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Production and vertical distribution of invertebrates on riprap shorelines in Chesapeake Bay: A novel rocky intertidal habitat

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ABSTRACT

Along the North American Mid-Atlantic coast, soft-sediment shorelines are armored with hard substrata, such as riprap (rock revetments), for erosion protection. These structures are valuable for determining anthropogenic effects on marine ecosystems, and riprap potentially represents a habitat similar to an “emerging ecosystem” with productive species assemblages. The goals of this project were to (i) quantify species diversity, secondary production, and vertical distribution associated with armored (i.e., riprap) habitats in various locations in Chesapeake Bay and (ii) compare benthic epifaunal production on riprap with infaunal production on natural soft-sediment habitats in a system where natural rocky intertidal habitats are absent. Density, diversity, and secondary production of benthic epifauna on riprap and benthic infauna were compared in adjacent habitats in lower (Lynnhaven River) and upper (Patuxent River) Chesapeake Bay. To compare riprap habitat between tributaries that differed in physical characteristics and with natural rocky intertidal habitats from other systems, oyster, mussel, and barnacle vertical distribution on riprap in southern (Lynnhaven River) and northern (Piankatank River) locations was quantified. The hypothesis was that riprap assemblages and secondary production would differ between rivers and among regions due to differences in physical variables such as temperature (thermal stress in northern locations), or osmotic stress (greater upriver), and patterns would be comparable to natural rocky habitats. We predicted that productivity would be relatively high and relate positively with diversity on riprap, suggesting that it is a habitat within an “emerging ecosystem” where new combinations of species and habitat appear. Benthic epifaunal production on riprap was sevenfold greater than natural infaunal production, and both tended to be highest in the Lynnhaven. Vertical distribution on riprap was similar to that on natural rocky intertidal habitats: oyster and mussel densities tended to be highest in the mid- and low-intertidal zones, whereas barnacle density was greatest in the high intertidal at the southern location and the low intertidal in the northern location. Secondary productivity on riprap was high relative to the natural, infaunal, soft-bottom habitat in this area. Species richness and epifaunal non-oyster production were positively related to oyster production. We demonstrate that intertidal riprap-armored shorelines are a productive novel habitat in an emerging ecosystem, and they enhance species diversity, abundance, and production. Thus, riprap shorelines mimic the ecological characteristics of natural hard-bottom habitats, and they may contribute substantially to ecosystem function throughout the Atlantic and Gulf of Mexico coasts due to riprap's widespread use and distribution.

1. Introduction

As coastal development increases, anthropogenic effects on coastal habitats may change the relative abundance and diversity of species in those habitats. In some cases, coastal ecosystems are altered into “emerging ecosystems” or “novel ecosystems,” where new combinations of species and habitat appear in abundances that have not previously occurred within a given biome (Milton, 2003). This definition was originally used in terrestrial ecosystems where land was cleared for commercial or industrial use and effects on ecological functions were unknown (Milton, 2003). In marine systems, ecological effects of coastal development are little known and are gaining importance in the scientific community (Bulleri and Chapman, 2010; Chapman and Underwood, 2011; Dugan et al., 2011; Gittman et al.,

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2016a,b). The study of emerging ecosystems, systems that emerge from anthropogenic use, is relatively new; therefore, little is known about the influences, trends, or ecological costs and benefits of these habitats. However, a cost for one species may be a benefit to another. One theory is that disturbed, man-made habitats are suboptimal to natural environments, especially when invasive species become well established on artificial structures (Bulleri and Chapman, 2010; Chapman and Underwood, 2011). However, "the assumptions that EEs [emerging ecosystems] are species-poor, dysfunctional, dominated by alien species, and a liability to humanity may need to be tested" (Milton, 2003). In some cases, emerging ecosystems characterized by altered species assemblages (Hobbs et al., 2006, 2009) may provide habitats with higher natural capital than those previously present, particularly in heavily impacted ecosystems (Milton, 2003). Moreover, increased diversity associated with novel ecosystems may enhance the resilience of an ecosystem due to functional redundancy (McCann, 2000).

Along the Mid-Atlantic U.S. and southeastern coasts of North America, the geology of a trailing-edge margin has led to a preponderance of natural soft-sediment systems along the shoreline, such as salt marshes, sandy beaches, and mudflats, which provide a gently sloping shoreline (Kennish, 2001) with few natural rocky intertidal habitats. There are no natural rocky intertidal habitats in the mid-Atlantic. These estuarine and coastal habitats are important nurseries and contribute >25% of coastal ecosystem services worldwide (Costanza et al., 1997; Scyphers et al., 2011), but are severely threatened by anthropogenic and natural disturbances (Vitousek et al., 1997). Due to proximity to the shoreline and recent increases in sea level (IPCC, 2014), coastal properties face shoreline erosion, particularly from wave action or storm events. This has resulted in the armoring of natural shorelines to protect the upland from erosion. Artificial structures form the dominant intertidal and shallow subtidal habitat in some urbanized coastal areas, and they are rapidly becoming ubiquitous along many coastlines (Bulleri and Chapman, 2010). One estimate is that 14% of the total US coastline (Atlantic and Pacific) is armored (Gittman et al., 2015). Armoring of shorelines can result in "coastal squeeze," whereby "the coastal margin is squeezed between the fixed landward boundary (artificial or natural) and the rising sea level" (Schleupner, 2008). Studies on the effects of hardened shorelines have focused on coastal habitats in Australia, Europe, and the Caribbean (Glasby and Connell, 1999; Bulleri et al., 2006; Glasby et al., 2007; Schleupner, 2008; Strain et al., 2018b), and some studies have focused on fouling communities (Tyrell and Byers, 2007; Geraldi et al., 2014), yet few studies have examined communities developing on riprap shorelines in the mid-Atlantic coast of the US where there are few natural hard substrates. Further study on communities developing on hardened shorelines is warranted, and this is especially relevant for the Western US Atlantic coastline where coastal armoring is expanding. For example, a recent meta-analysis of ecological effects of shoreline hardening demonstrated reduced ecosystem services in hardened versus natural shorelines (Gittman et al., 2016a) and concluded "the type and location of shoreline hardening could greatly affect habitat value."

One particular form of armoring, riprap (granite or rock revetment either placed against a sloping shoreline or stacked into the form of a sill at heights varying from 30 to 200 cm or more), is an ideal emerging ecosystem to study because its use has increased substantially in coastal habitats (Douglass and Pickel, 1999) and it may have effects on community structure and ecological functioning near the shore (Seitz et al., 2006, 2018; Airoldi and Beck, 2007; Bilkovic and Roggero, 2008; Seitz and Lawless, 2008). Other forms of armoring, such as bulkheads (vertical seawalls), have distinct detrimental ecosystem effects (Douglass and Pickel, 1999; Seitz et al., 2006; Kennish, 2002) including wetland loss when hardened shorelines prevent accumulation of sediments at a rate adequate to keep up with sea-level rise (Scavia et al., 2002) and increases in non-indigenous species (Bulleri and Airoldi, 2005). Conversely, riprap armoring may provide a novel anthropogenic habitat that contributes to ecosystem diversity, structure, and functioning.

In Chesapeake Bay, three types of artificial and natural shoreline habitats are common: natural marsh, riprap, and vertical seawall (referred to as "bulkhead") (Living Shoreline Summit Steering Committee, 2006). Subtidal soft-sediment benthic communities adjacent to natural marsh shorelines generally have greater density and diversity than those near bulkhead (vertical seawall) shorelines, whereas those near riprap shorelines often have similar subtidal density and diversity as those along natural marsh (Seitz et al., 2006; Bilkovic and Roggero, 2008; Seitz and Lawless, 2008). However, the density and productivity of epifaunal assemblages associated with riprap have been rarely studied (although see Bulleri and Chapman, 2010; Wong et al., 2011). In addition, vertical distribution and diversity of species on this created habitat have been investigated in European ecosystems (Airoldi et al., 2005; Vaselli et al., 2008, Firth et al., 2009, 2014), in lakes (Brauns et al., 2007), and in the Pacific (Pister, 2009), but not in the mid-Atlantic U.S. region. This habitat warrants study in the mid-Atlantic U.S. region to determine whether previous studies are generalizable to this region.

Location-specific environmental variables, such as salinity (King et al., 2005), sediment type (Diaz and Schaffner, 1990), dissolved oxygen (Long and Seitz, 2009, Seitz et al., 2009), and temperature (Bonsdorff and Blomqvist, 1993; Hummel et al., 1996) affect infaunal benthic communities. Estuarine faunal composition can also change with distance from the river mouth, attributed to changes in many environmental variables (Boesch, 2002). Salinity decreases upstream in estuaries, potentially reducing diversity of estuarine fauna (King et al., 2005), while nutrients from allochthonous inputs typically increase upstream in estuaries (Lenihan and Micheli, 2001). For example, in the York River tributary of Chesapeake Bay, the concentration of phytonutrients is highest upriver and decreases downriver, a pattern common in riverine estuaries (Boesch, 2002; Ouboter et al., 1998). Hence, faunal assemblages may differ by geographic location in Chesapeake Bay and distance upstream due to several factors that vary along a salinity gradient. Moreover, some benthic species (e.g., clams) are stressed by environmental variables such as high or low water temperatures, which can produce shifts in population abundance and distribution (Hummel et al., 1996).

