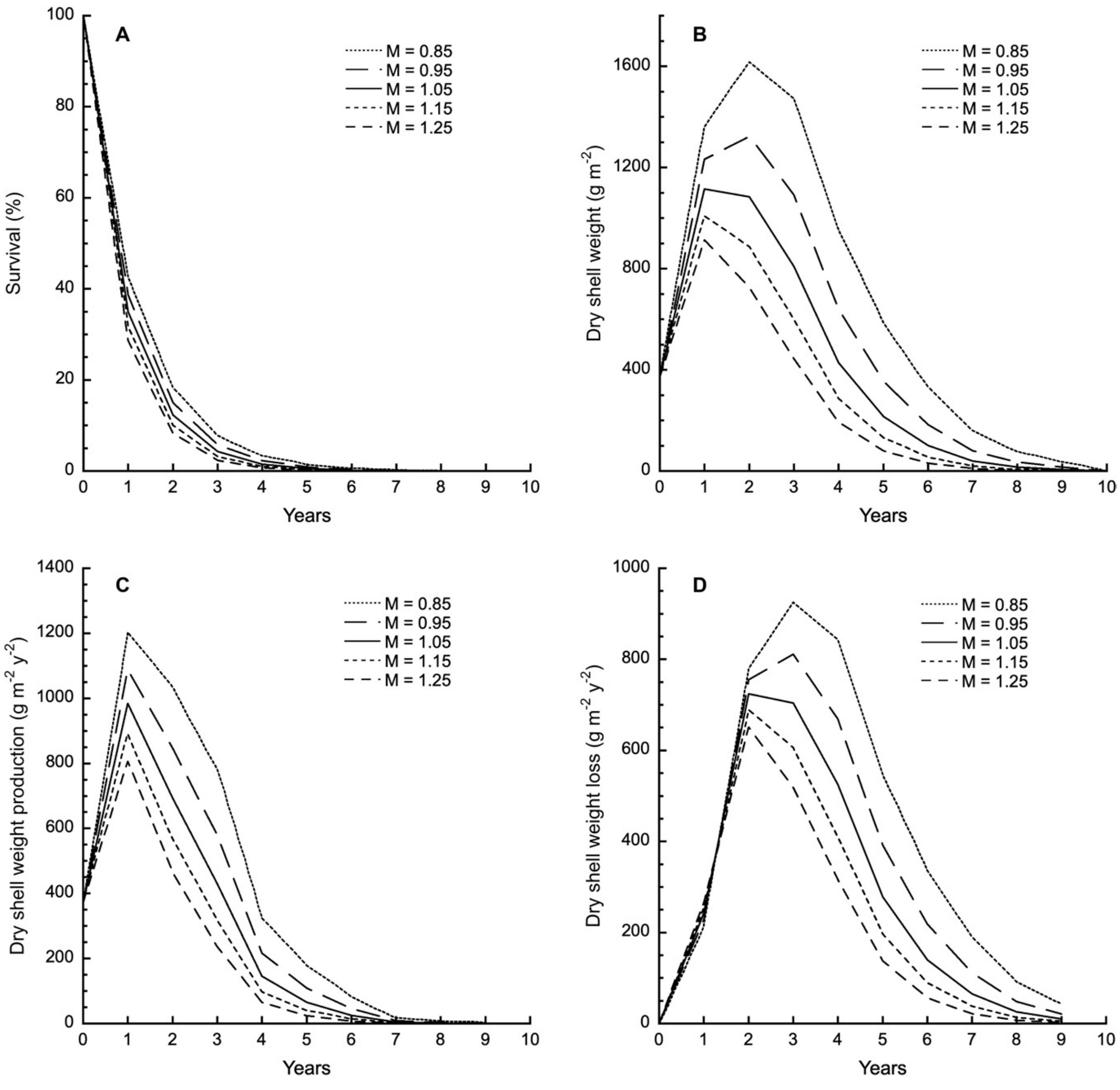

Figure 9. Simulations based on Figure 6 (see text). (A) Survival as a declining function wherein mortality, *M*, is a declining exponential of the form $Nt = No \times e^{-Mt}$. *M* values are consistent among panels between 0.85 and 1.25. (B) Standing stock of shell (g m^{-2}). (C) Annual shell production (g m^{-2} y^{-1}). (D) Annual shell loss (g m^{-2} y^{-1}).

