



# Reconstructing pre-colonial oyster demographics in the Chesapeake Bay, USA

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## ABSTRACT

Recent estimates of growth and mortality rates in extant Chesapeake Bay, USA oyster (*Crassostrea virginica*) populations are used to quantify changes in both population abundance (dN/dT) and shell accretion (dS/dT) associated with modern population demographics. The demographics of oyster populations that would be required to maintain reef accretion rates commensurate with sea level rise over geological time frames are examined using estimates of oyster longevity in pre-colonial (pre -1600) times combined with parallel estimates of pre-disease endemic mortality. The analysis demonstrates that modern populations, with their disease related, age-truncated demographics, are generally not capable of maintaining and building biogenic reefs through accretion. Estimates of filtration rates associated with Chesapeake Bay oyster populations prior to 1600 considerably underestimate actual benthic–pelagic coupling during that period. Pristine oyster populations would have supported water column turnover rates on the order of minutes to hours. Thus, the spatial footprint of oyster reefs was limited by available productivity in the estuary. Accretion rate calculations for pristine (pre-1600) oyster reefs describe the intimate relationship between benthic–pelagic coupling and the presence or absence of oyster reefs and the associated communities.

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## 1. Introduction

Oysters have survived over geological time by invading estuaries, typically ephemeral geological features at continental margins, and creating biogenic habitat, reefs, through gregarious settlement and metamorphosis followed by growth and eventual mortality. The distribution of the cupped *Crassostrea* form is in the sedimentary estuaries and coastal habitats of the northern hemisphere (Kennedy et al., 1996) where modern natural outcrops of hard substrate are rare to absent. Both DeAlteris (1988) and Smith et al. (2003) link the genesis of Chesapeake Bay oyster reefs during the Holocene with geologic features. These include ridge and swale topography (DeAlteris, 1988), and hard terrestrial terrace structure from Pleistocene (alluvial) or Tertiary (shallow marine) periods that were flooded by Holocene sea level rise (Smith et al., 2003).

Perpetuation of the subsequent oyster populations was and is inextricably wed to their ability to create habitat that accretes at rates commensurate with sea level rise. Oyster populations must exhibit positive growth in both abundance and shell (dN/dT and dS/dT > 0 respectively) in order to support viable (self-sustaining)

populations (Powell et al., 2006; Mann and Powell, 2007; Powell and Klinck, 2007).

Although oysters were historically long-lived (10–20 y, Powell and Cummins, 1985), oysters > 5 y old are rare in modern Chesapeake populations (Mann et al., 2009). Harding et al. (2008) and Mann et al. (2009) provide growth curves for pristine or pre-colonial (pre -1600) and modern James River, Virginia oyster populations. These age-at-length relationships facilitate the examination of modern population demographics (lengths) as age classes. Since the mid 1950s, oyster mortality from the diseases *Haplosporidium nelsoni* and/or *Perkinsus marinus* has been and continues to be a serious challenge to Chesapeake oyster populations in mid to high salinity waters (Andrews, 1996; Burreson and Ragone Calvo, 1996). Mann et al. (2009) describe mortality estimates, ranging between 38 and 92% for a single year class in the Age 1–3 cohorts, that underscore the continuing and uncontrolled contribution of disease to overall mortality in modern Chesapeake Bay populations. Thus, the spatial footprint of modern reefs that exhibit the required abundance and shell dynamics for long term survival at the population level is extraordinarily small.

The combination of growth rate estimates with values for oyster longevity and maximum size in the absence of disease and harvest and habitat changes post-European settlement (1607) allows exploration of the oyster demographics that would be required to support reef accretion rates commensurate with the formation of the Chesapeake Bay over the past 10,000 y (Hargis, 1999). Herein

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we examine the ability of oyster populations to accrete at rates in equilibrium with current and former sea level rise rates and estimate the filtration capacity of populations capable of exceeding the dual  $dN/dT$  and  $dS/dT > 0$  goal.