Secondary production (i.e., heterotrophic production of organic matter) represents the amount of food available to higher trophic levels and is indicative of habitat quality (Wilbur and Clarke, 1998). Moreover, secondary production is one commonly accepted currency in the evaluation of habitat restoration benefits (French McCay and Rowe, 2003; Peterson et al., 2003) and has been used in the evaluation here. Secondary production is a valuable metric because it is representative of ecosystem functioning. Further, secondary production scales with ecosystem services, integrates over time and space, synthesizes contributions to food resources, and accounts for benefits of habitat structure. Direct estimation of secondary production can be labor-intensive and cost-prohibitive (Wilbur and Clarke, 1998); however, indirect estimates can be accurate and reliable (Edgar, 1990; Cusson and Bourget, 2005; Sturdivant et al., 2014). Moreover, secondary production can be an estimate of estuarine health (Diaz and Schaffner, 1990; Dolbeth et al., 2005), as is diversity (Schaeffer et al., 1988; Costanza, 1992; Rapport et al., 1998). Both measures together can produce an estimate of the amount of carbon and the diversity of organisms available to higher trophic levels, which can help estimate ecosystem services provided by habitat on epifaunal structures (Peterson et al., 2003; Coen et al., 2007). Productivity integrates community respiration and consumption, and is influenced by both biological and physical (environmental conditions) variables (Edgar and Barrett, 2002; Cusson and Bourget, 2005); diversity can also change in response to similar variables (Pianka, 1966; Menge and Sutherland, 1976). Here, we use production theory and empirical models (Edgar, 1990, Sturdivant et al., 2014) to estimate benthic production and diversity associated with riprap habitats to evaluate the potential ecosystem functioning in both artificial and natural habitats. High epifaunal community secondary

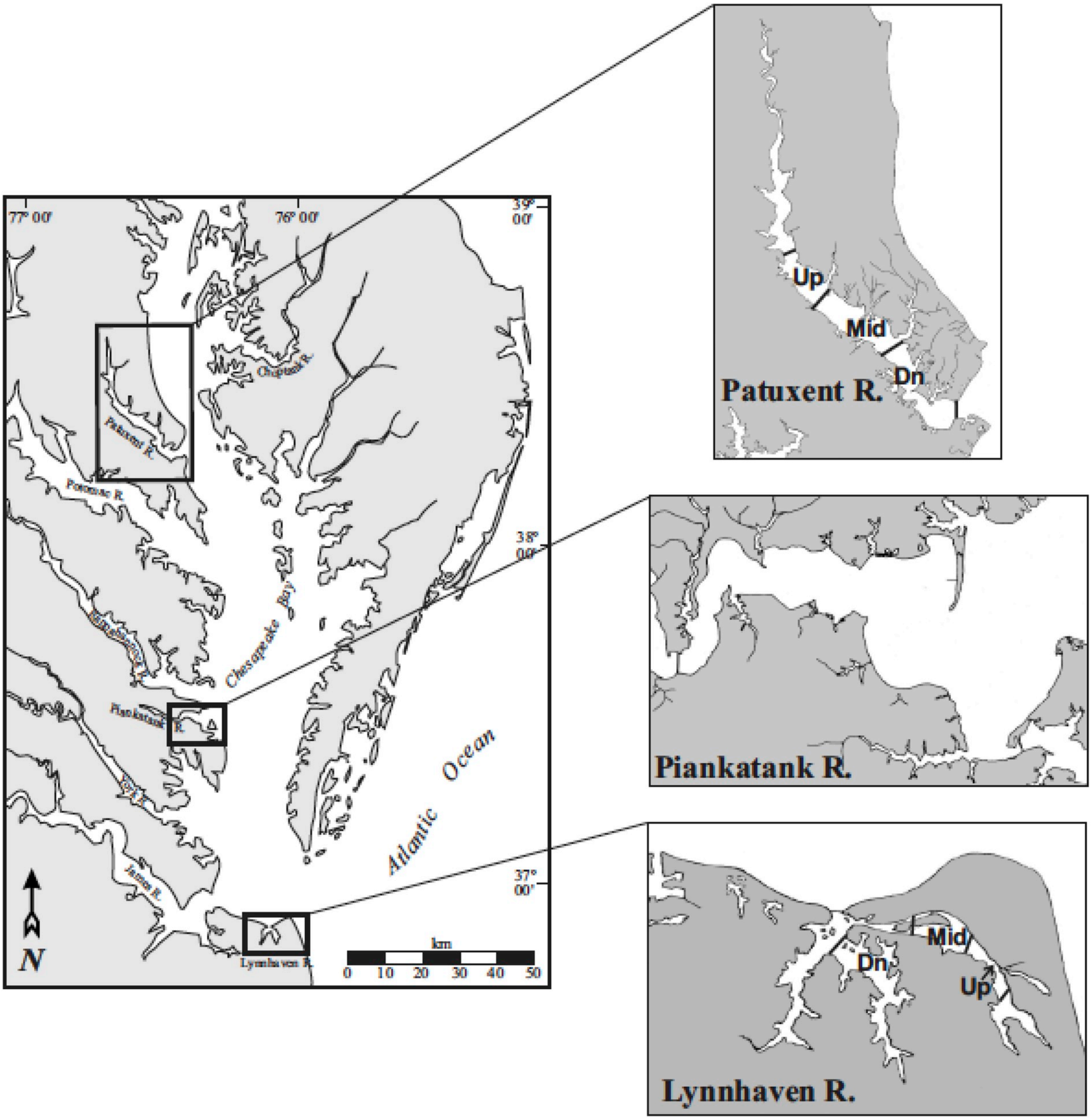

Fig. 1. Map of the Chesapeake Bay (left panel) with enlarged sampling rivers (right panels), the Patuxent River (with location of Regions Up [Up-River], Mid [Mid-River], and Dn [Down-River]), Piankatank River (zonation study only), and Lynnhaven River (with location of Regions Up, Mid, and Dn).

production would indicate a large amount of animal tissue, and therefore epifaunal structure present, but it is also important to examine how this production is divided among different species, or whether it is related to the presence of only one dominant species (e.g., oysters). The Lynnhaven River is a relatively productive system in terms of macrofaunal biomass (Seitz and Lawless, 2008), whereas the Patuxent River is highly developed and less productive (Lovall et al., 2017). One would expect that increased epifaunal secondary production due to oysters might provide increased structure for recruitment of a variety of other organisms, thus allowing for increased abundance and diversity (Peterson et al., 2003; Karp et al., 2018). It is unclear whether community production on riprap, or whether production in the absence of oyster production, would produce the same relationship with diversity, and therefore this relationship requires examination.

Vertical distribution of natural rocky intertidal epifaunal assemblages has been documented worldwide and is driven by a suite of biological and physical factors (Paine, 1966; Connell, 1972; Menge and Sutherland, 1987), though in some locations the distribution of organisms in the intertidal is patchy without distinct zones (Underwood and Chapman, 1996). One unresolved ecological question is whether riprap assemblages on the Mid-Atlantic coast of the US have vertical distribution patterns similar to those of natural rocky habitats (e.g., Connell, 1972), and whether these patterns are consistent geographically.

In this study, secondary production and diversity of intertidal populations on man-made riprap structures and adjacent subtidal populations in natural soft-sediment were quantified in two selected tributaries of Chesapeake Bay, the Lynnhaven (lower Bay) and Patuxent (upper Bay) Rivers. The aim was to contrast faunal patterns in two rivers that differed in geographic location (i.e., physical characteristics) and productivity, as well as to compare anthropogenic riprap structures with natural soft-sediment habitats. The relatively productive Lynnhaven River system is in the lower Chesapeake Bay (Seitz and Lawless, 2008), whereas the highly developed, less-productive Patuxent

River (Bradley, 2011; Lovall et al., 2017) is in the upper Bay (Hartzell et al., 2010). Systems in the upper Bay also tend to be cooler and less saline. We also examined the relationship between secondary production and various physical and biotic variables (i.e., temperature, salinity, dissolved oxygen [DO], grain size, sedimentary carbon, chlorophyll *a*), which varied along the riverine gradient. In addition, we examined the relationship between diversity and production. Finally, the vertical distribution of organisms in intertidal zones on riprap in the Lynnhaven and Piankatank Rivers was also sampled to examine how these man-made habitats compare with natural rocky intertidal habitat (absent in the mid-Atlantic) and to understand whether riprap epifaunal communities are responding to environmental factors in similar ways as their rocky intertidal counterparts (Connell, 1972). The hypotheses were that: (1) diversity and secondary production of riprap assemblages would be greater in the southern tributary and downriver in each tributary because of differences in temperature (i.e., greater thermal stress in northern locations), osmotic stress (greater upriver), and other physical variables; (2) productivity on riprap would be high compared to natural soft-sediment habitats (based on large-bodied epifauna on riprap); (3) productivity would be positively related to diversity on riprap given the presence of oysters, ecosystem engineers, and this habitat's similarity to natural rocky intertidal habitats; and (4) vertical distribution of riprap epifauna would differ by intertidal zone in Chesapeake Bay. Thus, the data would support the argument that these riprap habitats are components of "emerging ecosystems" by encompassing novel species and high productivity on these man-made structures as compared to natural habitats.

2. Materials and methods

2.1. Epifaunal and infaunal production and diversity

During June and July 2009, epifauna on riprap and infauna adjacent to riprap shorelines were sampled and secondary production was estimated at up-river, mid-river, and downriver regions (six replicates per river) in both the Patuxent and Lynnhaven Rivers (Fig. 1). Only riprap shoreline sites extending 50 m without intrusion by another shoreline type were used to preclude local influence of alternative shoreline types. Riprap was comprised of granite rocks 0.15–0.7 m in diameter. Shoreline maps from 2003 (http://www.vims.edu/ccrm/research/inventory/index.php) were used for site selection to ensure that each site had riprap established for at least six years, which is a sufficient amount of time for a man-made shoreline to allow development of a community similar to a natural system (Currin et al., 2010).

