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Comparison of *Crassostrea virginica* Gmelin (Eastern Oyster) Recruitment on Constructed Reefs and Adjacent Natural Oyster Bars over Decadal Time Scales

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and James A. Wesson³

Abstract - Since 1993, oyster reef replenishment efforts in the Virginia portion of the Chesapeake Bay have relied heavily on construction of oyster shell reefs with enhanced vertical relief. We evaluated the performance of six reefs constructed in proximity to natural subtidal oyster bars by comparing recruit densities (spat m⁻², where spat are young-of-the-year oysters with shell heights less than 50 mm) between habitats. Recruitment was higher on the reefs than bars during the first 1–3 yr post-construction, usually by at least an order of magnitude. Within 7 yr, recruitment was similar between reef-bar pairs although both reefs and bars received additions of shell, live oysters, or both during the study period. At decadal time scales, constructed oyster reefs did not show enhanced recruitment relative to adjacent natural oyster bars. The rapid decline in reef recruitment post-construction is likely related to three processes: (i) shell degradation by taphonomic processes, (ii) biofouling that occludes the shell surface to recruitment, and (iii) inability of extant oysters on the reef to produce new shell at a rate commensurate with losses to (i) and (ii). There appears to be a requirement for continued replenishment activity to maintain the shell base on these reefs, contrary to the dynamics of a healthy natural oyster population. The similarity in recruitment between constructed reefs and natural bars at decadal time scales suggests that subtidal shell plants or shell additions to natural bars may be a more cost-effective repletion strategy because they provide equal population enhancement per unit area.

Introduction

Crassostrea virginica Gmelin (Eastern Oyster) reefs were a dominant habitat in the Chesapeake Bay prior to European colonization (e.g., Hargis 1999, Newell 1988). The extensive reef fields that developed in the lower Chesapeake Bay during the Holocene epoch included fringing reefs as well as large intertidal three-dimensional reefs that were navigation hazards (Hargis 1999, Smith et al. 2003). The combination of post-colonization harvest pressure and environmental degradation drastically reduced oyster populations from their original spatial footprint and vertical extent such that by the 1890s the Commonwealth of Virginia commissioned Lt. J.B. Baylor to survey the remaining oyster resources (Baylor 1896). The decline in Virginia oyster populations continued through the 20th century (Andrews 1996, Haven et al. 1978, Rothschild

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et al. 1994) and was exacerbated by the introduction of *Haplosporidium nelsoni* Haskin, Stauber, and Mackin (MSX; Andrews 1968, Andrews and Wood 1967, Burreson et al. 2000) and environmental conditions in the 1980s that intensified *Perkinsus marinus* Mackin, Owen, and Collier (Dermo; Andrews 1996, Burreson and Ragone Calvo 1996). These diseases affect oysters in their second or third years and may increase the observed mortality of older oysters depending on site- and year-specific ambient environmental conditions (Andrews 1968, Burreson and Ragone Calvo 1996, Carnegie and Burreson 2011, Harding et al. 2010a, Mann et al. 2009a, Southworth et al. 2010). Neither disease directly impacts oysters within the first year post-settlement (recruits).

Natural subtidal oyster reef structures have a veneer of live oysters approximately 10 to 30 cm thick overlaying the reef core (DeAlteris 1988, Hargis 1999). The filling of the interstitial spaces or matrix in a natural reef is a gradual process that results from natural shell degradation and biodeposition. On a living reef, this infilling is balanced with reef accretion through growth of individuals and natural recruitment such that the living oyster layer expands outward over time (Hargis 1999, Powell and Klinck 2007).

The destruction of biogenic reef shell habitat is concurrent with the loss of the biological and ecological services provided by living oysters (Beck et al. 2011; Mann and Powell 2007; Mann et al. 2009a; Powell et al. 2009a, b; Woods et al. 2005). Oyster shell half life is typically on the order of 3–6 yr in mid-Atlantic estuaries (Powell et al. 2006); thus, natural accretion rates for equilibrium or growing reef systems must match or exceed rates of shell degradation combined with sea-level rise (Mann et al. 2009a, Powell and Klinck 2007). Extant Virginia oyster population demographics have been truncated by disease and environmental conditions such that 3–4 yr olds are rare (Harding et al. 2010a; Mann et al. 2009a, b; Southworth et al. 2010), and the existing shell base lacks the fundamental contribution originally made by larger, older individuals (DeAlteris 1988, Mann et al. 2009b). Annual variability in recruitment or replacement ratios (Harding et al. 2010a, Mann et al. 2009a, Southworth et al. 2010) also skews oyster population demographics within Virginia trap-type estuaries like the Piankatank and Great Wicomico rivers (Andrews 1979). Even within trap-type estuaries where hydrodynamics facilitate recruitment, defensible stock-recruit relationships based on long-term (>10 yr) data sets are absent (Harding et al. 2010a, Southworth et al. 2010) and indicative of the wide interannual fluctuations in natural recruitment that have been observed since at least the 1930s (e.g., Galtsoff et al. 1947). Natural oyster reef development and maintenance (= accretion) require longer time frames, broad population demographics, and relatively high replacement ratios (Harding et al. 2010a; Mann et al. 2009a; Powell et al. 2009a, b; Southworth et al. 2010).

The Commonwealth of Virginia has included construction of three-dimensional oyster shell sanctuary reef as part of its long-term oyster resource rehabilitation and fishery management program since the early 1990s. The term “reef” is used here in reference to a shell-based structure with vertical relief, while the term “bar” is used to refer to a shell-based structure that is

subtidal with limited, if any, vertical relief. Since construction of Palace Bar reef in the Piankatank River (Fig. 1) in 1993 (Bartol and Mann 1997), more than 50 similar reef structures have been built in the Virginia portion of the Chesapeake Bay. The resulting reefs were intended to mimic the original, natural reefs that developed on hard substrate during the Holocene epoch (e.g., DeAlteris 1988, Hargis 1999, Smith et al. 2003) and restore relief or replace