can occur. Decreasing M to 0.95 moves the inflection to year 2 at 1,323 g m^{-2} just prior to oysters being available for market harvest. As M is decreased to 0.85, the inflection point remains at year 2 as the maximum shell density increases to 1,616 g m^{-2}. The range of M values provide standing stocks of shell that are similar to reefs described in Figure 6. The purpose of Panels C and D in Figure 9 is to dissect the standing stock value of Panel B into annual live shell Production (addition of shell to the live pool through growth, Panel C) and Loss (decline in production associated with mortality and transfer of shell from live to brown shell pools, Panel D) rates. Note that Panels C and D address dynamics of the live pool only; they do not address taphonomic loss. The relevant estimators are:

Production (g m^{-2} y^{-1}) = # surviving oysters × increase in shell weight where interval ($t_1 - t_0$) = one year

Shell loss (g m^{-2} y^{-1}) = # oysters lost to mortality × shell weight at beginning of interval (one year)

The dynamic nature of the shell pool is evident from these plots. Early on, productivity increases as growth is relatively rapid. Over time, as growth slows and cumulative mortality increases, the balance shifts towards productivity decline. For example, even though shell standing stock in year 2 at $M = 0.85$ is 1,616 g m^{-2}, the production for that year is 1,034 g m^{-2} and loss is 780 g m^{-2}. For the higher $M = 1.05$, shell standing stock is 1,083 g m^{-2} and the production is 917 g m^{-2} and loss is 766 g m^{-2}. At the highest rate of $M = 1.25$, shell standing stock is 1,083 g m^{-2} and the production is 693 g m^{-2} and loss is 724 g m^{-2}. These pools of shell have very high turnover rates that may or may not be exacerbated by harvest on a locality-specific basis. Whereas the maximum shell standing stock values in Figure 9 are in the range 912–1616 g m^{-2} ($M = 1.25$ and 0.85, respectively) the total shell production and loss (because the year class passes through completely) over the 10-y period for the year class varies between 1,975 and 3,968 g m^{-2} ($M = 1.25$ and 0.88, respectively).

How do these calculations influence our view of the stability of shell on extant reefs and the live shell to brown shell relationship that accompany mortality? Table 4 provides a summary of live shell standing stock (LIVE, units dry shell, g m^{-2}), brown shell (BROWN, units dry shell, g m^{-2}), and the live/brown ratio (L/B) for VA area aggregations from 2006 to 2019 with all values rounded to the nearest whole unit. This is a numerical summary of live and brown data plotted in Figure 6 but in units of weight rather than volume. Of importance is the ratio L/B and the mean value for the 11-y period, underlined in Table 4. These means vary between 0.14 and 0.30. Assuming that brown shell reflects a balanced input from live and a loss to burial, taphonomy, and harvest, then the first approximation is that the L/B ratio represents a turnover or loss rate from the brown pool, that is, between 14% and 30% of the pool is replaced annually. This first approximation is misleading because the L/B ratio underestimates the input from the live pool as illustrated by the plots in Figure 9 and the mortality rate–dependent values given in the previous paragraph. In the range of mortality rates ($M = 0.85$–1.25) examined, total shell production exceeds peak standing stock by a factor of approximately 2.24 through 2.05 (3,632/1,611 = 2.24 at $M = 0.85$ through 1,605/912 = 1.76 at $M = 1.25$). As noted, Figure 8 estimates a residual brown shell volume at no live shell presence of approximately 4 L m^{-2}. With an increasing brown shell presence to approximately 15 L m^{-2}, there is an associated increase in live shell to approximately 4 L m^{-2}, which is an approximately 4:1 proportion of brown:live shell. If the live shell represents approximately one third of the total in this range, then a 2-fold turnover of the live component annually represents two thirds of the total in this range of brown shell densities. This is extraordinarily dynamic and reinforces both the half-life estimates of Powell and Klinck (2007) in addition to supporting the general guidelines implemented in the Virginia Marine Resources Commission Oyster Replenishment Program of shell planting every three years to approximately double standing shell stock on managed reefs.