In a stratified-random sampling design to examine geographical variation in assemblages, each river was divided into three regions with Region Up (i.e., Up-River) farthest from the river mouth, Region Mid (Mid-River), and Region Dn (Down-River) closest to the mouth, though the morphology of each river resulted in a slightly different distribution of Regions in each river (Fig. 1). Two replicate sites from each Region were randomly selected for sampling. Water temperature, salinity, and dissolved oxygen (DO) were measured using a YSI Pro-Plus Multi-Parameter Water Quality meter, and sediment and faunal samples were taken at each site (see below). All variables were compared between the two tributaries, the Lynnhaven and Patuxent Rivers, and by Region (Up, Mid, and Dn) using a 2-way Analysis of Variance (ANOVA) with River and Region as fixed factors. Note that Region Dn in the Lynnhaven was a different fork of the river but only tended to have higher salinity than Regions Up and Mid. Significance was determined at $\alpha = 0.1$. This level was chosen based on the desire to examine differences that are biologically meaningful given a system with high variability, and this is a more relaxed threshold that can act as an early warning signal to show the impact of different levels of the factor (Nuzzo, 2014). When significant interactions occurred, means of one factor were compared separately for each level of the other factor with Tukey tests (Underwood, 1997). The assumption of homoscedasticity was examined using Bartlett's and Levene's tests; data were square-root transformed to meet assumptions of normality and homogeneity of variance when necessary. Sediment grain size and faunal density were compared using linear regression.

Epifauna were sampled in the intertidal zone at each site by placing a 0.25-m^2 PVC quadrat randomly on the riprap rocks in the mid-intertidal zone. Each quadrat was photographed, and the epifauna on the surfaces of the riprap stones were scraped and collected; samples were washed through a 500-μm sieve. Organisms were identified to the lowest taxonomic level (usually species); diversity was determined using species richness (number of species), as well as the Shannon index ($H' \log_e$)(Krebs, 1989), and Simpson's index (1-dominance) to use as a comparison (Magurran, 2004). Species richness is a basic measure of diversity, and the Shannon index incorporates both species richness and the number of individuals belonging to each species and is also a robust diversity measure (Krebs, 1989; Spellerberg and Fedor, 2003). Quadrat photos were analyzed for number of taxa (usually phylum or class) with the NOVA Southeastern University computer program Coral Point Count extension (CPCe) using 100 random points on each photo (Kohler and Gill, 2006). This allowed a comparison between the two methods of (1) using a visual estimate of diversity with (2) using a destructive, collection-based method of estimating diversity. Both methods are presented in diversity results with an explanation of which method was used for which figures. Mobile organisms on the rocks were not quantified.

The relationship between the physical variables and epifaunal secondary production across both rivers was examined using multiple regression. Community relationships were also examined with ANOSIM non-parametric tests (one outlier from the Lynnhaven with only one species was removed from ANOSIM analysis) and nMDS plots using PRIMER v6 (Clarke and Gorley, 2006).

Subtidal infauna were sampled at each site approximately 5 m from shore using a suction apparatus with a 3-mm-mesh collecting bag, and a cylinder of 0.11-m^2 cross-sectional area. The cylinder was inserted 30 cm into the sediment and cylinder contents excavated to the bottom of the cylinder using a suction dredge (Seitz et al., 2006). At each subtidal site, a 30-mL syringe core of 2.5 cm diameter was used to extract the top 2–3 cm of sediment for grain size and carbon-hydrogen-nitrogen (CHN) analysis. The percentage composition of sand, gravel, silt, and clay were calculated following standard wet sieve and pipette procedures (Folk, 1980; Plumb, 1981). In addition, a 10-mL syringe of 1 cm diameter was used to collect the top 1 cm of sediment for chlorophyll *a* analysis.

Ash-free dry weight was determined for each taxonomic group and used to calculate biomass. Daily secondary production was calculated for each taxon using an empirical model ($P = 0.0049B^{0.80}\,T^{0.89}$), where B = AFDW biomass and T = temperature at the site (Edgar, 1990). In this model, daily secondary production (P μg d^{-1}) for each invertebrate is related to body mass (B μg AFDW/AFDM) and temperature (T, °C). The production values in μg were converted to mg when they were >1000 μg AFDW $m^{-2}\,d^{-1}$, for easier viewing. This method has been validated to estimate secondary production for organisms in Chesapeake Bay (Hagy, 2002; Sturdivant et al., 2014). It requires very limited sampling and is relevant for estuarine species in water temperatures of 5–30 °C (Edgar, 1990). One change we made from Edgar's method, which used the mean AFDW from organisms retained on a series of sieves, was to combine individuals within each taxonomic group (*sensu* Sturdivant et al., 2014). In addition, mainly to use as a comparison with other studies that used the production-to-biomass-ratio (P:B) method of annual production estimation, P:B ratios for different taxa (Diaz and Schaffner, 1990) were used to estimate annual production from the biomass values. Secondary production was estimated as: Annual production (g AFDW $m^{-2}\,yr^{-1}$) = Biomass (g m^{-2}) x P:B ratio (yr^{-1}). The P:B ratios were 2.9 for molluscs, 5.7 for crustaceans, 4.9 for polychaetes, and 2.3 for chordates (Diaz and Schaffner, 1990). Samples from infauna and epifauna were standardized per m^2. One limitation is that seasonal biomass was not available, so secondary production was only estimated from summer biomass and temperature, yet P:B ratios are based on annual rates.

To examine production versus diversity (i.e., species richness), we conducted Major Axis regression (= Type II regression with errors in x and y) using the 'SMATR' package in R (Warton et al., 2012). Analyses employed data from both rivers and from the Lynnhaven River alone due to the absence of oyster biomass in the Patuxent River. The functions plotted in figures of biomass, secondary production, and species richness were first validated by the statistical analyses in R, and then fitted to all data by nonlinear least squares regression in SigmaPlot. When necessary to meet assumptions of normality and homogeneity of variance, variables were transformed as $\log_{10}(x+1)$.

2.2. Vertical distribution

Vertical distribution of epifauna on riprap was compared between the Lynnhaven and Piankatank Rivers (but not Regions within rivers) to examine differences in systems at different latitudes with varying physical conditions (Lynnhaven River ~50 miles farther south), with potential varying associated thermal stress on epifaunal organisms exposed at low tide. In each river, eastern oyster (*Crassostrea virginica*), hooked mussel (*Ischadium recurvum*), and barnacles (mainly *Chthamalus fragilis* and *Balanus eburneus*) were sampled at four random sites. At each site, the vertical intertidal-subtidal shoreline was divided into four tidal zones of 50-cm vertical elevation measured from the spring low tide mark: high (spring high to mean high tide), mid (mean high to mean low tide), low (mean low to spring low tide), and subtidal (below spring low tide). Within each tidal zone, rocks of similar size (~15 cm × 15 cm) were haphazardly chosen for collection. One rock from each tidal zone was collected at each of four replicate sites within a river (16 rocks per river). The rocks were bagged, their orientation (front/back) was noted, and they were placed on ice. All oysters, mussels, and barnacles were counted. Oysters were measured, and barnacles were removed for identification. Densities of oysters, mussels, and barnacles were analyzed with 2-way ANOVA models using River (Lynnhaven and Piankatank) and Tidal Zone (High-, Mid-, Low-, and Sub-tidal) as fixed factors; significance was determined at $\alpha = 0.1$.

3. Results

3.1. Physical variables

Salinity tended to be higher in the Lynnhaven River than the Patuxent River, but there was a significant River by Region interaction (Table 1). In the Patuxent River, salinity increased in regions closer to the river mouth (Tukey HSD test, $p = 0.003$: Region Up < Mid < Dn), whereas in the Lynnhaven River salinity did not differ by region (Table 2; Tukey HSD test, $p = 0.568$). In the Up, Mid, Dn Regions separately, salinity was higher in the Lynnhaven than the Patuxent (Tukey HSD test, $p < 0.005$, $p = 0.002$, and $p = 0.001$, respectively). Dissolved oxygen (DO) was significantly higher in the Lynnhaven than in the Patuxent River, the Region and interaction effects were not significant (Tables 1 and 2), and all DO levels were normoxic ($>6.8\,\mathrm{mg\,L^{-1}}$). Temperature did not differ by River but differed significantly by Region; it decreased closer to the river mouths (Tables 1 and 2), and there was no significant interaction. Sedimentary total nitrogen (TN), total organic carbon (TOC), and chlorophyll *a* did not differ by River or Region and there were no interaction effects (Table 1). Mean sedimentary nitrogen values were three times greater in the Lynnhaven River than in the Patuxent River, but variability was high, especially in the Lynnhaven (Table 2).

The Patuxent River had six times more gravel than the Lynnhaven River (Table 3), and this difference was significant with no River × Region interaction (Table 1). The Lynnhaven and Patuxent Rivers had similar fractions of sand, silt, and clay, with no significant differences (Table 3).

Table 1
Statistical results for two-way crossed ANOVAs for fixed factors River (Lynnhaven and Patuxent) and Region (Up, Mid, and Dn) for physical variables and chlorophyll *a* in production study. Source = factor, DF = degrees of freedom, Adj MS = adjusted mean squares. DO = dissolved oxygen, Temp = temperature, Sed N = sedimentary nitrogen, Sed TOC = sedimentary total organic carbon, Chl *a* = chlorophyll *a*, % Gravel = percent of gravel in sediment grain-size analysis. Bold indicates significant differences at $\alpha < 0.10$.