## 2. Estimating population demographics to support accretion at rates in equilibrium with current sea level rise estimates

The data requirements for this task are location specific rates of sea level rise, estimates of oyster recruitment, growth rate, maximum size, mortality in the absence of disease, shell weight and volume at each year class, and rate of degradation of shell to biological and taphonomic processes post mortality.

Modern rates of sea level rise in the Chesapeake Bay range from 2.7 to 4.5 mm/y with a mean value ( $n = 6$ ) of 3.5 mm/y (Pyke et al., 2008). Relative sea level rise (corrected for land subsidence) at the Chesapeake Bay entrance is estimated at 4 mm/y (Zhang et al., 2004). For the current exercise, we use 3.5 mm/y.

Oyster growth rates for pre-colonial (Harding et al., 2008) and modern (Harding et al., 2008; Mann et al., 2009) oyster populations are based on population demographics in the James River, Virginia using the method of Bhattacharya (1967). The resulting length-at-age relationships are linear models ( $SL = m \times x + b$ , Table 1) where  $SL$  = length (mm, distance from hinge to the shell margin, correctly termed height but described here as length in accordance with common use), and  $x$  = Age (y).

The data of Harding et al. (2008) and Mann et al. (2009) are for a presumed July 1 birth date but reporting for lengths on November 1 at ages of 0.33, 1.33, and so on with annual increments. Linear models have been used for oyster age-at-length descriptions (Harding et al., 2008; Mann et al., 2009) instead of the traditional von Bertalanffy model (Bertalanffy, 1938). The challenge in the current exercise with all reported linear fits is that no maximum size ( $SL_{max}$ ) is proffered because the collection for Harding et al. (2008) demonstrated no growth rate reduction with size and the demographics described by Mann et al. (2009) are truncated because oysters either died, probably from disease, or were harvested while at a moderate age and size. Nonetheless an estimate of  $SL_{max}$  is required.

DeBroca (1865) stated that “Specimens (oysters) are sometimes found measuring 15 English inches in length,  $3\frac{1}{2}$  in width.” This translates to approximately 450 mm length and 90 mm width. DeBroca’s oyster descriptions also note “its great length, compared with its width” and that at this time a bushel from Maryland and Virginia contained “from 200 to 250, according to the size of the oyster” underscoring the general large size, compared to current standards, of harvested oysters. The question of adherence to a growth curve resulting in an asymptotic maximum length remains open to discussion. Again, DeBroca (1865) notes in his description of the Virginia oyster that the species has “a narrow shell, increasing gradually in size from the top and moderately

curved in the plane of the intersection of the valves when it is allowed free development. The specimens taken from the natural banks are generally distorted, an account of certain conditions affecting their growth...”. We interpret this to mean that an isodiametric growth form was absent and that oysters on reefs (=banks of DeBroca) were probably crowded and distorted in shape. The impact of the choice of growth curve for the  $>4$  y olds is manifested in the contribution of the dead oysters to the shell budget for the local habitat after death. A linear length-at-age relationship will, for a chosen age, produce a greater length than a non linear von Bertalanffy form and, using the length (and hence age) conversions for shell mass and volume (described below) suggest a higher shell contribution. It will thus provide lower estimates of population density to provide accretion at equilibrium with sea level rise than would a von Bertalanffy fit. The linear is then the “best case” scenario in that should very high population densities result from the following calculation, the choice to employ a von Bertalanffy fit will dictate the need for even higher densities for an equilibrium situation.

Estimates of biomass, wet shell weight and shell volume are based on the following relationships (Mann et al., 2009)

$$\text{Biomass, } B(g) = 0.0000712 \times \text{Shell length, } SL(mm)^{2.15}; \\ R^2 = 0.80, n = 73 \quad (1)$$

$$\text{Wet shell weight, } W(g) = 0.002374 \times \text{Shell length, } SL(mm)^{2.21}; \\ R^2 = 0.64, n = 73 \quad (2)$$

$$1 \text{ L of wet James River shell} = 587.3g \pm 22g \quad (3)$$

Relationship (3) is based on intact valves collected en masse and volume assessed in a bucket with gradations. Much of the volume is open space between the collected valves and fragments. The specific gravity of the sample will only approach that of calcium carbonate when the entire shell collection is crushed.