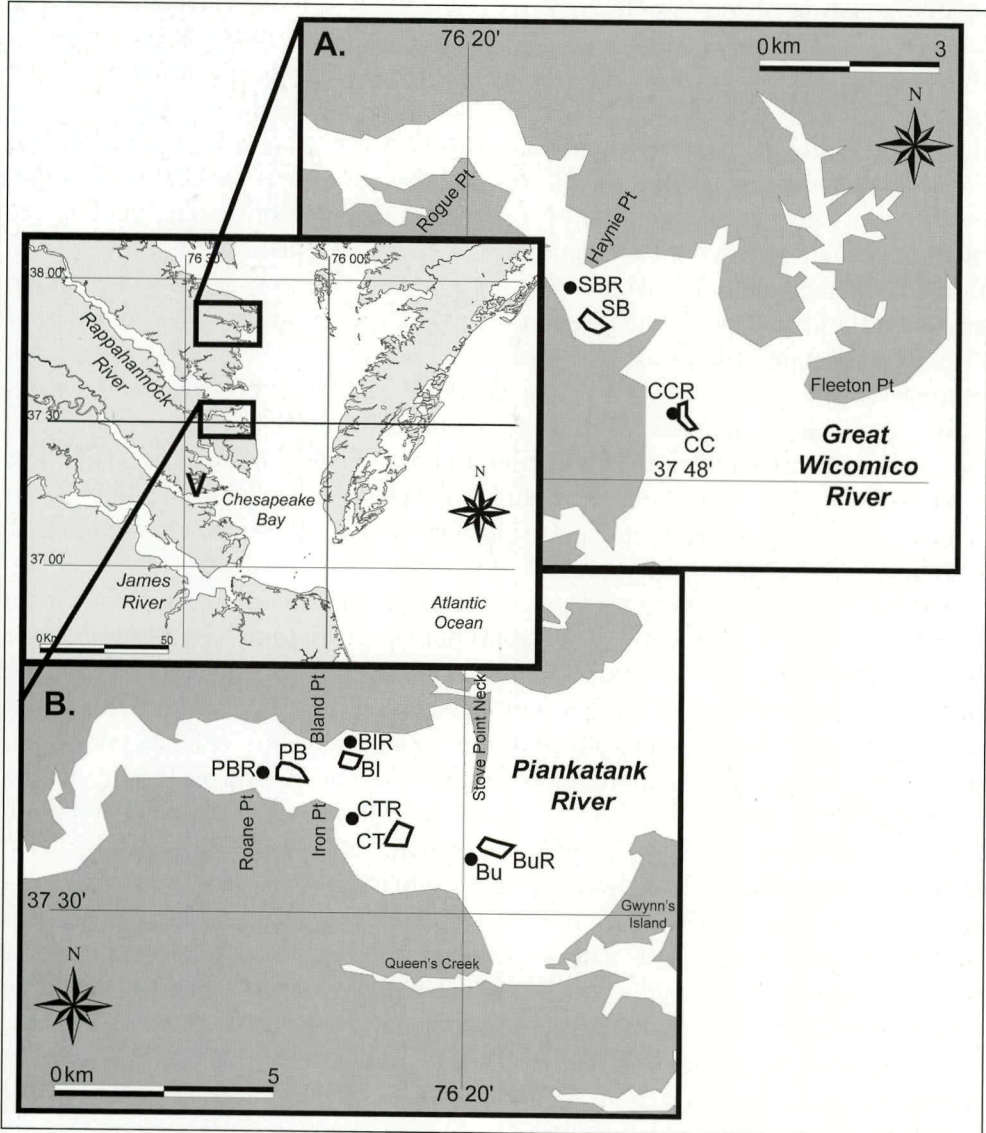


Figure 1. Map of the Virginia portion of the Chesapeake Bay showing the reef and bar locations studied in the Great Wicomico (A) and Piankatank (B) rivers. Site abbreviations are as follows: CC = Crane's Creek bar, CCR = Crane's Creek reef, SB = Shell Bar, SBR = Shell Bar reef; BI = Bland Point bar; BIR = Bland Point reef, Bu = Burton Point bar (equal to Burton Point 1 in Harding et.al. [2010a]), BuR = Burton Point reef, CT = Cape Toon bar, CTR = Cape Toon reef, PB = Palace Bar, PBR = Palace Bar reef, V = VIMS oyster pier.

reefs that have been reduced or destroyed by a combination of environmental and anthropogenic factors (Hargis and Haven 1999, Wesson et al. 1999). The stated goals for Virginia's oyster reef construction program include the establishment of self-sustaining oyster populations on the constructed reefs. Regular recruitment is a requirement for self-sustaining oyster populations.

Oyster reef restoration efforts have often been examined in the context of the resulting ecological services (e.g., Breitburg 1999; Coen and Luckenbach 2000; Coen et al. 1999, 2007; Kennedy 1996; Peterson et al. 2003). Reef construction is usually described as "restoration", but these projects are rarely evaluated quantitatively in terms of subsequent sustainability and biogenic carbonate production. Live oyster density, biomass, and/or demographics (e.g., Luckenbach et al. 2005, Powers et al. 2009) have been proposed as metrics of restoration success. While these are certainly relevant criteria, they do not directly address the maintenance and growth of biogenic shell habitat with time that is fundamental to the persistence of self-sustaining reef structures across multiple years (Mann and Powell 2007). Constructed three-dimensional sanctuary reefs are essentially thick (>50 cm) intertidal shell plants or shell layers spread evenly over the target bottom (Haven et al. 1978, Kennedy and Sanford 1999). Over time, the composite shells are redistributed by wave action or settle or subside, resulting in subtidal structures in the absence of continued shell addition by either natural or artificial processes. In addition to leveling out, spaces between the shells fill with biodeposits, sediment, and other materials including shell fragments (Abbe 1988, O'Beirn et al. 2000, Powell et al. 2006).

Oyster shell is a limiting resource for modern Virginia oyster replenishment and management programs (Hargis and Haven 1999, Wesson et al. 1999). If there are no differences in oyster recruitment between three-dimensional constructed reefs and two-dimensional natural bars, then the limited shell resource may be more cost effectively used to cover larger spatial areas as shell plants. Shell plants 20–30 cm thick are a proven strategy to encourage and sustain oyster recruitment in the Chesapeake Bay (Abbe 1988; Harding et al. 2010a; Hargis and Haven 1999; Haven et al. 1978, 1981; Mann et al. 2009b; Southworth et al. 2010) as well as other estuaries (Kennedy and Sanford 1999, Moore 1897).

Natural subtidal oyster bars adjacent to constructed reefs provide a baseline from which to evaluate the performance of constructed reefs with regard to recruitment. Six oyster reefs built in Virginia between 1993 and 1998 are in proximity to natural oyster bars (Fig. 1). Annual estimates of oyster spat density, a descriptor of recruitment success, are available for both reefs and bars from reef construction through 2006, including at least 9 yr of data for each reef-bar pair. Evaluation of recruitment trends must include multi-year time scales that are long enough to encompass oyster life-span (3–6 yr; Harding et al. 2010, Powell and Cummings 1985, Southworth et al. 2010), oyster generation time (≈ 1 yr; Harding et al., in press), and shell half-life (3–6 yr; Harding et al. 2010a, Powell and Klink 2007, Southworth et al. 2010) within these rivers.