Variable	Source	DF	Adj MS	F-value	P-value
Salinity	**River**	**1**	**181.90**	**3693.14**	**<0.0005**
	Region	**2**	**1.20**	**24.00**	**0.001**
	River x Region	**2**	**0.68**	**13.54**	**0.006**
DO (mg/L)	**River**	**1**	**130.68**	**15.22**	**0.008**
	Region	2	11.51	1.34	0.330
	River x Region	2	20.25	2.36	0.176
Temp (°C)	River	1	0.14	0.37	0.565
	Region	**2**	**3.94**	**10.40**	**0.011**
	River x Region	2	0.09	0.25	0.789
Sed N	River	1	0.005	2.02	0.205
	Region	2	0.004	0.78	0.500
	River x Region	2	0.001	0.47	0.644
Sed TOC	River	1	0.36	1.53	0.262
	Region	2	0.10	0.42	0.674
	River x Region	2	0.08	0.33	0.731
Chl *a*	River	1	161.9	0.26	0.626
	Region	2	468.9	0.76	0.506
	River x Region	2	42.3	0.07	0.934
% Gravel	**River**	**1**	**906.7**	**3.86**	**0.098**
	Region	2	11.8	0.05	0.952
	River x Region	2	75.9	0.32	0.738

3.2. Epifaunal production and diversity

Mean epifaunal secondary production on riprap ranged from 20 to 400 mg AFDW $\mathrm{m^{-2}\,d^{-1}}$ (Table 4; Fig. 2), with the majority of the production from oysters. There were no epifaunal oysters in the Patuxent. For epifaunal secondary production, there was a significant River by Region interaction (Table 4). In the Lynnhaven, epifaunal secondary production was highest in the upriver Region and lowest in the downriver Region (Fig. 2a; Tukey HSD test, $p = 0.094$), but it did not differ significantly by Region in the Patuxent River (Fig. 2b; Tukey HSD, $p = 0.601$). Overall, epifaunal secondary production averaged around 200 mg AFDW $\mathrm{m^{-2}\,d^{-1}}$ in the Lynnhaven River, which was eightfold greater than that in the Patuxent River (Fig. 2c; Table 4; Tukey HSD $p = 0.041$). In the Up-River Region, epifaunal secondary production was higher in the Lynnhaven than the Patuxent River (Tukey HSD test, $p = 0.066$), and for Mid- and Down-River Regions, it was not significantly different by River (Tukey HSD test, $p = 0.221$, $p = 0.503$, respectively). Non-metric multi-dimensional scaling (nMDS) analysis showed some separation between epifaunal communities in the Lynnhaven and Patuxent rivers, with stress = 0.05 (Fig. 3). Epifaunal species Richness from photo quadrats did not differ significantly by River or Region (Fig. 4; Table 4). Epifaunal Shannon H′ diversity did not differ by River ($p = 0.555$) or Region ($p = 0.533$) with no interaction ($p = 0.713$). One site with a single individual precluded a statistical analysis with Simpson's diversity (Table 5).

Epifaunal secondary production was significantly and positively related to temperature, DO, and sedimentary carbon (Table 6). The overall multiple regression additionally including salinity, chl *a*, and percent gravel was significant, with a large amount of variation explained by the combination of variables ($R^2 = 92\%$), though this high R^2 could be a result of the few data points used.

3.3. Infaunal production and diversity

Infaunal secondary production in natural soft-sediment habitats ranged from 15 to 250 mg AFDW $\mathrm{m^{-2}\,d^{-1}}$ (Fig. 5), was substantially lower (four- to 10-fold) than epifaunal production on riprap structures

Table 2
Average measures of physical variables in the infaunal secondary production study in two rivers (Lynnhaven: Lynn, and Patuxent: Pax) and three regions (Reg) per river (Up: farthest from mouth, Mid: mid-river, Dn: closest to mouth), and mean (mn) from two sites per region. DO = dissolved oxygen; N = nitrogen; Temp = temperature; Sal = salinity; Chl *a* = chlorophyll *a*.

River	Reg	Sal (psu) ± SE	Temp (°C) ± SE	DO (mg L^{-1}) ± SE	N (%) ± SE	Chl *a* (ug cm^{-2}) ± SE
Lynn	**Up**	17.46 ± 0.04	27.90 ± 0.10	18.65 ± 1.65	0.039 ± 0.024	28.13 ± 1.75
	Mid	17.44 ± 0.30	27.05 ± 0.05	13.10 ± 2.30	0.027 ± 0.014	38.63 ± 11.82
	Dn	17.73 ± 0.15	26.05 ± 0.55	11.20 ± 4.20	0.093 ± 0.078	45.33 ± 1.92
	mn	17.54 ± 0.10	27.00 ± 0.37	14.00 ± 1.93	0.053 ± 0.025	37.36 ± 5.00
Pax	**Up**	8.81 ± 0.00	28.05 ± 0.15	7.05 ± 0.25	0.018 ± 0.003	19.32 ± 1.06
	Mid	9.73 ± 0.16	27.60 ± 0.40	7.30 ± 0.20	0.013 ± 0.000	25.64 ± 0.02
	Dn	10.72 ± 0.11	26.00 ± 0.80	8.80 ± 0.10	0.020 ± 0.007	45.09 ± 0.06
	mn	9.75 ± 0.35	27.21 ± 0.46	7.70 ± 0.36	0.017 ± 0.002	30.02 ± 0.33

(compare to Fig. 2; note y-axis scale change), and there were no subtidal oyster populations in these habitats. The Lynnhaven River tended to have greater infaunal secondary production than the Patuxent River (Fig. 5; Table 4). When the epifaunal and infaunal secondary production estimates were combined, the Lynnhaven River far surpassed the Patuxent River, with more than seven times the combined secondary production as the Patuxent River (Figs. 2c and 5c; Table 4), whether calculated using the Edgar (1990) method or the P:B-ratio method (Table 5), as the density of oysters and other invertebrates was higher in the Lynnhaven.

Infaunal diversity was two-fold greater in the Lynnhaven River than the Patuxent River, and the difference was significant (Fig. 6a and b; Table 4; see Appendix for details of infaunal species assemblages, densities, and production, Table A.1., Fig. A.1 and Fig. A.2). In both rivers, infaunal diversity did not differ significantly by Region (Fig. 6a and b), and infaunal diversity was not significantly related to average infaunal production (Regression p = 0.353).

3.4. *Relationship between species richness and secondary production*

We analyzed the relationship between oyster secondary production, non-oyster secondary production, and species richness using data from both rivers, and separately using data from the Lynnhaven River due to the absence of oyster biomass in the Patuxent River. Species richness was a highly significant, asymptotic function of oyster secondary production whether with only Lynnhaven River data ($r^2 = 0.93$, $p < 0.002$, $\log_{10}$-transformed data) or with data from both rivers (Fig. 7a, $r^2 = 0.72$, $p < 0.004$). In contrast, non-oyster secondary production was not significantly related to species richness for the Lynnhaven River ($r^2 = 0.27$, $p = 0.286$, untransformed data) nor for the Patuxent River ($r^2 = 0.21$, $p = 0.365$, untransformed data). Non-oyster epifaunal secondary production was significantly related to oyster secondary production (Fig. 7b). In addition, epifaunal species richness was a significant asymptotic function of oyster biomass (Fig. 8), similar to that for oyster secondary production.

Table 4
Statistical results for two-way crossed ANOVAs for fixed factors River (Lynnhaven and Patuxent) and Region (Up, Mid, and Dn) for biological variables in production study (all calculated using Edgar method), and for Zone and River (Lynnhaven and Piankatank) in vertical distribution study. Source = factor, DF = degrees of freedom, Adj MS = adjusted mean squares. *C. virginica* = *Crassostrea virginica*, *I. recurvum* = *Ischadium recurvum*, barnacles = *Chthamalus fragilis* and *Balanus eburneus*. Bold indicates significant differences at α < 0.10.

Variable	Source	DF	Adj MS	F-value	P-value
Epifaunal 2° production	**River**	**1**	**93148**	**15.65**	**0.007**
	Region	**2**	**36937**	**6.20**	**0.035**
	River x Region	**2**	**29920**	**5.03**	**0.052**
Epifuanal Photo quad Richness	River	1	6.750	2.19	0.189
	Region	2	3.250	1.05	0.405
	River x Region	2	3.250	1.05	0.405
Infaunal 2° production	River	1	6318	1.08	0.338
	Region	2	13788	2.36	0.175
	River x Region	2	15022	2.58	0.156
Infaunal Diversity (H′)	**River**	**1**	**0.5821**	**3.79**	**0.099**
	Region	2	0.0465	0.30	0.749
	River x Region	2	0.0259	0.17	0.848
Epi- and infaunal 2° production	**River**	**1**	**147990**	**10.17**	**0.019**
	Region	**2**	**91750**	**6.31**	**0.033**
	River x Region	**2**	**86232**	**5.93**	**0.038**
C. virginica density	**River**	**1**	**10047**	**8.31**	**0.008**
	Zone	2	2629	2.18	0.117
	River x Zone	2	2566	2.12	0.124
I. recurvum density	River	1	84.5	0.20	0.658
	Zone	2	207.1	0.49	0.691
	River x Zone	2	426.1	1.01	0.405
Barnacle density	**River**	**1**	**61075.1**	**4.09**	**0.054**
	Zone	2	28338.3	1.90	0.157
	River x Zone	**2**	**44852.5**	**3.01**	**0.050**

Table 3
Mean percent of sediment as different grain-size categories in the two rivers (Lynnhaven: Lynn, and Patuxent: Pax) and three regions (Reg) per river (Up: farthest from mouth, Mid: mid-river, Dn: closest to mouth), and mean (mn) from two sites per region sampled for the infaunal secondary production study.