The VA data have thus been summarized. Can similar calculations be made for the MD survey brown shell density on a per unit area basis? Swept area estimates of brown shell per unit area in MD surveys were generated from tow length, dredge width, and bushel collected values. These were then converted to shell dry weight per unit area values using the following relationships:

1 MD bushel = 2810 cu in = 45.9L,

1L wet shell = 597 g wet weight (Mann et al. 2009a, 2009b), and

dry shell weight (g) = 0.93* wet shell (g) = 0.555 g dry weight ($r^2 = 0.99$, $n = 300$ based on haphazard samples from 2013 MD condition sample oysters).

The conversion of wet shell volume to wet weight may appear illogical in that this gives wet shell a specific gravity of 0.597, less than that of water! This value is generated from loosely packed shell volume in collections made on the VA survey and reflects the fact that most of the volume in a bushel of oyster shell is air space between the shells. Hence, the reason for the apparent nonsensical value. Applying the above conversions to the shell weights per unit area results, across the entire swath of sampled MD reefs, results in brown shell estimates that are comparable to that of the live shell per unit area.

Unlike the VA data as reported in Table 4, the MD relationship is variable and inconsistent both within and among reef sites, a product of towed dredge function as it effectively samples the reef surface layer but displays decreasing efficiency with increasing depth into and hardness of the reef structure. As the underlying structure hardens, penetration is reduced and the brown shell layer is under-sampled relative to the live oysters, precluding an examination of the quantitative relationship between the two and forcing the focus of discussion on simple turnover rates of shell in the live portion alone.

How do the shell production and loss rates described herein compare with evolutionary targets for *Crassostreid* species whose very survival over evolutionary time requires that they build reefs at rates commensurate with or in excess of sea level rise (Mann & Powell 2007)? What sea level rise values should we consider? Mann et al. (2009a) provide a short summary. The glaciated late Tertiary (30 MYA–1.8 MYA) and Quaternary (1.8 MYA to present; Vail & Mitchum 1979, Pitman 1978 in Kennett 1982) periods had higher rates than the early Tertiary (30–60 MYA) period. Rates of sea level rise during the early Holocene transgression (7,000–17,000 y ago) were approximately 8 mm y^{-1} (Kennett 1982, based on Curray 1965, Milliman & Emery 1968) with a short phase at 7,000–10,000 y ago with a higher rate of 10 mm y^{-1} (Kennett 1982). The combination of sea level rise and/or the crossing of hydrographic or topographic barriers caused the Chesapeake estuary to change from fresh to

TABLE 4.

Summary of live shell standing stock (LIVE, units dry shell, g m^{-2}), brown shell (BROWN, units dry shell, g m^{-2}), and the live/brown ration (L/B) for the VA areas from 2006 to 2016.

	Chesapeake Bay			Great Wicomico			Tangier			Pocomoke		
	LIVE	BROWN	L/B	LIVE	BROWN	L/B	LIVE	BROWN	L/B	LIVE	BROWN	L/B
2006	260	3599	0.07	348	4211	0.08	278	3595	0.08	272	5341	0.05
2007	194	2748	0.07	2061	5191	0.40	668	3985	0.17	807	4003	0.20
2008	270	1837	0.15	1815	4902	0.37	957	4861	0.20	967	4649	0.21
2009	477	4178	0.11	1317	3943	0.33	719	3789	0.19	544	3634	0.15
2010	393	3509	0.11	794	3643	0.22	633	3477	0.18	427	2538	0.17
2011	781	4554	0.17	1354	7179	0.19	826	4445	0.19	1149	4905	0.23
2012	990	4161	0.24	1275	6344	0.20	848	4029	0.21	1707	3979	0.43
2013	975	3909	0.25	2563	6926	0.37	666	3452	0.19	994	3415	0.29
2014	985	3733	0.26	2203	5688	0.39	762	3878	0.20	779	2719	0.29
2015	1111	4501	0.25	1537	4878	0.32	473	3646	0.13	157	2875	0.05
2016	1251	3326	0.38	1961	5806	0.34	775	3771	0.21	242	5429	0.04
2017	2064	5846	0.35	1584	4759	0.33	715	3086	0.23	179	4057	0.04
2018	2270	5899	0.38	1141	3769	0.30	670	3114	0.22	179	2934	0.06
2019	1628	5987	0.27	957	4267	0.22	953	4416	0.22	760	3847	0.20
			0.22			**0.29**			**0.19**			**0.17**