The exponents in equations (1) and (2) are remarkably close, indicating that a traditional meat weight:shell weight condition index (e.g. Walne and Mann, 1975; Mann, 1978) is approximately constant with size. An estimate of natural mortality is required. High post-recruitment (to the benthos) predation related mortality is an accepted feature of oyster populations (Newell et al., 2000) although there is indication of increasing predator refuge with increasing shell height. Eggleston (1990) notes that oysters  $>30$  mm shell height (equivalent to shell length in this discussion) may be near the critical size for crushing by large crabs. This size corresponds approximately to the young-of-the-year age class and thus we propose to consider scenarios that begin with recruits to the year 1 age class and employ a constant mortality rate after that age wherein a linear relationship exists between the logarithms of mortality rate and maximum observed age. This is consonant with the approach of Hoenig (1983). Note that this is critically different to current day scenarios where the impacts of disease may require considerable incubation periods to result in death and also result in non-conformity to the linear fit suggested by Hoenig (1983). For simplicity we describe annual mortality rate,  $M$ , as a proportional value between 0.0 (all survived) and 1.0 (all died). Survival is  $(1-M)$  for a period of one year or  $(1-M)^q$  for a period of  $q$  years. For the current exercise we develop estimates of mortality rates corresponding to maximum longevity of 5 through 12 y at intervals of 1 y, and for 14, 16 and 19 y, the maximum value being set by the approximate correspondence of the 450 mm SL from DeBroca (1865) with age 19 and SL of 433 mm using the modern growth curve from Mann et al. (2009).

**Table 1**

Summary of linear models used to describe oyster length-at-age relationships for pre-colonial (Harding et al., 2008) and modern (Harding et al., 2008; Mann et al., 2009) oyster populations.  $n$ : the number of oysters that contributed to the length-at-age regression,  $m$ : the slope, SE: standard error,  $b$ : y-intercept value,  $R^2$ : coefficient of determination.

Source	$n$	$m$	SE $m$	$b$	SE $b$	$R^2$
Pre-colonial <sup>a</sup>	484	31.67	1.84	7.15	3.75	0.95
Modern <sup>a</sup>	3350	21.57	1.11	14.43	2.86	0.94
Modern <sup>b</sup>	81,369	21.60	1.48	30.22	3.17	0.93

<sup>a</sup> From Harding et al., 2008.

<sup>b</sup> From Mann et al., 2009.

Reef accretion is the net end product of growth, mortality, and shell degradation. We applied the growth and mortality rates to estimate shell accretion with mortality and cumulative shell addition from a single cohort. The annual contribution to the shell budget was estimated assuming constant recruitment, growth and mortality over many years. This is not, however, the accretion rate because shell loss occurs over the same period. We employ a loss rate of 30% of the exposed shell per year based on the half-life estimates of Powell et al. (2006), Powell and Klinck (2007) and Mann et al. (2009). Thus an accretion rate of 3.5 mm/y requires shell production of 4.55 mm/y or 4.55 L/m<sup>2</sup>/y.

Estimates of annual mortality, and densities of oysters in the year 1 age class required to balance this accretion budget for defined maximum ages are presented in Table 2. Thus the growth estimator of Harding et al. (2008) for historic oysters with a maximum age limit of 5 would require a density of 68 oysters/m<sup>2</sup> of 1-year old oysters and  $M=0.56$  to balance a shell budget. Increasing the maximum age to 10 y with the same growth curve requires only 18 oysters/m<sup>2</sup> of 1-year old oysters with  $M=0.22$ . With a life span of 19 y, the density at 1 y of age is reduced to 4.5 oysters/m<sup>2</sup> and  $M=0.07$ . Comparable values of  $N$  and  $M$  for maximum ages 5, 10 and 19 using the modern growth curve from Mann et al. (2009) are  $N=77$  oysters/m<sup>2</sup> of 1-year old oysters and  $M=0.62$ ,  $N=34$ /m<sup>2</sup> and  $M=0.31$ , and  $N=9$ /m<sup>2</sup> and  $M=0.11$  respectively.