We compared spat densities (number of spat m^{-2}) between 6 constructed three-dimensional reefs and adjacent natural two-dimensional bars to quantitatively

test the hypothesis that three-dimensional constructed reef structures have enhanced recruitment (higher spat densities) relative to natural oyster bars over multi-year time scales. We pose this hypothesis to test the assumption that observed recruitment trends at a location are driven by substrate availability rather than larval supply. Recruitment trends within each of these rivers are widely variable from year to year (Harding et al. 2010a, Haven et al. 1978, Southworth et al. 2010). Given that the reef-bar pairs are in proximity, the point is to compare the 2 habitat types (constructed 3D vs. natural 2D) as recruitment habitat. If both provide similar recruitment (spat density) signals, then both are an equally good use of shell resource. If one habitat provides a signal that shows higher recruitment in terms of annual numbers, long-term consistency or both, then the use of that habitat is a better investment.

Materials and Methods

Study sites

The Piankatank and Great Wicomico rivers (Fig. 1, Table 1) were chosen as sites for three-dimensional reef construction because of their history as trap-type estuaries (Andrews 1979) and seed-production rivers (Hargis and Haven 1988, Haven and Whitcomb 1986, Haven et al. 1978). By design, reef-construction sites were located on the geologic footprints of natural oyster reefs delineated by the Baylor survey (1896) and adjacent to public oyster grounds resurveyed by Haven et al. (1981; also Haven and Whitcomb 1986). These natural bars have been actively managed by the Virginia Marine Resources Commission (VMRC) since at least 1963 (Haven et al. 1981). The reef/bar names used herein match the historic names used by Baylor (1896) and Haven et al. (1981).

A total of 4 reefs were built in the Piankatank River between 1993 and 1995 (Fig. 1, Table 1): Palace Bar Reef (June 1993, reef footprint = $8.1 \times 10^3 \text{ m}^2$) and Bland Point Reef, Cape Toon Reef, and Burton Point Reef (all June 1995, $4.05 \times 10^3 \text{ m}^2$ each). Subsequently, 2 reefs were built in the Great Wicomico River (Fig. 1, Table 1): Shell Bar Reef (summer 1996, $8.1 \times 10^3 \text{ m}^2$) and Crane's Creek

Table 1. Summary of site-specific information for the constructed reef-natural bar pairs examined in the Great Wicomico River and Piankatank River, VA. Details for site-specific replenishment measures are provided in text. Yr RC = year of 3D reef construction. Areas are reported as m^2 . Burton Point bar is equal to Burton Point 1 in Harding et al. (2010a).

| River/site | Yr RC | Reef abbreviation | Reef area | Bar abbreviation | Bar area |
|----------------|-------|-------------------|--------------------|------------------|--------------------|
| Great Wicomico | | | | | |
| Crane's Creek | 1998 | CCR | 8.10×10^3 | CC | 5.08×10^4 |
| Shell Bar | 1996 | SBR | 8.10×10^3 | SB | 7.16×10^4 |
| Piankatank | | | | | |
| Bland Point | 1995 | BIR | 4.05×10^3 | Bl | 1.01×10^5 |
| Burton Point | 1995 | BuR | 4.05×10^3 | Bu | 1.58×10^5 |
| Cape Toon | 1995 | CTR | 4.05×10^3 | CT | 1.68×10^5 |
| Palace Bar | 1993 | PBR | 8.10×10^3 | PB | 1.66×10^5 |

Reef (summer 1998, $8.1 \times 10^3 \text{ m}^2$). All reefs were built at water depths of $\approx 3 \text{ m}$ with reef shells extending from the substrate through the water column to the air-water interface.

Each constructed reef was located within 1 km of a natural two-dimensional oyster bar that supported a self-sustaining oyster population throughout the time period examined (Piankatank bars: Harding et al. 2010a; Great Wicomico bars: Southworth et al. 2010). Note that Burton Point bar in the Piankatank River referenced here corresponds to the bar referred to as Burton Point 1 in Harding et al. (2010a). Natural bars varied in size from 5.08×10^4 to $1.68 \times 10^5 \text{ m}^2$ (Table 1). Maximum water depths over the subtidal natural bars were also $\approx 3 \text{ m}$.

Oyster and/or shell resources on constructed three-dimensional reefs and natural bars were supplemented periodically from 1993 through 2006 (Table 2). Repletion activities included additions of wild broodstock oysters, cultured individual oysters (hereafter cultchless oysters), clean oyster shell, and/or shell to which cultured oysters have been allowed to metamorphose in high density via remote setting (hereafter spat on shell).

Temperature and salinity data

Hydrographic conditions at Palace Bar reef (Fig. 1) and Shell Bar reef (Fig. 1) are representative of ambient hydrographic conditions at the natural bars and constructed reefs examined in the Piankatank and Great Wicomico rivers, respectively (Harding et al. 2010a, Southworth et al. 2010). Weekly water temperature and salinity data were calculated from bottom-water temperature ($^{\circ}\text{C}$) and salinity data recorded by automated monitoring stations (15-minute intervals) on Palace Bar reef (Piankatank River) and Shell Bar reef (Great Wicomico River) from June

Table 2. Summary of replenishment activity on natural bars (B) and constructed reefs (R) including shell planting (SP), addition of wild broodstock or cultchless oysters (Oy), and addition of spat-on-shell (SOS). "C" indicates the year of construction for reefs. * indicate years prior to reef construction. - indicates years in which no replenishment activity occurred.

| Year | Site | | | | | | | | | | | | | |
|------|---------------|-------|-----------|------|-------------|---------|--------------|----|-----------|----|------------|----|----|-----|
| | Crane's Creek | | Shell Bar | | Bland Point | | Burton Point | | Cape Toon | | Palace Bar | | | |
| | B | R | B | R | B | R | B | R | B | R | B | R | | |
| 1993 | * | * | * | * | * | * | * | * | * | * | * | * | - | C |
| 1994 | * | * | * | * | * | * | * | * | * | * | * | * | - | - |
| 1995 | * | * | * | * | - | C | - | C | - | C | - | - | - | - |
| 1996 | * | * | - | C,Oy | - | - | - | - | - | - | - | - | - | - |
| 1997 | * | * | SP | Oy | - | - | - | - | - | - | - | - | - | Oy |
| 1998 | - | C, Oy | SP | Oy | SP | - | - | - | - | - | - | SP | Oy | Oy |
| 1999 | SP | - | SP | Oy | SP | Oy | SP | Oy | - | Oy | SP | Oy | SP | Oy |
| 2000 | - | - | - | Oy | SP | Oy | SP | Oy | - | Oy | SP | Oy | SP | Oy |
| 2001 | - | - | - | Oy | SP | - | - | - | - | - | SP | Oy | SP | Oy |
| 2002 | - | Oy | - | Oy | - | - | - | Oy | - | - | - | Oy | - | Oy |
| 2003 | - | - | SP | Oy | SP | - | - | - | - | - | - | - | - | - |
| 2004 | - | Oy | SP | Oy | SP | Oy | - | - | - | Oy | SP | - | SP | - |
| 2005 | - | - | SP | Oy | - | SOS | SP | - | - | - | SP | - | SP | - |
| 2006 | - | - | SP | Oy | - | Oy, SOS | SP | - | - | - | - | - | - | SOS |