	Upper Rappahannock			Lower Rappahannock			Piankatank			York & Mobjack		
	LIVE	BROWN	L/B	LIVE	BROWN	L/B	LIVE	BROWN	L/B	LIVE	BROWN	L/B
2006	285	3376	0.08	54	2747	0.02	278	3744	0.07	41	3282	0.01
2007	427	3158	0.14	176	2215	0.08	764	3347	0.23	621	5207	0.12
2008	565	3496	0.16	627	2426	0.26	868	3339	0.26	1444	5258	0.27
2009	608	3188	0.19	486	2418	0.20	951	3644	0.26	533	2594	0.21
2010	553	3856	0.14	142	2841	0.05	993	4550	0.22	209	3818	0.05
2011	557	3310	0.17	157	2504	0.06	2390	5615	0.43	429	4070	0.11
2012	1258	4169	0.30	417	2057	0.20	2101	6422	0.33	648	3040	0.21
2013	990	3344	0.30	236	2542	0.09	1610	4502	0.36	915	3392	0.27
2014	1047	3326	0.31	198	1793	0.11	1903	4603	0.41	841	3531	0.24
2015	932	3904	0.24	459	2702	0.17	1812	4071	0.45	794	3392	0.23
2016	1200	4237	0.28	607	2581	0.24	2082	4380	0.48	1320	4977	0.27
2017	1307	4324	0.30	622	3290	0.19	1279	4388	0.29	1203	3911	0.31
2018	1131	4820	0.23	323	3396	0.09	874	3805	0.23	1026	3739	0.27
2019	1685	5700	0.30	654	4419	0.15	1079	4296	0.25	1655	5972	0.28
			0.23			**0.14**			**0.30**			**0.20**

	Upper James			Middle James			Lower James		
	LIVE	BROWN	L/B	LIVE	BROWN	L/B	LIVE	BROWN	L/B
2006	1960	7161	0.27	544	2422	0.22	158	1455	0.11
2007	1534	7609	0.20	568	2478	0.23	236	1672	0.14
2008	1644	7620	0.22	473	2288	0.21	223	2387	0.09
2009	2008	7296	0.28	586	2709	0.22	217	2037	0.11
2010	2243	7713	0.29	749	2972	0.25	221	3960	0.06
2011	2937	8504	0.35	914	2884	0.32	419	3885	0.11
2012	2092	7903	0.26	729	2702	0.27	352	2617	0.13
2013	1755	8213	0.21	651	2644	0.25	539	3149	0.17
2014	2095	7419	0.28	804	2506	0.32	617	2167	0.28
2015	2184	7950	0.27	672	2148	0.31	716	3212	0.22
2016	2234	6937	0.32	837	2541	0.33	1493	5049	0.30
2017	2281	7588	0.30	840	2860	0.29	1289	4001	0.32
2018	1007	6529	0.15	601	2397	0.25	1141	3504	0.33
2019	1707	7574	0.23	553	1815	0.30	1431	3565	0.40
			0.26			**0.27**			**0.20**

All values are rounded to the nearest whole unit. The mean L/B value for each region are underscored. VA, Virginia.

brackish in nature between 7,400 and 8,200 y ago (Bratton et al. 2003). As the headwaters of the estuaries filled with sediment and rates of sea level rise decreased, the oyster populations retreated in a seaward direction leaving fossil oyster beds in the northern Chesapeake Bay and upstream areas of the Potomac River (Bratton et al. 2003). Thus, the Holocene transgression value of 10 mm y^{-1} sets an evolutionary target for oyster reef accretion. This may arguably be increased for taphonomic loss and burial at approximately 30%, or even higher based on production to standing stock ratios in Figure 9, a shell production rate to maintain equilibrium at a corrected 13 mm y^{-1} or 13 L m^{-2} y^{-1} (one L covers one square meter to a depth of 1 mm) is 7,217 g m^{-2} y^{-1} dry shell. This estimate is approximately six times higher than the maximum production rate in Figure 9C, and should a higher turnover rate in the brown shell pool be invoked, the disparity increases. The only countering argument is that Figure 9 represents a single year class and that multiple year classes progressing simultaneously will appropriately increase total production rate—but even 4 or 5 y classes in unison fail to exceed the required production to accommodate a 10 mm y^{-1} sea level rise rate.