River	Reg	Grain Size (±SE)			
		% Gravel	% Sand	% Silt	% Clay
Lynn	**Up**	1.75 ± 1.62	94.11 ± 2.07	0.07 ± 0.05	4.09 ± 0.37
	Mid	7.65 ± 7.16	88.78 ± 7.58	1.04 ± 0.01	4.61 ± 0.43
	Dn	0.80 ± 0.42	50.57 ± 29.51	30.34 ± 20.52	18.29 ± 9.41
	mn	3.40 ± 2.33	77.80 ± 11.7	10.49 ± 8.22	9.00 ± 3.82
Pax	**Up**	19.09 ± 14.84	78.78 ± 13.86	1.25 ± 0.16	6.71 ± 1.47
	Mid	16.35 ± 14.13	72.95 ± 13.21	0.49 ± 0.32	5.21 ± 0.04
	Dn	26.91 ± 15.37	67.23 ± 18.00	1.00 ± 0.74	5.11 ± 1.62
	mn	20.78 ± 6.91	73.04 ± 7.11	0.91 ± 0.26	5.68 ± 0.65

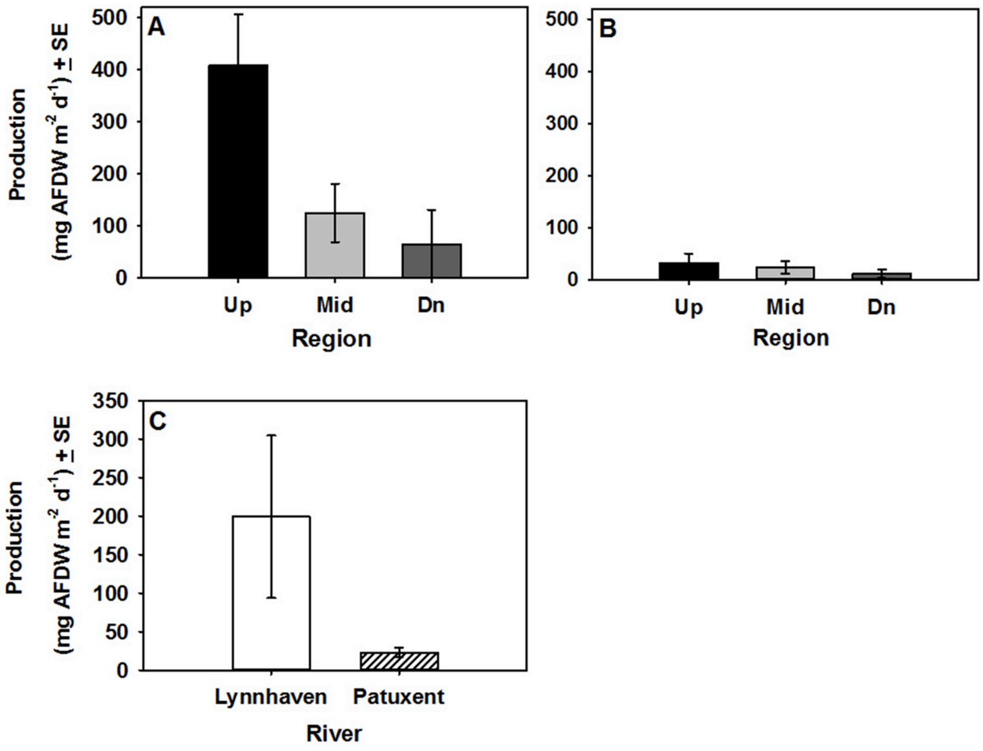

Fig. 2. Mean daily epifaunal secondary production (Edgar method) by Region in the A) Lynnhaven River and, B) Patuxent River, from two sites per river region, and C) secondary production averaged among Regions to compare between Rivers (from six sites per river).

3.5. Vertical distribution

Densities of oysters, *Crassostrea virginica*, were significantly greater (six-fold) in the Lynnhaven River than in the Piankatank River and tended to be highest in the mid- and low-intertidal zones (Fig. 9a; Table 4). The hooked mussel, *Ischadium recurvum*, had similar densities in both rivers and was spread relatively evenly across tidal zones (Fig. 9b; Table 4). Vertical distribution patterns of barnacles, mainly *Chthamalus fragilis* and *Balanus eburneus*, showed a significant interaction (Table 4), partly because different species dominated the different rivers. Patterns in the high intertidal zone differed by River at $\alpha = 0.1$ (Tukey HSD). In the Lynnhaven River, barnacles were primarily (>95%) *Chthamalus fragilis*, density was greatest in the high intertidal zone, and this was significant at $\alpha = 0.1$ (Tukey $p = 0.093$), whereas in the Piankatank River, barnacles were primarily (>95%) *Balanus eburneus*, density tended to be greatest in the subtidal zone and moderate in mid- and low-intertidal zones. This difference was not significant (Fig. 9c; Tukey HSD: $p = 0.116$).

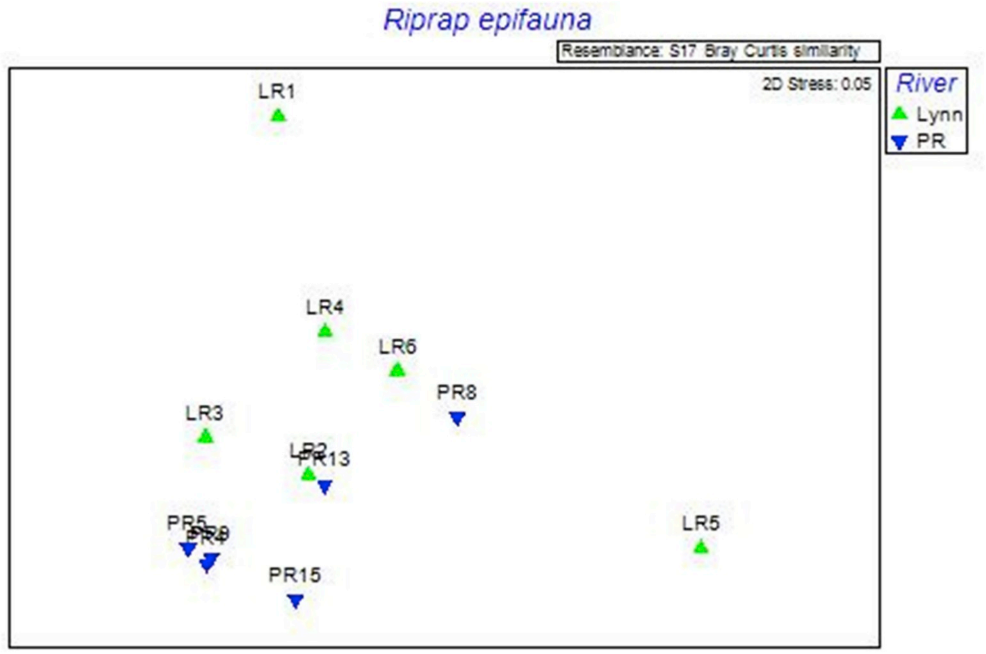

Fig. 3. Non-metric multidimensional scaling (nMDS) plot of Lynnhaven River (Lynn) and Patuxent River (PR) community epifaunal abundance (with site numbers after the river designation). Global R of 0.227 ($p < 0.05$) and stress are from ANOSIM analysis. LR3 & 4 = Up-River, LR1 & 2 = Mid-River, LR5 & 6 = Down-River, PR4 & 5 = Up-River, PR8 & 9 = Mid-River, and PR13 & 15 = Down-River.

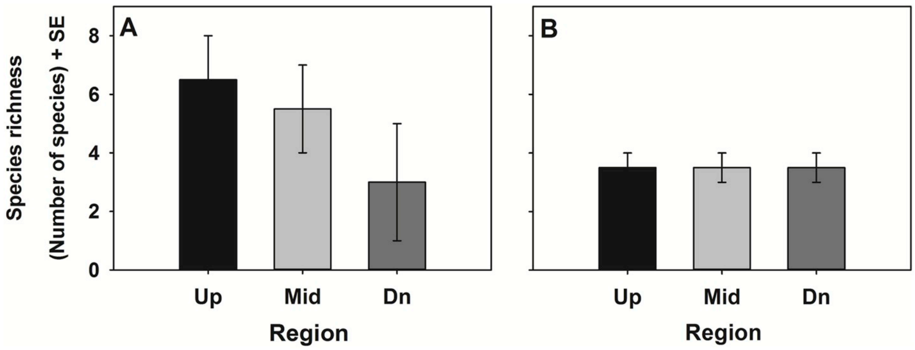

Fig. 4. Mean epifaunal species richness by Region of the A) Lynnhaven River and B) Patuxent River from photo quadrats using NOVA Southeastern University computer program Coral Point Count extension (CPCe) (N = 2 per Region).

4. Discussion

Secondary production on riprap habitats was high in comparison to infaunal production in nearby natural habitats (this study) and in comparison to secondary production in other Chesapeake Bay systems (e.g., Sturdivant et al., 2014). Moreover, vertical distribution of epifaunal organisms on riprap in the Chesapeake Bay resembled that of natural rocky intertidal habitats of the U.S. west and northeast coasts (Connell, 1972), with *Chthamalus* densities greatest in the high intertidal zone and *Balanus* lower in the intertidal. Epifaunal production was much greater than infaunal production due to the high biomass of oysters (*Crassostrea virginica*) on riprap, as in other studies (Wong et al., 2011), which also led to a difference in epifaunal production between the two river systems. These riprap habitats with abundant oysters as ecosystem engineers acted similar to other intertidal hard-bottom habitats, and to subtidal hard substrates such as oyster castles and reef balls (Soniat and Burton, 2005; Burke, 2010; Theuerkauf et al., 2015; Lipcius and Burke, 2018). In both river systems, bivalves contributed most to infaunal secondary production, and polychaetes contributed secondarily to infaunal production (Table A.1, Fig. A.2), similar to other natural, infaunal systems (Wilson, 1989; Edgar, 1990; Hagy, 2002). However, the availability and areal coverage of infaunal habitat in the mid-Atlantic U.S. coast is much greater than hard substrate, which has ramifications for ecosystem processes.

Epifaunal species richness was strongly related as an asymptotic function to oyster secondary production and biomass, but not to non-oyster secondary production. Production of epifaunal organisms besides oysters was also related to oyster production. This suggests that oysters on riprap structures can act as ecosystem engineers (Gutiérrez et al., 2003; Jackson et al., 2008), corresponding with both increased diversity and increased production of the epifaunal community. Thus, the biomass of oysters not only provides habitat for other species, but oysters and other filter-feeding bivalves also provide important ecosystem services such as filtration (Coen et al., 2007; Grizzle et al., 2008). Oysters did not occur on the riprap structures in the Patuxent River, and this lack of oyster biomass was associated with lower epifaunal production in that system. It is possible that this resulted from differences in dissolved oxygen between the rivers, although no DO levels were hypoxic (i.e., all above 6.8 mg L^{-2}). The most likely explanation for the difference in oysters between rivers is that extreme winter freezes killed settled oyster larvae in the Patuxent River (though evidence of settlement was not investigated herein), as the more northern location of the Patuxent experiences harsher winters than the Lynnhaven. Hence, the productivity of riprap structures will depend on environmental conditions of the ecosystem (Wong et al., 2011).