2005 through December 2006. Average weekly water temperatures and salinities at both reefs prior to 2005 were predicted using measured temperatures and salinities from a similar station deployed in the York River (Fig. 1, Gloucester Point VA, 37°14'47"N, -76°30'23"W, VIMS Data archive) with linear regressions from Southworth et al. (2010, Shell Bar reef) and Harding et al. (2010a, Palace Bar reef).

Predicted measurements were supplemented with water temperature and salinity data collected weekly at reefs and bars ($n > 3$) from June through September (Piankatank: 1993–2006, Great Wicomico: 1998–2006). From 1993–2004, water samples were collected approximately 0.5 m off the bottom. Temperature was measured with an alcohol thermometer within 5 minutes of water-sample collection and salinity was measured with a hand-held refractometer. Beginning in 2005, water temperature and salinity were measured with a hand-held digital probe suspended 0.5 m from the bottom.

Oyster spat surveys

Natural recruitment on natural oyster bars was surveyed each fall (November, 1995–2006) following the methods described by Mann et al. (2009a, James River), Southworth et al. (2010, Great Wicomico River), and Harding et al. (2010a, Piankatank River). Oysters were collected from the R/V *J.B. Baylor* with a hydraulic patent tong using a random sampling design. The open dimensions of the tong were such that it sampled one square meter of bottom to a depth of 30 to 50 cm through the oxic or taphonmically active layer (Davies et al. 1989). Upon retrieval of each sample (= patent tong grab; $n > 7 \text{ bar}^{-1} \text{ yr}^{-1}$), the longest dimension from the hinge to the growth margin was measured (shell height [SH] in mm) for all oysters. Oysters < 50 mm SH were subsequently categorized as spat. Thus, we define an oyster spat as a young-of-the-year animal that has a maximum dimension from hinge to growth edge of less than 50 mm (shell height) and does not have a cupped left valve. Standardized quantitative surveys were not conducted prior to 1995 on either natural bars or constructed sanctuary reefs.

Beginning in September 1995, natural spat densities (number m^{-2}) on constructed reefs were determined using an annual dive survey. Divers randomly placed a 0.25- m^2 quadrat on the reef surface and then removed all material (live oysters and oyster shell) within the quadrat to a depth of at least 30 cm. All material was subsequently examined on board the survey vessel, and live spat were enumerated for each quadrat sample ($n > 6 \text{ reef}^{-1} \text{ yr}^{-1}$). The number of spat observed per 0.25- m^2 sample were multiplied by 4 to yield spat densities m^{-2} .

Data analyses

Annual spat densities (number m^{-2}) were compared for each constructed reef-natural bar pair using reef-bar pair and year-specific two-tailed non-parametric Mann-Whitney U tests. Mann-Whitney U tests were used because the data were not normally distributed and included large ranges of observed spat densities. Significance levels were established at $\alpha = 0.05$ a priori.

Within a site, the average annual change in observed spat density was calculated by taking the average of spat densities within year 1 and subtracting the average density in year 1 from the average density in year 2 and so on. Differences in average annual changes in spat density between reef-bar pairs were also evaluated with Mann-Whitney U tests for consecutive years in which there were data available for both reefs and bars.

Results

Temperature and salinity data

Water temperatures in the Piankatank and Great Wicomico rivers followed similar trends from 1993–2006 (Fig. 2) with observed seasonal minima of ≈ 0 –4 °C and maxima of 28–30 °C. Great Wicomico water temperatures measured during July and August were 1–2 °C warmer than Piankatank water temperatures in 2000, 2001, 2003, and 2004. The summers of 1996 and 1997 were relatively cooler than other years.

Salinities in both rivers were generally 8–20 psu (Fig. 3). Observed minima (5–10 psu) generally occurred during the late winter/early spring wet period. Observed salinity maxima (18–26 psu) corresponded to lower rainfall conditions

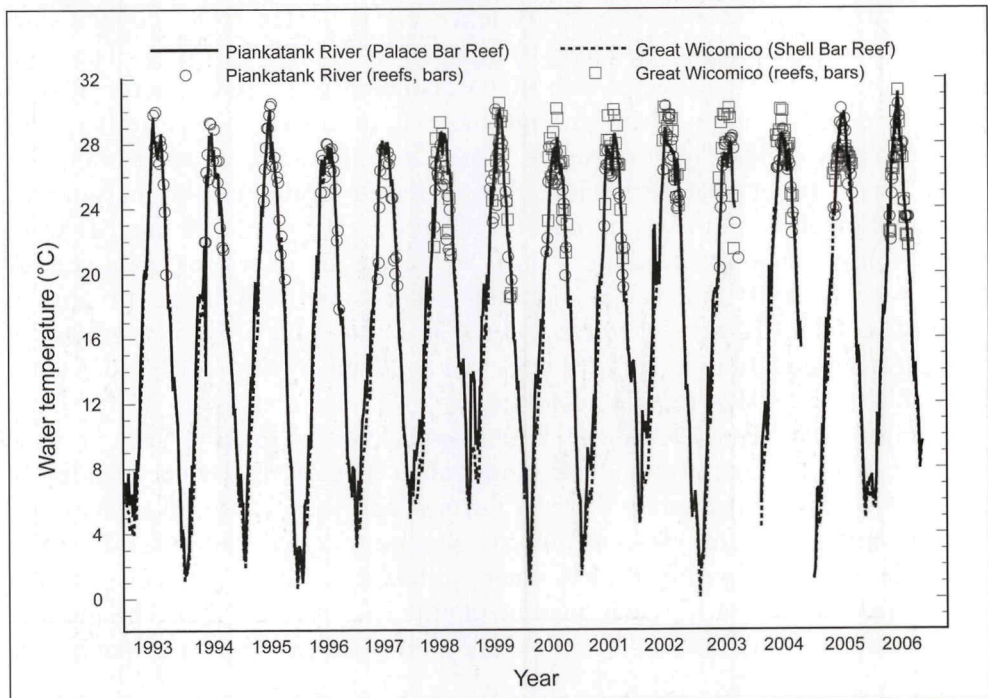


Figure 2. Weekly average water temperature (°C) in the Piankatank and Great Wicomico rivers from 1993 through 2006. Predicted values from 1993 through May 2005 were estimated from York River (V in Fig. 1) measurements using Harding et al. (2010a) and Southworth et al. (2010), respectively, as described in text. Year-round measurements at Shell Bar and Palace Bar reefs are available from June 2005 through December 2006. Measured values during May through September of 1993 through 2006 are averages from a minimum of 3 bars within each system.

typically observed during late summer and fall in the Chesapeake region. Salinities measured during summer and fall of 1999 and 2002 were higher than predicted but similar between rivers. Relatively low salinities were observed during summer and fall of 1996 and 2004.