There is generally good agreement between these progressions, although the larger, older pre-colonial oysters explain the relatively lower  $N$  values compared to modern populations for that projection. Comparison of density and mortality values from the modern populations with pre-colonial values underscores the enormous impact of increasing longevity on the equilibrium calculation. Conversely, truncating the population at maximum ages less than 5 y of age places a prerequisite for continued high recruitment ( $> \sim 80$ /m<sup>2</sup>) to the year 1 age class that is observed in very few locations in modern populations (Mann et al., 2009).

A particularly intriguing question posed by Table 2 is that of accretion rate associated with periodic or even sustained levels of recruitment of the young-of-year corresponding to the highest observed rates in current systems. Moon Rock is one of the few reefs in the modern James River at equilibrium with respect to accretion, maintained by high recruitment (mean year 1 age class = 98/m<sup>2</sup>, 1998–2006, Mann et al., 2009) in the face of high

mortality. If such recruitment, currently exhibited in an acknowledged stressed system, were available in arguably more pristine pre-colonial conditions the prospective accretion rate would be extraordinary. Substituting an  $N$  value of 100 in Table 2 for even the most conservative growth projection, that of Harding et al. (2008) for modern data, with a modest life expectancy of 10 y results in a net accretion rate of 11.3 mm/y! Such calculations, even considering the cumulative errors involved in extrapolation, underscore the invasive ability of oysters to occupy new spatial footprints by accretion to create biogenic habitat. All extant “restoration” activities pale by comparison, 11.3 mm/y is the equivalent of adding 785 bushels/acre/y of shell as a repletion action on a continuing basis. We suggest that the maximal rate of accretion was probably considerably less than 11.3 mm/y, and was potentially limited by the productivity of the estuary.

A recent historical estimate of “bioaccumulation”, approximating the accretion rate estimates presented here, is given in Figure 6 of DeAlteris (1988) who calculated that the cumulative contribution of feces, pseudofeces and shell material at Wreck Shoal in the James River was 5 mm/y for the period 1000 through 1855 AD. DeAlteris (1988) also presented an estimate of “bioaccumulation” for a “healthy” oyster reef in the James River in the early 1980s assuming 50% mortality per year. To quote: “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 or 3.5 L/m<sup>2</sup>/y. 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 (DeAlteris, 1988).” This is 5.0 mm/y or 5.0 L/m<sup>2</sup>/y. Note that DeAlteris did not correct for shell degradation. Repeating the calculation of DeAlteris (1988) for current James River data taken from Mann et al. (2009) gives a mean density for Moon Rock of 1211 bushels/acre (484 bushels/ha) and 51 bushels/acre (20.5 bushels/ha) for Wreck Shoal, the latter illustrating degradation of the reef in the two-decade period between the studies.

**Table 2**

Scenarios supporting equilibrium accretion rates for defined maximum age.  $M$ : annual mortality rate as a proportional value between 0.0 (no mortality) and 1.0 (all died).  $N$ : number of age 1 oysters (per m<sup>2</sup>) required to balance accretion at the defined maximum age and annual mortality rate.  $A$ : the estimated accretion rate (mm/y linear or L/m<sup>2</sup>/y by area).