In southern California, riprap habitats have similar diversity and community composition as natural rocky habitats (Pister, 2009), but this is not the case in other locations. In many places, hardened habitats, including riprap, bulkhead (vertical seawall), or other man-made structures, do not function similarly to natural rocky habitats because man-made structures can cause fragmentation and modify natural dispersal patterns, thereby altering local and regional biodiversity (Fahrig, 2003; Goodsell et al., 2007; Bulleri and Chapman, 2010). Previous studies suggest integrating natural habitat elements into urban structures to reduce negative impacts (Bulleri and Chapman, 2010; Strain et al., 2018a; Liversage and Chapman, 2018), which can be accomplished in Chesapeake Bay and elsewhere with living shorelines that incorporate natural features in man-made structures (Davis et al., 2006;

Table 5
Comparison of secondary production (prod.) estimated by two methods, annual production using P:B ratios (Diaz and Schaffner, 1990) in g AFDW m^{-2} yr^{-1} (P:B prod.) and daily production using the Edgar method (Edgar, 1990) in mg AFDW m^{-2} d^{-1} (Edgar prod.) in two rivers (Riv.), the Lynnhaven (LR) and Patuxent (PR), in various Regions (Reg.); as well as infaunal (Inf.) or epifaunal (Epi.) Diversity using Richness (Rich.; number of species), Shannon H' (Shan. H') (nats $individual^{-1}$), and Simpson's Index (Simps.)(1 - dominance).

Riv.	Site No.	Reg.	P:B prod.	Edgar prod.	Inf., Epi. Rich.	Inf. Shan. H′	Epi. Shan. H′	Inf. Simps. index	Epi. Simps. index
LR	1	Mid	49.09	69.38	2, 4	0.562	1.023	0.500	0.593
LR	2	Mid	202.07	181.26	9, 7	1.927	1.102	0.863	0.595
LR	3	Up	702.8	506.77	3, 8	0.898	0.709	0.603	0.295
LR	4	Up	358.24	308.09	6, 5	1.627	1.269	0.859	0.703
LR	5	Dn	0.07	0.18	3, 1	1.099	0	1	
LR	6	Dn	148.11	131.3	3, 5	0.956	1.140	0.667	0.622
PR	4	Up	13.79	15.44	3, 3	0.756	0.704	0.440	0.497
PR	5	Up	74.1	51.29	1, 4	0	0.687	0.000	0.464
PR	8	Mid	12.37	11.45	4, 3	0.281	0.815	0.112	0.540
PR	9	Mid	48.48	37.32	4, 4	1.209	0.829	0.659	0.514
PR	13	Dn	2.01	3.51	2, 4	1.121	0.856	0.051	0.543
PR	15	Dn	23.8	20.72	3, 3	0.779	0.531	0.4891	0.331

Table 6
Multiple regression of physical factors and epifaunal secondary production (calculated using Edgar method) with Analysis of Variance across both rivers. Coef = coefficient, SE coef = standard error of the coefficient. DF = degrees of freedom, SS = sum of squares, MS = mean squares. Bold indicates significant differences at α < 0.10. Regression: R-Squared = 96.4%, R-Squared (adjusted) = 92.0%.

Predictor	Coef	SE Coef	T-value	P-value
Constant	−1385.3	556.9	−2.49	0.055
Salinity (psu)	−17.55	11.75	−1.49	0.195
Temp.(C)	**44.93**	**19.75**	**2.28**	**0.072**
DO (mg l^{-1})	**50.353**	**7.286**	**6.91**	**0.001**
TOC %	**178.13**	**55.49**	**3.21**	**0.024**
total chl	−1.861	1.483	−1.26	0.265
% Gravel	0.797	2.255	0.35	0.738

Analysis of Variance

Source	DF	SS	MS	F-value	P-value
Regression	**6**	**456552**	**76092**	**22.14**	**0.002**
Residual Error	5	17185	3437		
Total	11	473737			

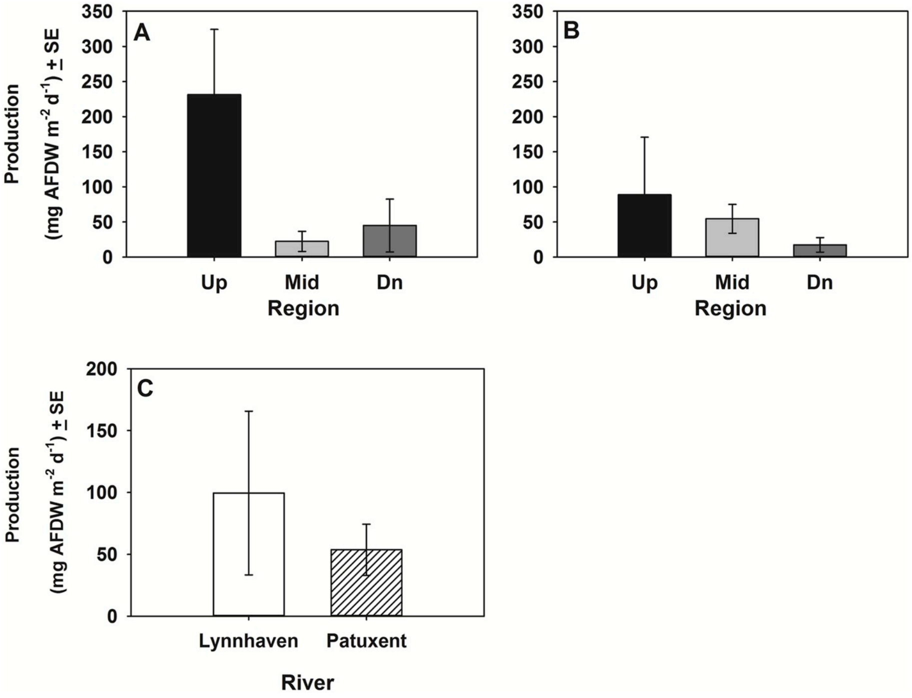

Fig. 5. Mean daily infaunal secondary production (Edgar method) by Region in the A) Lynnhaven River, B) the Patuxent River, from two sites per river region, and C) averaged daily production among Regions for each river for comparison between rivers (from six sites per river).

Currin et al., 2010; Scyphers et al., 2011; Davenport et al., 2018).

The complex structure of the riprap allowed a relatively diverse epifaunal community to grow adjacent to a less-productive benthic infaunal community. This epifaunal community added substantially to the overall production of each river. The epifaunal productivity also increased diversity, as bivalve ecosystem engineers, primarily oysters,

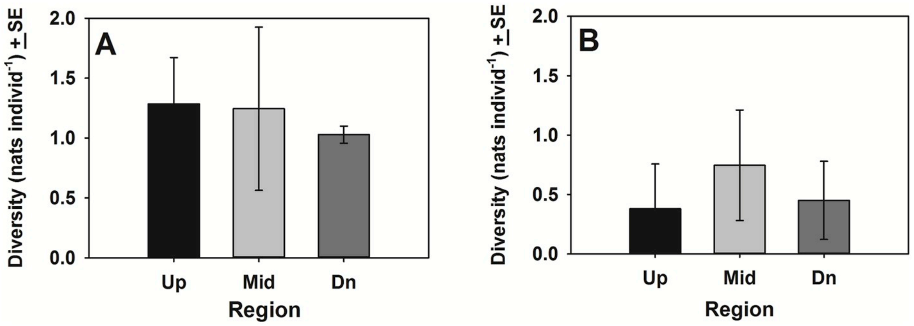

Fig. 6. Mean infaunal Shannon diversity (nats individual^{-1}) by Region in the A) Lynnhaven River and B) Patuxent River.

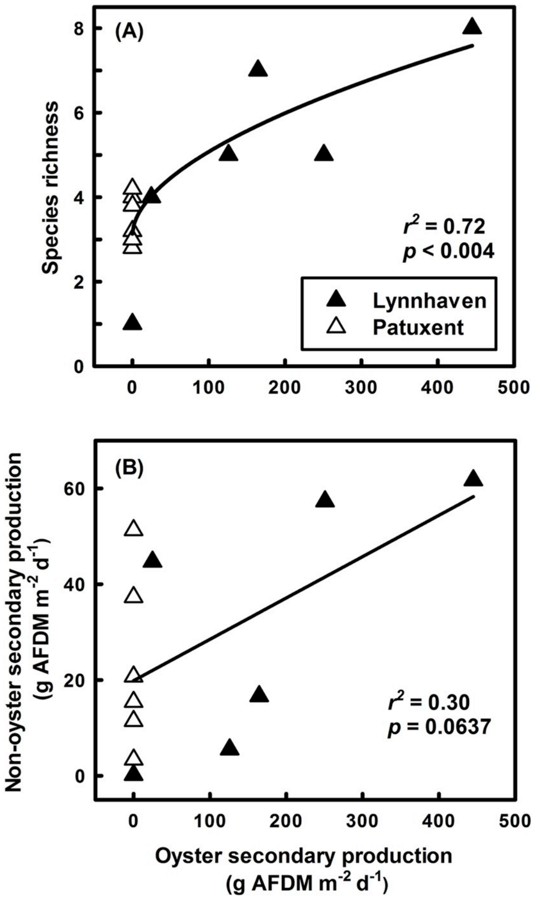

Fig. 7. A) Mean epifaunal species richness (number of species) compared with oyster epifaunal daily secondary production (Edgar method; data have been jittered (offset) across species richness for the Patuxent) and B) Non-oyster epifaunal daily secondary production (Edgar method) compared with oyster epifaunal secondary production for the Lynnhaven and Patuxent Rivers.