Spat density

Oyster spat densities on the reefs and bars have been described with quantitative surveys since 1995. Annual fall surveys on both reefs and bars provide quantitative estimates of recruitment for each habitat type. Patent tong survey data were not available for any Piankatank River bars in 1997 and for Burton Point Bar and Cape Toon Bar in 1999.

Oyster recruitment onto constructed reefs was high during the reproductive season immediately following reef construction (Fig. 4). The highest recruitment observed throughout the study at Crane's Creek Reef and Shell Bar Reef occurred immediately after the reefs were built (Fig. 4). A strong recruitment signal was also evident on the three Piankatank reefs built in June 1995 (Bland, Burton, Cape Toon) when they were surveyed in September 1995 (Fig. 4). The initial recruitment event was not sustained at any of these reefs during the second year

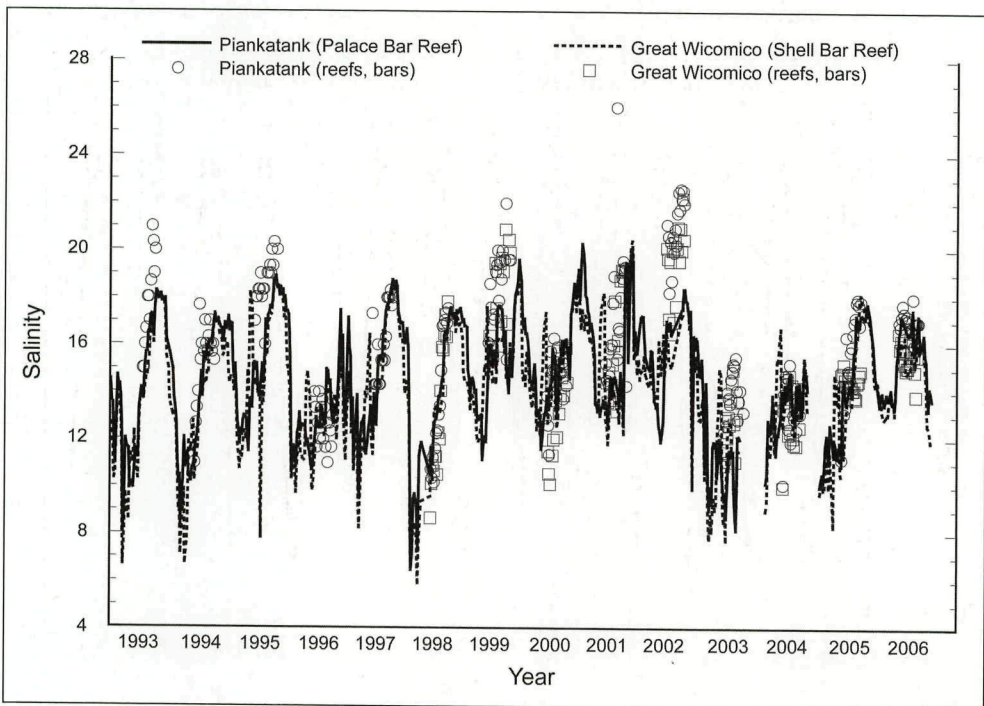


Figure 3. Weekly average salinities in the Piankatank and Great Wicomico rivers from 1993 through 2006. Predicted values from 1993 through May 2005 were estimated from York River (V in Fig.1) measurements using Harding et al. (2010a) and Southworth et al. (2010), respectively, as described in text. Year-round measurements at Shell Bar and Palace Bar reefs are available from June 2005 through December 2006. Measured values during May through September of 1993 through 2006 are averages from a minimum of 3 bars within each system.

post-construction. Spat densities on constructed reefs were significantly higher than spat densities on adjacent natural bars during the first 1 to 6 yrs post construction for these 5 reef-bar pairs (all but Palace Bar; Fig. 4, Table 3). By 6–7 yr post reef construction, observed spat densities on the constructed reefs were not significantly different than those recorded on adjacent natural bars. The recruitment observed on Shell Bar, Bland Point, and Cape Toon reefs during 2006, after the addition of large numbers of broodstock oysters to each of these sites (Table 2, Fig. 4), is the exception to this trend (Table 3).

River and year-specific variations in recruitment are evident in the observed patterns of recruitment on both bars and reefs. Recruitment in both the Great Wicomico and Piankatank Rivers was unusually high during 2002 (Harding et al. 2010a; Southworth et al. 2003, 2010) and the strength of this year class was evident at all reefs and bars (Fig. 4). Recruitment onto natural bars in the Piankatank River during 2002 was the highest observed between 1995 and 2006 for Bland Point, Burton Point, and Cape Toon bars (Fig. 4C, D, E) and the second highest bar recruitment for Palace Bar (Fig. 4F). Recruitment on the natural oyster bar at the Palace Bar site was highest during 1999 (Fig. 4F) commensurate with