Source		Maximum age (y)												
		3	4	5	6	7	8	9	10	11	12	14	16	19
Pre-colonial <sup>a</sup>	$M$	0.78	0.65	0.56	0.49	0.38	0.32	0.27	0.22	0.2	0.18	0.14	0.1	0.07
	$N$	120	90	68	53	38	30	23	18	15	13	9	6.5	4.5
	$A$	4.55	4.58	4.53	4.53	4.54	4.66	4.56	4.56	4.57	4.72	4.59	4.49	4.42
Modern <sup>a</sup>	$M$	0.82	0.7	0.6	0.52	0.45	0.39	0.33	0.28	0.25	0.22	0.17	0.14	0.10
	$N$	187	151	121	98	79	64	51	40	33	28	20	15	10
	$A$	4.57	4.56	4.55	4.57	4.57	4.59	4.61	4.52	4.52	4.61	4.64	4.61	4.53
Modern <sup>b</sup>	$M$	0.81	0.7	0.62	0.52	0.45	0.4	0.36	0.31	0.28	0.24	0.19	0.15	0.11
	$N$	106	90	77	64	54	46	39	34	28	23	17	13	9
	$A$	4.59	4.57	4.55	4.56	4.59	4.58	4.52	4.74	4.53	4.47	4.47	4.55	4.53
Pre-colonial applied to Holocene at 10 mm per yr	$M$	0.84	0.72	0.62	0.54	0.46	0.40	0.35	0.30	0.27	0.24	0.19	0.15	0.11
	$N$	353	275	213	167	128	101	80	63	52	43	30	22	14
	$A$	12.99	13.01	13.00	13.03	13.04	13.10	13.06	13.10	13.08	13.14	13.20	13.50	13.02

<sup>a</sup> From Harding et al., 2008.

<sup>b</sup> From Mann et al., 2009.

### 3. Estimating filtration rate of a population of oysters with accretion at equilibrium with sea level rise

The estimates of Newell (1988) that the volume of the Chesapeake Bay could, in pre-colonial times, be filtered in 3.5 days have driven subsequent studies concerning the need to restore such benthic-pelagic coupling to the Bay and underscored the importance of oysters in provision of habitat and as ecological engineers (Coen and Luckenbach, 2000; Gutierrez et al., 2003). These studies did not provide rates of biogenic habitat creation. This is the first such effort. Table 3 progresses from the demographics of Table 2 and estimates the maximum filtration rate,  $F_{\max}$ , in L/hr/m<sup>2</sup> of occupied reef for the various demographics assuming a Q10 of 2 and a summer maximum temperature of 26 °C. Maximum temperatures of 28–29 °C have been observed in the James River, Virginia in July and August of some years (Mann et al., 2009), thus 26 °C is a conservative estimate. A second value,  $F_{20}$ , is also reported – this being the estimated filtration rate of the same demographic at 20 °C. Note that the  $F_{\max}$  values based on Newell et al. (2005) are approximately five times larger than those reported by Powell et al. (1992). Recent field work by Southworth et al. (2009) in large scale oyster farms in the Chesapeake Bay region found good agreement of filtration rate estimates with those of Powell et al. (1992).

The  $F_{\max}$  values (Table 3) indicate the ability of the equilibrium population, assuming a maximum age of 12 y, at maximum summer temperatures to filter the volume of water overlaying one square meter of bottom at one-meter depth (1000 L) in 0.33 to 0.47 h (20 to 28 min)! Reducing the temperature to 20 °C and employing the five-fold lower filtration rate of Powell et al. (1992), changes this range to 2.3–3.4 h, which is still a rapid processing of the water column. These times to filter the overlaying water column are lower than estimates of doubling times in phytoplankton populations (Jackson, 1980; Cloern et al., 1985). The filtration of the overlaying water is even faster if oysters older than 12 y are included in the population calculation.