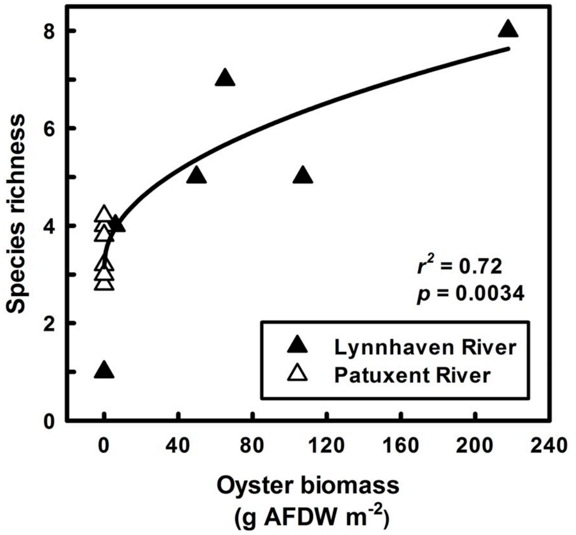

Fig. 8. Mean epifaunal species richness versus oyster biomass for the Lynnhaven and Patuxent Rivers (data have been jittered across species richness for the Patuxent).

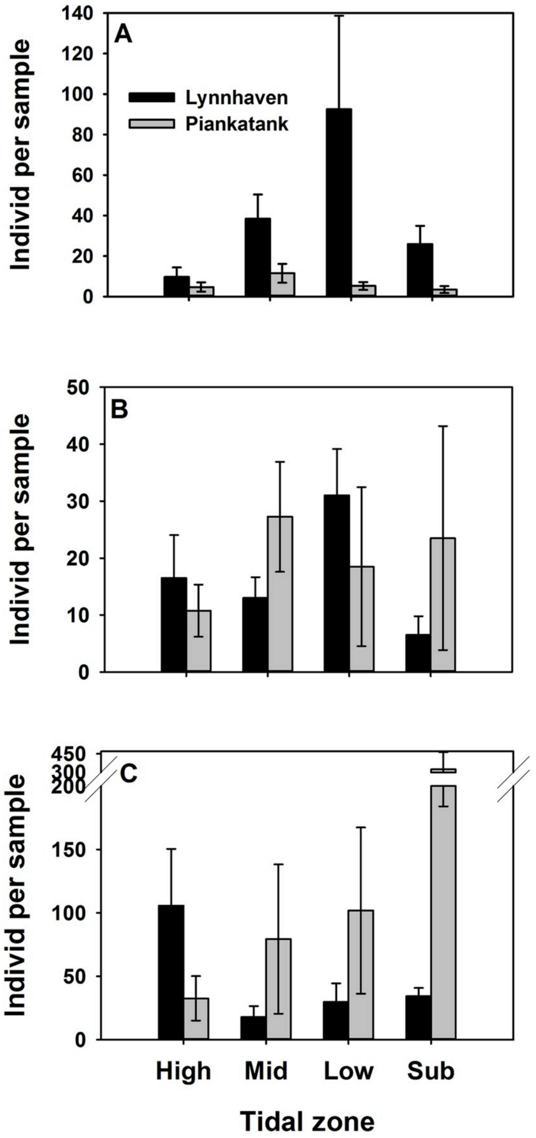

Fig. 9. Density of A) oysters *Crassostrea virginica*, B) mussels *Ischadium recurvum*, and C) barnacles (including *Chthamalus fragilis* and *Balanus eburneus*) in high intertidal (High), mid-intertidal (Mid), low-intertidal (Low) and subtidal (Sub) zones, in two river systems, the Lynnhaven and Piankatank, VA.

were associated with high species diversity. The high productivity of the epifauna likely contributes to ecosystem services, such as water filtration with numerous filter-feeding organisms like oysters and mussels (Grizzle et al., 2008; Bilkovic and Mitchell, 2013), and food for higher trophic levels, thus highlighting the importance of this emerging assemblage of organisms.

Comparing secondary production between locations, both infaunal and epifaunal production tended to be greater, and total secondary production was more than three times greater, in the southern location, the Lynnhaven River, as compared to the northern location, the Patuxent River. The physical differences between the two rivers may have contributed to differences in infaunal production, as higher dissolved oxygen, sedimentary total organic carbon, and temperature were associated with greater production in the Lynnhaven River. In addition, the productive infaunal species in this study were mainly deposit feeders (Diaz and Schaffner, 1990), which thrive in silty habitats with high organic content, emphasizing the importance of grain size to the overall production. The Lynnhaven River, in the lower Chesapeake Bay, experiences elevated salinities and less-severe winters than the Patuxent River (D'Elia et al., 2003) in upper Chesapeake Bay. This may have contributed to the ability of epifaunal bivalves to survive on intertidal substrata (intermittently exposed to extreme temperatures) with reduced thermal stress in the Lynnhaven River compared to the Patuxent River. The tidal range of the Patuxent River is also lower than that of the Lynnhaven River (Boynton et al., 2008; Sisson et al., 2010), potentially contributing to differences in exposure of intertidal organisms as well as areas available for organisms to occupy.

Compared to other Chesapeake Bay systems, infaunal production in the Lynnhaven River was relatively high (Diaz and Fredette, 1982; Diaz et al., 1982; Sturdivant et al., 2014), and epifaunal production was at least double that of infaunal production. In comparison to other benthic systems in Chesapeake Bay, daily infaunal production (calculated using the Edgar method) in the Lynnhaven (~100 mg AFDW m^{-2} d^{-1}) was more than double the mean production at normoxic sites over time (1996–2004) throughout the Bay (39 mg AFDW m^{-2} d^{-1}) and on par with that observed in a year with maximum production (~97 mg AFDW m^{-2} d^{-1})(Sturdivant et al., 2014). Compared to annual production calculated using P:B values, the Lynnhaven River had an average of 30 g AFDW m^{-2} yr^{-1} for infauna and 243 g AFDW m^{-2} yr^{-1} for epifauna (Table 5), whereas comparable subtidal flats have infaunal secondary production values of 18–20 g AFDW m^{-2} y^{-1} (Diaz and Fredette, 1982), or of 14.4 g m^{-2} y^{-1} in mid-Bay locations (Hagy, 2002), and epifaunal production on riprap sills of 60–120 g AFDW m^{-2} y^{-1} (Wong et al., 2011). Notably, the patterns for production between Locations and among Regions in this study were similar whether examined using the Edgar method or the P:B-ratio method (Table 5), suggesting that either method works well for a summertime snapshot of productivity. The use of empirical methods (e.g., Edgar method) may be beneficial for production studies when seasonal biomass over changing temperatures is available.

In comparison to other benthic systems, the Patuxent River was relatively low for both infaunal (5 g AFDW m^{-2} y^{-1}) and epifaunal (20 g AFDW m^{-2} y^{-1}) annual production, but these were comparable to annual production values in other systems (Wong et al., 2011). These comparisons suggest that the Patuxent River is not highly productive, but average (Bradley, 2011; Lovall et al., 2017). In addition, production in Chesapeake Bay is highest in polyhaline regions compared to habitats with lower salinity (Sturdivant et al., 2014), agreeing with the trend of higher production in the high-salinity river (Lynnhaven). Moreover, the vastly higher epifaunal production versus infaunal production in both systems points out the role of riprap and oyster reefs to create habitat in which other species can survive.

In previous studies (Wong et al., 2011), annual secondary production of oyster reefs was greater than that of marshes, seagrass, and subtidal flats. This pattern was corroborated by the results of this study, as the greatest contributor to secondary production was by epifaunal oysters in the Lynnhaven River. The increase in production and diversity due to the presence of riprap demonstrates the importance of this habitat in contributing to new combinations of species and also its similarity to an emerging, or novel, ecosystem (Milton, 2003). As natural oyster shell becomes less available for settlement (Piazza et al., 2005; Powell et al., 2006), alternative substrata for oyster settlement will become more important (Soniat and Burton, 2005; Burke, 2010; Theuerkauf et al., 2015; Lipcius and Burke, 2018). In some subtidal habitats, these man-made structures contribute to less-abundant and less-diverse communities compared to adjacent natural subtidal habitats, such as marshes (Peterson et al., 2003; Seitz et al., 2006; Wong et al., 2011), and therefore their additions to the ecosystem must be weighed carefully for each region.

Though natural rocky intertidal habitats do not exist in Chesapeake Bay, the vertical distribution of epifauna on the riprap structures was similar to that in typical rocky intertidal habitats of the Northeast or West coasts of the US (Menge and Branch, 2001). Densities of oysters and mussels were highest in the mid- and low-intertidal zones where desiccation stress at low tide and predation at high tide are minimized. Barnacle densities were highest in the high-intertidal zone in the southern site, similar to that on other rocky intertidal coasts, as the main species, *Cthamalus fragilis*, is more tolerant of heat or desiccation than other epifauna, yet they tend to succumb to competitors at lower tidal ranges (Wethey, 1983, 2002). The slightly greater subtidal densities of barnacles in the northern location are typical of the main species there, *Balanus eburneus*, and may be partially explained by competition with other epifaunal species in the high-intertidal zone, as occurs north of Cape Cod, Massachusetts (Wethey, 2002).

Epifaunal oysters were not found at the northern location, potentially because of extreme cold or freezing of intertidal habitats in the winter (Büttger et al., 2011), the smaller tidal range, or reduced larval influx (Shumway, 1996). In a field survey of oysters on riprap in the Great Wicomico River (south of the Patuxent River) there was a mass mortality of oysters in the mid-intertidal and high-intertidal following an extremely cold winter (R. Lipcius, personal observation), suggesting that cold winter temperatures similarly affect riprap assemblages in other northern locations, such as the Patuxent River.