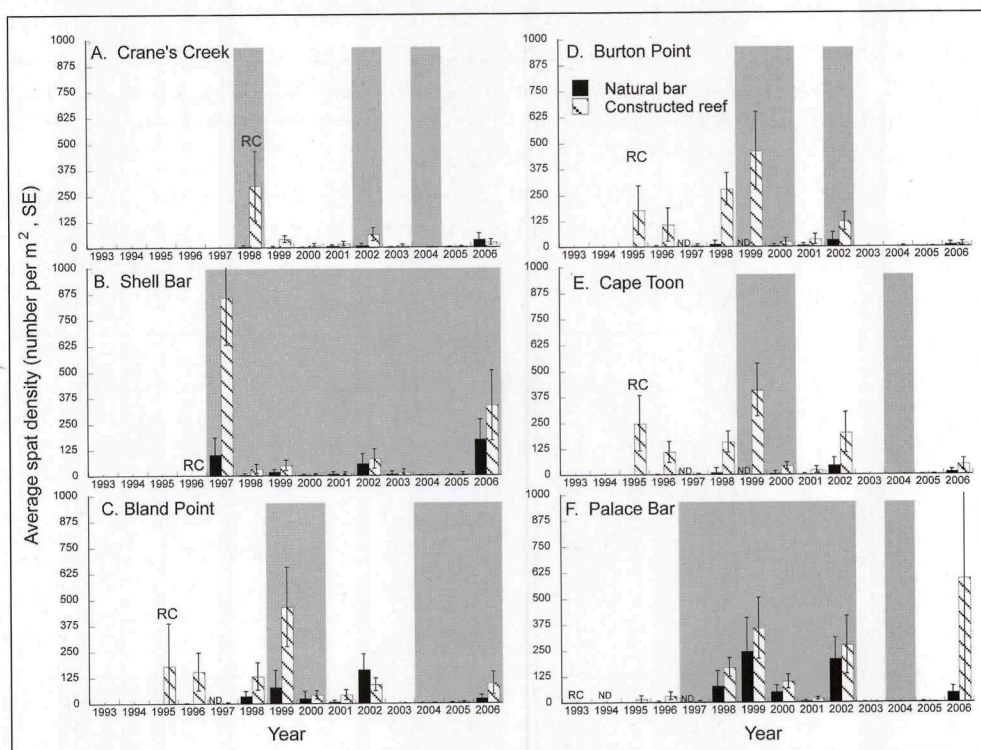


Figure 4. Average spat density (m^{-2} , standard deviation) for each reef-bar pair by year from reef construction (RC) through 2006. Crane's Creek (A) and Shell Bar (B) are in the Great Wicomico River. Bland Point (C), Burton Point (D), Cape Toon (E), and Palace Bar (F) are in the Piankatank River. No data (ND) were available for Palace Bar or Palace Bar reef (F) in 1993 and 1994, all of the natural bars in the Piankatank River during 1997, and Burton Point (D) and Cape Toon (E) bars in 1999. Years in which replenishment activities on reefs were completed are indicated by shaded rectangles.

another strong recruitment signal throughout the Piankatank system (Harding et al. 2010a). In the Great Wicomico River, the highest observed recruitment for the two natural bars (Crane's Creek Bar and Shell Bar) was in 2006 (Fig. 4A, B). Recruitment was relatively high throughout the Great Wicomico River in 2006 (Southworth et al. 2007, 2010).

After initial construction, all of the reef-bar combinations examined received at least one addition of clean shell and/or live oysters to the bar, the reef, or both within the same year during the 8–9 year study period (Table 2, Fig. 4). However, repletion activity was not always followed by an increase in site-specific recruitment within the same year (Figs. 4, 5). The Palace Bar (Piankatank) and Shell Bar (Great Wicomico) reef-bar pairs serve as good examples. The reefs at each site are two of the earliest reefs built and have received regular replenishment since construction. The adjacent bars have also received regular repletion during the study period (Table 2; also Harding et al. 2010a, Southworth et al. 2010). When repletion activity coincided with years of system-wide high recruitment (1999, 2002, 2006 as discussed above), the replenished sites showed an increase in observed recruitment relative to the previous year (Figs. 4, 5). During years when system-wide recruitment was not high, recruitment levels at replenished sites were approximately the same or less (Fig. 5) than those observed in the previous year. Decreases in recruitment observed on Palace Bar in 2000 and 2001 after replenishment were lower in magnitude than those observed on Palace Bar reef (Fig. 5).

Oyster recruitment onto constructed reefs should at least be equal to recruitment observed on the adjacent natural bar within the same year (1:1 relationship, diagonal dashed line in all Fig. 6 panels). If reefs receive higher recruitment than bars, the data points will all be above the 1:1 line. If bars receive higher

Table 3. Summary of *P* values resulting from year- and site-specific Mann-Whitney U tests comparing constructed reefs (R) with adjacent natural bars (B). No data = no data available from either reef or bar. ns = not significant. R > B or B > R = bar or reef data all zero while the other site was non zero. NC = no comparison because data from both reef and bar were all 0.

| Year | Site | | | | | |
|------|---------------|-----------|-------------|--------------|-----------|------------|
| | Crane's Creek | Shell Bar | Bland Point | Burton Point | Cape Toon | Palace Bar |
| 1993 | | | | | | No data |
| 1994 | | | | | | No data |
| 1995 | | | R > B | R > B | R > B | R > B |
| 1996 | | No data | <0.01 | <0.01 | <0.01 | <0.01 |
| 1997 | | <0.01 | No data | No data | No data | No data |
| 1998 | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 |
| 1999 | <0.01 | <0.01 | <0.01 | No data | No data | ns |
| 2000 | ns | ns | ns | <0.01 | <0.01 | <0.01 |
| 2001 | 0.02 | ns | <0.01 | <0.01 | <0.01 | ns |
| 2002 | <0.01 | ns | 0.01 | <0.01 | <0.01 | ns |
| 2003 | 0.05 | ns | ns | NC | B > R | B > R |
| 2004 | R > B | ns | ns | R > B | NC | B > R |
| 2005 | ns | ns | ns | ns | ns | B > R |
| 2006 | ns | 0.03 | <0.01 | ns | <0.01 | ns |

recruitment than the reefs, data points will all be below the 1:1 line. If oyster populations receive regular recruitment, data points should either stay approximately equal or increase moving forward in time. Examination of natural recruitment onto reef-bar pairs for the decade post-reef construction reveals several trends. None of the reefs show either a stable number of recruits or a regular increase in recruitment from the year of construction forward (Fig. 6). Reef and bar spat densities vary from year to year regardless of repletion and river. Even with additions of shell, live oysters, or both to all reefs and bars, the spat densities on constructed reefs in 2006 are less than the spat densities observed in the year of construction and are within the same order of magnitude as spat densities on the adjacent bars (all reefs but Palace Bar; Fig. 6).