These calculations do not account for movement of water over the reef that continually replenishes the food supply, but they do suggest indicate that pre-colonial oyster populations may have been food limited. For comparison we note that Gerritsen et al. (1994) came to a similar conclusion for bivalve populations in the mesohaline portion of the Potomac River. Their modeling suggested that resident bivalves filter between 80 and 100% of the river volume in spring and summer months. Modeling by Cerco and Noel (2007) to evaluate the effects of a 10 fold increase in Chesapeake oyster populations from 2000 levels shows that food limitation will prevent the attainment of this goal in areas with highest oyster densities (average of 6.2 g DW m<sup>-2</sup>, 1998–2002, James and lower Rappahannock Rivers, Virginia). Note that the biomass values used by Cerco and Noel (2007) are at least an order of magnitude lower than the cumulative B values presented herein for even the smallest demographic (Table 3).

Questions addressing the ability of pre-colonial, presumably accretion equilibrium oyster populations to filter the volume of the Chesapeake Bay should not be posed as “days to filter volume” but rephrased in terms of the spatial limit of the oyster reef footprint set by prevailing productivity. Examination of the historic spatial footprints of oyster reefs presents an opportunity to test the hypothesis that pristine oyster populations were food limited. The spatial footprints of oyster reefs have been mapped in the Chesapeake Bay (Winslow, 1882; Baylor, 1896; Haven et al., 1981; Haven and Whitcomb, 1983; Haile, 1998) and elsewhere (TX: Moore, 1907; DE: Moore, 1911; FL: Dangle, 1917) where *Crassostrea virginica* is or was the dominant benthic species for over a century. The spatial distribution of oyster reef footprints within an estuary was and is highly structured with respect to tidal flow. Reefs are “phytoplankton consumption” regions. Zones between reefs (inter-reef areas) receive nutrients excreted from the oyster reefs, are mixed by wind and tidal turbulence channeled by the reef structure, and serve as primary productivity incubators which regenerate phytoplankton (Officer et al., 1982). This spatial coupling is very obvious in the modern Apalachicola Bay, Florida as well as Texan estuaries,

**Table 3**  
Estimates of filtration rate (L/hr/m<sup>2</sup>, Newell et al., 2005) associated with the population demographics reported in Tables 1 and 2. N: number of age 1 oysters (per m<sup>2</sup>) required to balance accretion at the defined maximum age and annual mortality rate. SL (mm): max length of oyster in demographic. Cum B: cumulative biomass (g dry weight) of all individuals and year classes in the demographic.  $F_{\max}$ : estimated summer maximum filtration rate at 26 °C (9.62 L h<sup>-1</sup> g<sup>-1</sup> dry weight, Newell et al., 2005 converted to L/hr/m<sup>2</sup> for demographics in Table 2).  $F_{20}$ : estimated filtration rate at 20 °C.

Source		Maximum age (y)												
		3	4	5	6	7	8	9	10	11	12	14	16	19
Pre-colonial <sup>a</sup>	N	120	90	68	53	38	30	23	18	15	13	9	7	5
	SL	102	134	165	197	229	260	292	324	355	387	450	514	609
	Cum B	48	64	78	93	131	166	198	316	276	318	402	560	788
	$F_{\max}$	466	618	752	896	1264	1594	1903	3041	2653	3063	3872	5388	7582
	$F_{20}$	326	433	526	627	885	1116	1332	2128	1857	2144	2710	3772	5307
Modern <sup>a</sup>	N	187	151	121	98	79	64	51	40	33	28	20	15	10
	SL	79	101	122	144	165	187	209	230	252	273	316	360	424
	Cum B	49	61	75	90	108	129	159	253	219	258	345	423	596
	$F_{\max}$	475	587	718	866	1040	1245	1530	2436	2107	2479	3319	4065	5730
	$F_{20}$	332	411	503	606	728	872	1071	1705	1475	1735	2323	2845	4011
Modern <sup>b</sup>	N	106	90	77	64	54	46	39	34	28	23	17	13	9
	SL	95	117	138	160	181	203	225	246	268	289	333	376	441
	Cum B	56	66	75	93	111	127	141	237	187	220	283	370	507
	$F_{\max}$	541	635	722	898	1070	1222	1356	2284	1803	2115	2722	3555	4882
	$F_{20}$	379	444	506	629	749	856	949	1599	1262	1480	1906	2489	3417
Pre-colonial applied to Holocene	N	353	275	213	167	128	101	80	63	52	43	30	22	14
	SL	102	134	165	197	229	260	292	324	355	387	450	514	609
	Cum B	116	150	189	230	287	345	405	682	550	631	818	1077	1432
	$F_{\max}$	1119	1445	1815	2213	2760	3318	3898	6564	5293	6068	7871	10363	13778
	$F_{20}$	783	1012	1271	1549	1932	2323	2729	4595	3705	4247	5509	7254	9644