Are there options to examine accretion rates in more recent times? DeAlteris (1986, 1988) provides data commensurate with absence or minimal fishing in the Chesapeake Bay before colonial settlement. DeAlteris (1986) notes in describing Wreck Shoal in the James River that "From the 1550s to the 1850s the oyster reef developed vertically almost 1.5 m." DeAlteris (1988, Fig. 6) extends this time period estimating the accumulation of feces, pseudofeces, and shell material at Wreck Shoal at 5 mm y^{-1} for the period 1000 through 1855 AD. DeAlteris (1988) presented an estimate of "bioaccumulation" for a "healthy" oyster reef in the James River in the early 1980s assuming 50% mortality per year as follows: "With a standing crop of 500 bushels (26,250 L) per acre (0.4 ha), this yields a contribution of 250 bushels (13,125 L) of shells per year to the oyster reef. To set this in perspective, it would take about 100 y for an oyster reef to accumulate a layer of shells 35 cm thick due to the natural mortality of the oyster population." This is 3.5 mm y^{-1} or slightly below the value from 1,000 through 1855 AD. DeAlteris continues, "The void space in an oyster shell reef is approximately 50% depending on the shell size. This space may be filled with fecal deposits that contribute to reef growth. If there were negligible resuspension and transport of fecal biodeposits, a productive oyster reef could develop vertically at a rate in excess of 50 cm/100 y, resulting from the deposition of oyster shells and fine fecal muds in a dense matrix." This is 5.0 mm y^{-1} or 5.0 L m^{-2} y^{-1}. Sadly, DeAlteris (1986) also notes that "From the 1850s to present the oyster reefs have lost more than 1.0 m of elevation due to intense harvesting activity." DeAlteris (1986) describes Wreck Shoal as a hard rock "characterized by a relatively thick oyster shell layer, higher densities of live oysters, a coarser interstitial sediment, and negligible sediment cover." Additionally, "the hard rock oyster reef, with high bottom shear stress is rarely depositional with respect to fine sediments." The pre-exploitation accretion rate approximates to 5 mm y^{-1}, slightly higher than sea level rise rates, and requires an additional reef volume of 0.05 m^{-3} y^{-1}. Assuming that this volume of consolidated oyster reef shell and mud approximates to the loosely packed shells used to generate estimates of shell volume to weight conversions described earlier in this text with coarse grain infill (as described by DeAlteris (1988)), a reasonable assumption given the shear stress environment, then the volume of shell in this increase has a mass of 2,775 g m^{-2} y^{-1}.

Mann et al. (2009a) provide a discussion of accretion rates based on a combination of estimated longevity of up to 19 y recalculated from a report of a maximum 450 mm SL by DeBroca (1865) using growth estimators from Harding et al. (2008) and Mann et al. (2009b), a declining exponential mortality rate as for Hoenig (1983), and sustained recruitment rates comparable to those observed in the James River (Mann et al. 2009b). With the target accretion of 3.5 mm y^{-1} and longevity of 5, 10, and 19 y, respectively, the required initial density of 1-y-old oysters and mortality rates (M) are 68 m^{-2} and $M = 0.56$, 18 m^{-2} and $M = 0.22$, and 4.55 m^{-2} and M = 0.07. These values of M are proportional by year, with a value between 0.0 (no mortality) and 1.0 (all died). Survival is $(1-M)$ for a period of 1 y or $(1-M)^q$ for a period of q years. Corresponding Z values (where Z = M+F, effectively $Z = M$ where F =0) in the form $N_t = N_o \times e^{-Zt}$, are 1.7, 0.14, and 0.08, respectively.