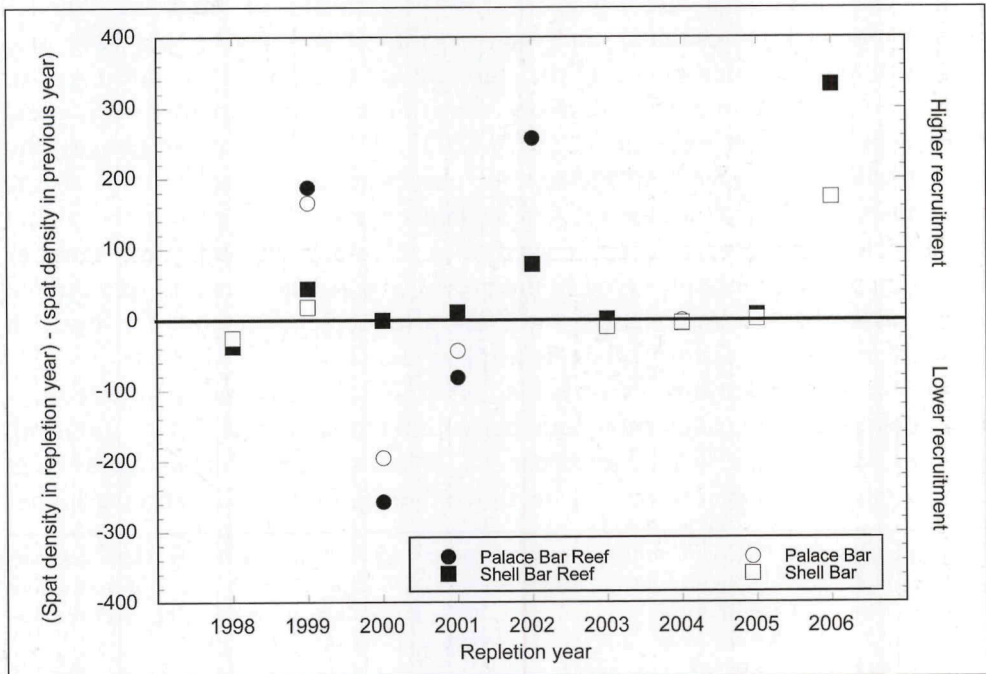
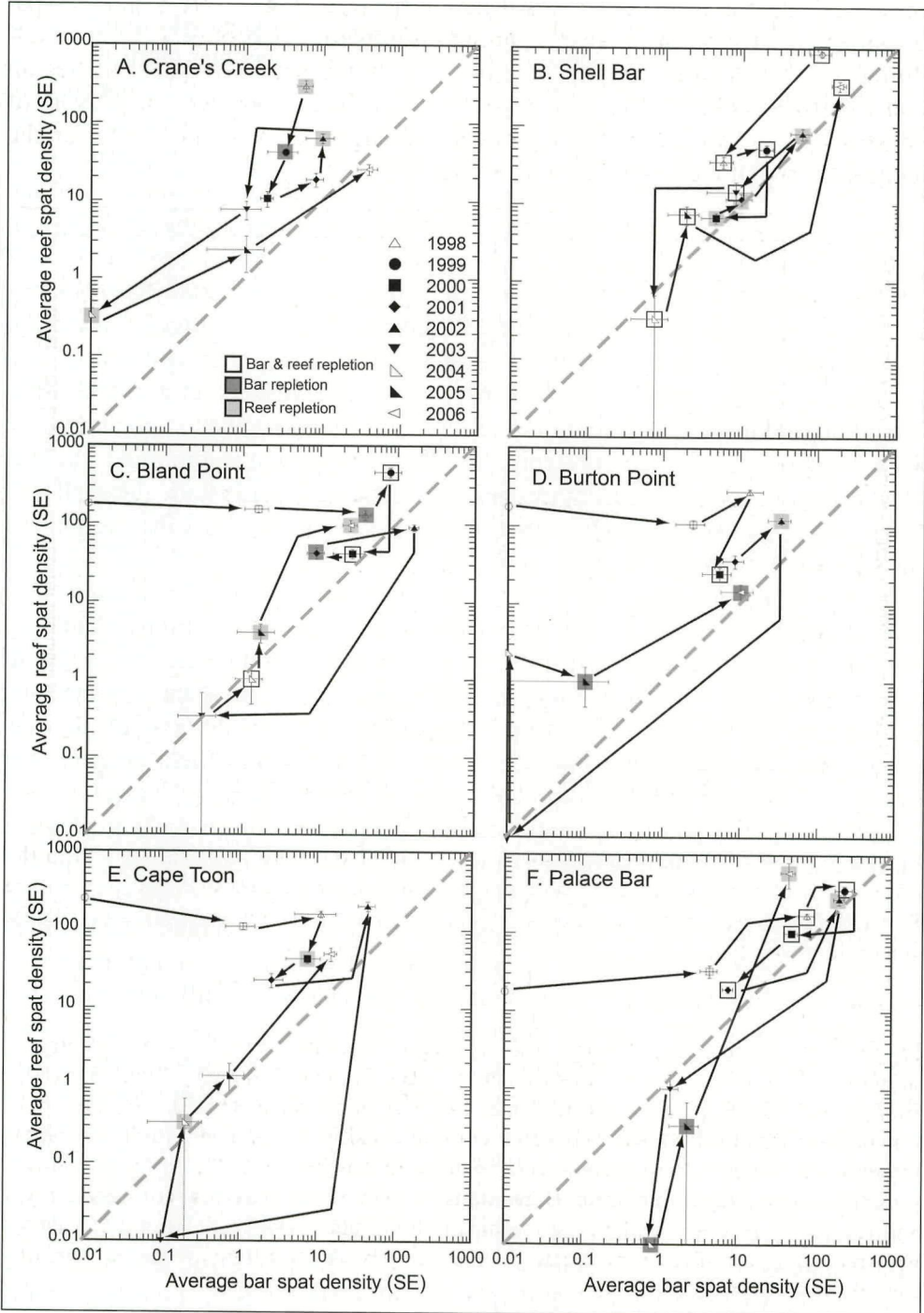


Figure 5. Trends in spat density and repletion activity in one year with regard to the observed spat density in the previous year where no repletion occurred for Palace Bar and Palace Bar reef (Piankatank River) and Shell Bar and Shell Bar reef (Great Wicomico River).

Figure 6 (opposite page). Comparison of average spat density (SE, standard error) on natural bars with adjacent constructed reefs for Crane's Creek (A), Shell Bar (B), Bland Point (C), Burton Point (D), Cape Toon (E), and Palace Bar (F). The diagonal line indicates the location where bar and reef spat densities are equal (1:1 relationship). Observed densities of zero oysters were changed to densities of 0.001 oysters to allow presentation on a logarithm scale. Data points in years where bars and reefs, bars only, and reefs only received repletion are indicated by a black-bordered rectangle, a dark grey rectangle, or a light grey rectangle, respectively. Arrows indicate the passage of time from one year to the next.