<sup>a</sup> From Harding et al., 2008.

<sup>b</sup> From Mann et al., 2009.

e.g. San Antonio Bay (Bouma, 1976). These inter-reef areas in the pre-colonial Chesapeake Bay would have been regions of high water clarity where extensive submerged aquatic vegetation beds thrived. The complex circulation of the Chesapeake Bay dictates that oyster reef footprints would have been complicated to achieve the balance between phytoplankton production and oyster consumption. Examination of the orientation of the original Point of Shoals reef in the James River, Virginia (Woods et al., 2005) underscores this obvious relationship between reef spatial extent, orientation, and the physical habitat.

#### 4. Impacts of accretion and filtration estimates over geological time

Oysters have survived over geological time by invading ephemeral estuarine environments in accordance with sea level rise and fall, and with continental drift over the past 200 million years (approximating the presence of oysters in the geological record, Stenzel, 1971). Over this vast time period the basic form of the oyster has changed little (compare fossil *Gryphaea* with extant *Crassostrea*, although speciation in the latter may have been influenced by some of these geological upheavals) and we suggest that the calculations herein for accretion have applied, with minor modification if any, for estuarine *Crassostrea* oyster populations over at least a 50 million year period. To test this assertion we pose the question “can the proposed population dynamics sustain an accretion rate commensurate with maximum sea level rise in the past 50 million year period?” The early Tertiary (30–60 MYA) may have experienced much less rapid sea level rises and falls than the glaciated late Tertiary (30 MYA – 1.8 MYA) and Quaternary (1.8 MYA to present Pitman, 1978; Vail and Mitchum, 1979 in Kennett, 1982). Rates of sea level rise were higher in the early Holocene transgression (7000 to 17,000 y ago) at 8 mm/y (Kennett, 1982, based on Curray, 1965; Milliman and Emery, 1968). The most rapid phase of the Holocene transgression was at 7000–10,000 y ago with a rate of 10 mm/y (Kennett, 1982). The Chesapeake estuary experienced a relatively rapid transition from fresh to brackish water conditions between 7400 and 8200 y ago commensurate with sea level rise and/or the crossing of hydrographic or topographic barriers (Bratton et al., 2003). Landward intrusion of salt-water is marked by fossil oyster beds in the northern Chesapeake Bay and upstream areas of the Potomac River with subsequent oceanward retreat beginning about 6000 y ago as rates of sea level rise decreased and the headwaters of the estuaries began to fill with sediment (Bratton et al., 2003). Shell production rate to maintain equilibrium with sea level rise of 10 mm/y is estimated, again with a 30% loss/y to degradation processes, to be 13 mm/y or 13 L/m<sup>2</sup>/y. Table 2 applies Harding et al. (2008) historic growth rate function to estimate values of *M* and *N* commensurate with this Holocene shell production rate. A density of 101 oysters/m<sup>2</sup> at one year of age, again comparable to that observed at Moon Rock in the James River for the per 1998–2006 (Mann et al., 2009) combined with a proportional mortality of 0.40 and a maximum life expectancy of 8 y will maintain the required accretion rate. These calculations provide a basis for the description of the original dynamics of estuarine biogenic habitats on a global scale by examining river sediment dynamics, the presence or absence of vertically accreting biogenic reefs, and the spatial extent of these structures, even with the variations in global climate during the past 50 million years (Sambol and Finks, 1977; Ivany et al., 2004).

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