Current relative sea level rise, including both sea level rise and land subsidence, approximates to 4.5 mm y^{-1} depending on location within the Chesapeake Bay. Whereas the rate decreases in an upward direction, the overall rate is trending upwards (https://www.vims.edu/bayinfo/tidewatch/index.php). For oysters, this challenge may be compounded by location dependent sedimentation (see Hobbs et al. 1990; also note historical perspective Bratton et al. 2003) acknowledging the comments of DeAlteris (1986) that hard rocks do not suffer sedimentation whereas lower density, deeper water rocks are susceptible. Even at current sea level rise rates, it is evident that extant shell production may, depending upon location in the Bay, be inadequate to accommodate ongoing sea level rise. The only options that comfortably accommodate such a rise rate are, as demonstrated by the calculation above, either far greater longevity of individuals or consistent extremely high recruitment in combination with reduced mortality rates.

Required accretion rates estimated for both the Holocene transgression and the precolonial period compare well to descriptions of present day invading populations of *Crassostrea gigas* at three sites in the Dutch Ooesterschelde by Walles et al. (2015) where shell addition to the reef matrix by mortality was estimated at 10.7 kg m^{-2} y^{-1} for the reef at Viane, 12.3 kg m^{-2} y^{-1} at St. Annaland, and 5.1 kg m^{-2} y^{-1} at Kats. This corresponds to volumetric additions of 14.6 L m^{-2} (or mm y^{-1} vertical accretion) at Viane, 16.9 L m^{-2} at St. Annaland, and 7.0 L m^{-2} at Kats. The *C. gigas* reefs in these locations have been actively accreting because the species' first record of presence in 1964 and stand as significant geological and ecological structures in this otherwise eroding environment (Markert et al. 2013).

How do these shell production and loss rates compare with those of other molluscs? Four decades ago, Beukema (1980) reported on shell carbonate production by the infaunal *Macoma balthica* on the intertidal flats of the Dutch Wadden Sea. Annual standing stock values varied from 16–34 g m^{-2} at Balgzand region, a 50 km^2 tidal flat area in the westernmost part of the Wadden Sea, with a 11-y average of 23.6 g m^{-2}. For the overall Dutch Wadden Sea, the average standing stock was 18 g m^{-2} with 95% confidence interval (CI) of 13–22 g m^{-2}. Production rates varied from 9 to 18 g m^{-2} y^{-1} with P:B ratios declining from approximately 0.81 to approximately 0.32 as the population aged and became more dominated by older year classes. In a subsequent study, Beukema (1982) described carbonate standing stock and production for the cockle *Cerastoderma* (*Cardium*) *edule* in the Wadden Sea, incorporating data from the 1968 to 1982 period. Recruitment, survival, and thus local density varied within this period. Young of the year densities varied between 20 and 500 m^{-2}, whereas adult density varied between less than 5 and 80 m^{-2}, with the vast majority being present in the intertidal flats. The mean Z mortality value for the first half year post recruit was 1.88. Mortality decreased as cockles grew, and the mean value for cockles that survived through their first winter varied in the 14 y data set from 0.29 to 3.22 with a mean of 1.41 and 95% CI of 0.9–1.9. These values are not unlike those observed for oyster populations in this study. Shell standing stock varied both seasonally and between years, with high values being driven by high recruitment events. Cockle shell standing stock on the Balgzand tidal flat for the 1968–1982 period was 127 ± 22 g m^{-2} (n = 15) for late summer and 80 + 19 g m^{-2} (n = 14) for late winter. The annual mean was 104 ± 40 g m^{-2} (95% CI). The mean standing stock for the 1,300 km^2 of the entire Dutch Wadden Sea is estimated at 50–150 g m^{-2} with 90% being in the intertidal region. This is a highly dynamic system with annual shell carbonate production rates of between 33 and 338 g m^{-2} y^{-1} with a mean of 118 ± 23 g m^{-2} y^{-1} (n = 14, 95% CI). Annual loss rates vary between 29 and 240 g m^{-2} y^{-1} with a mean of 114 ± 17 g m^{-2} y^{-1} (n = 14, 95% CI). What is remarkable about this system is that annual mean values of standing stock, production, and loss are comparable. That is P:B approximately 1.0, and the entire shell mass in the system turns over annually. These values are remarkable for two reasons. First, they are at least an order of magnitude lower than the Holocene transgression and the precolonial *Crassostrea virginica* values and the present day invading *Crassostrea gigas* values. Second, they are approaching values comparable to a number of the extant, present day Chesapeake Bay oyster reefs as reported in Figure 6. High production and P:B values are driven by high recruitment events. Figure 9C indicates that a similar scenario prevails in present day oyster populations in the Chesapeake Bay. Indeed, age-specific mortality rates for oysters, as reported earlier in this text, are comparable to those for *Macoma* through age 4.5 y (Beukema (1980). Truly, oysters with life expectancy in the 10–20 y range should exhibit mortality rates similar to that of other large mactrids such as the surf clam *Spisula solidissima*, the fishery management plan for which employs a value of $F = M = 0.15$ (proptional) or $Z = 0.18$ (NEFSC 2016); however, this is far from the case.