At multi-year time scales, annual changes in spat density between reef-bar pairs were not significantly different (Mann-Whitney U: $P > 0.05$) indicating the reefs did not provide enhanced settlement habitat relative to the bars, and that larval supply rather than substrate limitation drives the observed recruitment trends within these rivers.



Discussion

At decadal time scales, constructed oyster reefs did not show enhanced recruitment relative to adjacent natural oyster bars. Recruitment on the constructed reefs was enhanced relative to the bars in the years immediately following reef construction and immediately following addition of supplemental shell or oysters as a repletion strategy. However, in the absence of continued addition of shell and/or live oysters, spat densities on constructed reefs declined until they were equivalent to spat densities observed on natural oyster bars that did not receive shell. The time course for the observed decline in reef recruitment was 1–7 yr post-reef construction. This time frame is approximately equal to the oyster shell half-life of 3–6 yr reported by Powell et al. (2006) and commensurate with the modern life span (2–3 yr) of oysters within these rivers (Harding et al. 2010a, Southworth et al. 2010).

The observed decline in recruitment onto constructed reefs likely corresponds to the condition of the shell resource. Immediately after construction, the clean shell provides available habitat for oysters as well as other epibenthic taxa including barnacles, bryozoans, and macroalgae (Luckenbach et al. 2005, Rheinhardt and Mann 1990). The timing of reef construction and shell planting with regard to the timing of oyster recruitment within the system is important. If clean shell is planted after the peak of oyster recruitment within a system, the shell will be colonized by other taxa. Oyster settlement in subsequent years may be limited by the availability of suitable substrate.

Oyster shells are degraded through physical and biological processes. In a natural reef, living oysters maintain their shells and thus the interstitial reef matrix, and increase the available shell surface area through individual growth. When an oyster dies, its shell begins to erode through chemical and mechanical processes. *Cliona* spp. (boring sponges) have been regularly observed at all six of the sites studied (reefs and bars) since 1995. On constructed reefs, when shells are deployed as single valves rather than incorporated into a heterogenous matrix, valves may be rolled or moved by waves and mobile fauna, hastening the mechanical breakdown of the shell. Pieces that have broken off shells combine with biodeposits within the interstitial spaces of the reef matrix (DeAlteris 1988). In a living oyster reef, reef accretion or expansion of the growth edges into the water column is greater than the infilling or biofouling of the interstitial shell matrix maintaining or increasing the availability of interstitial habitat. Interstitial spaces may fill quickly in constructed shell habitats as planted shells erode, subside, and compact (Abbe 1988, Nestlerode et al. 2007, O'Beirn et al. 2000). If the reef interstitial matrix has filled, only substrate on the exterior of the reef is available as recruitment habitat, drastically reducing the available settlement surface and increasing the risk of predation (Bartol and Mann 1999, Bartol et al. 1999).

The Great Wicomico and Piankatank rivers have a history of regular recruitment, and both of these rivers have been described as substrate limited rather than recruit limited since at least 1963 (Harding et al. 2010a, Haven et al. 1978, Southworth et al. 2010), although Galtsoff et al. (1947) describe

substrate limitation in the Piankatank River during the 1930s. The initial positive effects of the constructed reef habitats were reduced as the initial shell plants aged in the absence of sustained recruitment and the development of resident oyster populations with a multi-year demographic that enhances interstitial habitat. The observed 1–7-year time course for the decay of the recruitment signal post reef construction is also related to the life expectancy of oysters within these rivers. In general, the age structure of the oysters within these rivers is truncated by the diseases Dermo and/or MSX. Oysters greater than 3 years old are rare in both systems (Harding et al. 2010a, Southworth et al. 2010). Thus, oysters from recruitment events within 1–2 yr of shell planting grew, maintained the shell base, and then died. Occlusion and degradation of their shells after death resulted in poor substrate condition in the absence of continued recruitment or replenishment.

Recruitment variability between years further compounds the living oyster-oyster shell dynamic. While oyster generation time in these rivers is as little as 1 yr, the observed interannual recruitment variability within these systems often spans at least an order of magnitude (Galtsoff et al. 1947, Harding et al. 2010a, Haven et al. 1978, Southworth et al. 2010). If shells are planted or added in a year of poor recruitment, the shells will degrade prior to oyster settlement, although there is no guarantee that a low recruitment year will be followed by a year of high recruitment. Since spat recruit to shell, the lack of multiple successful recruitment events to a shell plant within the 1–7-year window will result in a decrease in available habitat as the shell base degrades. Substrate availability is a dynamic process whereby it is gained through recruitment, growth, and replenishment, but lost through mortality, occlusion, and degradation.

The reduction in larger, older oysters observed within these populations (Harding et al. 2010a, Southworth et al. 2010) reduces habitat heterogeneity (Paynter et al. 2010, Powell et al. 2006) and the availability of healthy oyster growth edges that may enhance settlement. The presence of very large broodstock oysters on Shell Bar Reef in 1997 (Southworth and Mann 1998) may have contributed to the intense recruitment event observed during 1997, which remains the highest observed recruitment event observed at that reef to date. The contribution of larger, older oysters to the reef shell surface layer, interstitial matrix, and base is fundamental to habitat stability over time and the continued reef accretion process (Mann et al. 2009b, Powell and Klinck 2007).

There appears to be a requirement for continued replenishment activity to maintain the habitat heterogeneity of the shell surface on these constructed reefs, contrary to the dynamics of a healthy natural oyster population. While the reefs and resident oysters provide ecosystem services (Beck et al. 2011, Coen and Luckenbach 2000, Coen et al. 2007) for a variety of associated species (e.g., Breitburg 1999; Coen et al. 1999; Harding and Mann 1999, 2001, 2003, 2010; Harding et al. 2010b; Wenner et al. 1996), these constructed reefs do not provide enhanced habitat for oysters over the long term relative to existing natural bars. Given the large volume of shell required to build each reef

and the current paucity of shell available for oyster repletion and habitat rehabilitation, these data support as the most cost effective use of shell continued two-dimensional oyster shell planting in Virginia with coverage on the order of the traditional range of 5,000–10,000 bu acre⁻¹ (Haven et al. 1978) or approximately 20 L m⁻² (Harding et al. 2010a, Mann et al. 2009a) rather than creation of additional intertidal constructed reefs. Such shell planting would increase the spatial footprint for oyster habitat rehabilitation well beyond that possible if three-dimensional reefs were built. The effectiveness of shell planting as an oyster replenishment strategy may be further enhanced when planting is followed by deployment of spat-on-shell, given the potential for spat-on-shell to increase habitat complexity akin to a natural living reef matrix (e.g., O’Beirn et al. 2000, Rodney and Paynter 2006).

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