The standing stock values reported by Beukema (1980, 1982) underscore the dominance of *Cerastoderma* over *Macoma* in the shell carbonate budget of the Wadden Sea system. Beukema (1982) notes that approximately 90% of the "annual yield" of shells in this location is 100,000–300,000 m^3, or 195,000 metric tonnes. Beukema (1980, 1982) expressed concern that fishing removal could exceed annual production for both species. This concern was also been expressed earlier in this text with respect to Chesapeake Bay oyster populations. Since Beukema (1980, 1982), there have been few direct measures of shell turnover in bivalve populations; however, production:biomass (P:B) ratios in bivalves provide direct analogs assuming a constant tissue weight:shell weight, often termed condition index (review in Mann 1978), throughout the life of the species in question. High P:B ratios are commensurate with high shell production to shell standing stock ratios. Mann et al. (2020; Table 1) review P:B ratios in 25 species encompassing a latitudinal range from Greenland to Namibia. The reported P:B ratios vary from 0.05 for *Mercenaria mercenaria* in Wassaw Sound GA, a stable population of old individuals, to five populations with ratios greater than 2.0: *Macoma balthica* in the Ythan estuary in Scotland, *Cardium edule* and *Mytilaster lineatus* in the Sea of Azov, *Scrobicularia plana* from the intertidal of Colwyn Bay in Wales, and *Mya arenaria* in Nova Scotia, Canada. All populations with high P:B ratios are characterized by small individual size, high recruitment rates, limited longevity, and high turnover rates.

The current report exposes a fundamental challenge with longevity for Chesapeake Bay oysters. As noted earlier, a simple declining exponential mortality descriptor may not be appropriate for oysters once a refuge from predation size is attained (see discussion of predation loss in Eggleston 1990, multicomponent mortality curves in Powell et al. 1994, Lockwood & Mann 2019). The continued high mortality of oysters within the presumed predator refuge but prior to attaining a market size of 76 mm SL, is abundantly clear in literally millions of measurements over extended time and space in Virginia oyster populations (https://cmap2.vims.edu/VOSARA/viewer/VOSARA.html). The presumed extended period of low mortality is not evident, and the losses cannot be simply explained by harvest removal or disease. A broader consideration of the Chesapeake Bay watershed and its input to the Bay should be carefully scrutinized to explain the high mortality and truncated age structure of Chesapeake Bay oysters. The implications of truncated population structure are not limited to the reduction of shell supply to the underlying reef structure and loss of shell substrate for continuing oyster recruitment. Failure to rebuild shell reserves represents a loss of carbonate from the alkalinity bank described by Waldbusser et al. (2013), with implications for near bottom chemical environments that are advantageous to metamorphosing invertebrates (Green et al. 2004, 2012, Waldbusser et al. 2010) and thus, food chain stability that builds on benthic prey (Baird & Ulanowicz 1989, Ulanowicz & Tuttle 1992). Finally, reef building is a mechanism for carbon burial (Fodrie et al. 2017, Lockwood & Mann 2019), an ecosystem service that has only recently received focused attention as part of a greater debate on climate change and its amelioration.

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