One estimate claimed that at least 35% of the world is an emerging ecosystem, and this percentage is expected to rise (Marris, 2009). Examples include new forests growing on deteriorated lands in Puerto Rico, tropical savannas in Brazil, re-inhabited kelp forests, and estuaries such as San Francisco Bay (Hobbs et al., 2006). Oil and gas platforms in the Gulf of Mexico allow dispersal of corals into new areas, thereby enhancing populations (Sammarco et al., 2004), and potentially represent an emerging ecosystem. Some emerging ecosystems enhance fish populations (Barwick et al., 2004; Guidetti et al., 2005). Many ecologists fear negative impacts that emerging ecosystems may have on balanced natural systems, but other scientists (Marris, 2009) suggest that these systems may be as or more productive than the natural systems they have replaced. It is important to understand the potential positive effects on secondary production of riprap habitats in Chesapeake Bay, given the trends in human development (Airoldi et al., 2005) and expansion of developed shorelines (Bulleri and Chapman, 2010).

Two attributes are necessary for a system to be an emerging ecosystem: novelty and human agency (Hobbs et al., 2006). The riprap habitat in this study is similar to an emerging ecosystem in that the novelty is the new benthic community established upon the riprap structure, and the human agency is the establishment of the man-made riprap structure, which is usually constructed to reduce shoreline erosion. Man-made habitats are increasing in prevalence and may be important for maintaining biodiversity in an urban landscape (Rebele, 1994; Savard et al., 2000; Sandstrom et al., 2006; Bulleri and Chapman, 2010). For sustainable development, an increased understanding of the ecology of such man-made habitats will be useful to managers and is warranted (Airoldi et al., 2005). As global warming continues to threaten the environment, sea level is estimated to rise 0.2–0.7 m by 2100 (IPCC, 2014), increasing erosion and necessitating additional erosion-protection structures. These structures can exist without completely compromising Chesapeake Bay's ecological health, and understanding these new habitats is important.

Riprap structures provide a compromise between preventing erosion with severe loss of habitat (as with the use of bulkheads)(Scavia et al., 2002) and maintaining biodiversity by serving as substrate for benthic epifauna; thus, they are preferential to other erosion-control measures such as bulkheads. They also may be used in concert with natural living shorelines, for example, as sills shoreward of a marsh (Gittman et al., 2016b), which would provide further benefits to the ecosystem (Living Shoreline Summit Steering Committee, 2006; Scyphers et al., 2011; Wong et al., 2011). Secondary productivity on and adjacent to riprap is high and on par with oyster reefs (Wong et al., 2011), though productivity may be lower than that of marsh or seagrass habitats. The high oyster and mussel biomass and secondary production on these structures also can contribute substantially to ecosystem services such as filtration of phytoplankton and seston, habitat for other epifaunal molluscs and mobile species, and benthic–pelagic coupling (Coen et al., 2007). Hence, this novel, hard-substratum, riprap habitat has promise as a productive component of an emerging ecosystem.

Caution is needed against interpreting these results as evidence that riprap is “good” for the environment, as there is likely a threshold of shoreline development beyond which it would be difficult for the environment to respond (Seitz and Lawless, 2008). However, it is recognized that human alteration of habitats will result in ecosystem changes that must be understood to efficiently protect and restore these habitats.

Ethics statement

Permits and approvals were not necessary for field collections, as only plants and invertebrates were sampled. Land was accessed by boat and homeowners were contacted when appropriate. Field studies did not involve endangered or protected species and no protected species were sampled or kept in captivity. The locations of the study in the Lynnhaven River were Broad Bay (N 36°54′, W 76°03′), Linkhorn Bay (N 36°53′, W 76°00′), and Eastern Branch (N 36°53′, W 76°04′). Sites in the Patuxent River were between N 38°30′, W 76°39′ and N 38°19′, W 76°25′ and in the Piankatank River they were between N 37°54′, W 76°26′ and N 37°54′, W 76°05’.

Author contributions

RDS and RNL conceived and designed the experiments. SA and MW performed the experiments. RDS, SA, RNL, and MW analyzed the data. RDS, SA, RNL, and MW wrote the paper.

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Appendix A

Table A.1
Infaunal species' Latin name (or Group name), abbreviations (used in Fig. A.2), and taxonomic identification (in order of combined abundance across both the Lynnhaven and Patuxent Rivers).

Latin name/Group name	Abbreviation	Taxon
Tagelus plebeius	*T. plebeius*	Bivalve
Limecola (formerly *Macoma*) *balthica*	*L. balthica*	Bivalve
Ensis (formerly *directus*) *leei*	*E. leei*	Bivalve
Gemma gemma	*G. gemma*	Bivalve
Mya arenaria	*M. arenaria*	Bivalve
Mixed polychaetes	Polys	Polychaete
Ameritella (formerly *Macoma*) *mitchelli*	*A. mitchelli*	Bivalve
Mulinia lateralis	*M. lateralis*	Bivalve
Macoploma (formerly *Macoma*) *tenta*	*M. tenta*	Bivalve
Kelliopsis (formerly *Aligena*) *elevata*	*K. elevata*	Bivalve
Glycera dibranchiata	*G. dibranchiata*	Polychaete
Alitta (formerly *Neanthes/Nereis*) *succinea*	*A. succinea*	Polychaete
Drilonereis longa	*D. longa*	Polychaete
Leitoscoloplos sp.	*Leitoscoloplos*	Polychaete

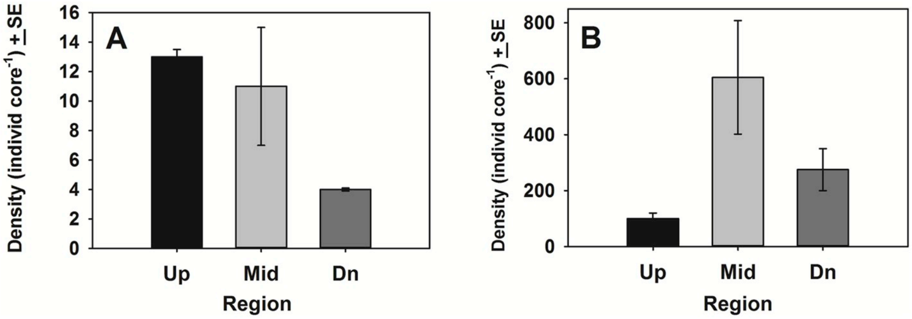

Fig. A.1. Mean infaunal density by Region in the A) Lynnhaven River and B) Patuxent River (note difference in y-axis scale).

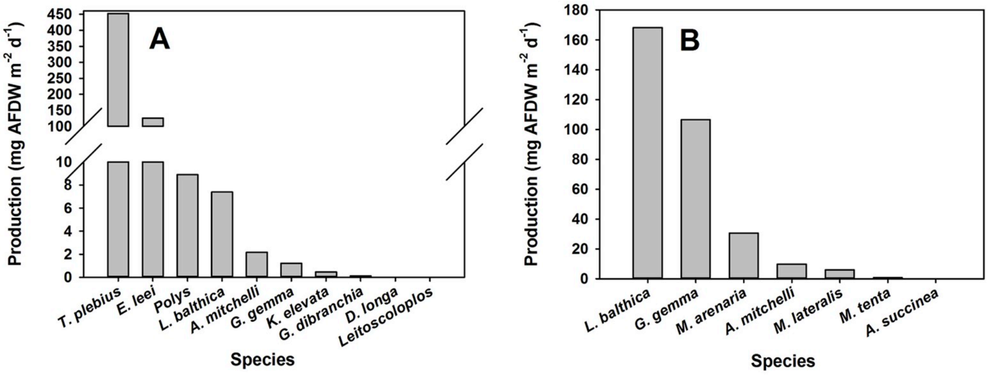

Fig. A.2. Total daily secondary production (Edgar method) summed across sites for most abundant infaunal species in the A) Lynnhaven River and B) Patuxent River (note difference in y-axis scale). (Full species names given in Table A.1.)

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.106357.

References

Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal habitats of Europe. Oceanogr. Mar. Biol. Annu. Rev. 45, 345–405.

Airoldi, L., Abbiati, M., Beck, M.W., Hawkins, S.J., Jonsson, P.R., Martin, D., Moschella, P.S., Sundelöf, A., Thompson, R.C., Åberg, P., 2005. An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. Coast Eng. 52, 1073–1087.

Barwick, R.D., Kwak, T.J., Noble, R.L., Barwick, D.H., 2004. Fish populations associated with habitat-modified piers and natural woody debris in Piedmont Carolina reservoirs. N. Am. J. Fish. Manag. 24, 1120–1133.

Bilkovic, D.M., Mitchell, M.M., 2013. Ecological tradeoffs of stabilized salt marshes as a shoreline protection strategy: effects of artificial structures on macrobenthic assemblages. Ecol. Eng. 61, 469–481.

Bilkovic, D.M., Roggero, M.M., 2008. Effects of coastal development on nearshore estuarine nekton communities. Mar. Ecol. Prog. Ser. 358, 27–39.

Boesch, D.F., 2002. Challenges and opportunities for science in reducing nutrient overenrichment of coastal ecosystems. Estuaries 25, 886–900.

Bonsdorff, E., Blomqvist, E.M., 1993. Biotic couplings on shallow water soft bottoms—examples from the northern Baltic Sea. Oceanogr. Mar. Biol. Annu. Rev. 31, 153–176.

Boynton, W.R., Hagy, J.D., Cornwell, J.C., Kemp, W.M., Greene, S.M., Owens, M.S., Baker, J.E., Larsen, R.K., 2008. Nutrient budgets and management actions in the Patuxent River estuary, Maryland. Estuar. Coasts 31, 623–651.

Bradley, C., 2011. Impacts of Shoreline Development on Shallow-Water Benthic Communities in the Patuxent River, MD. Master's Thesis. College of William & Mary, pp. 93.

Brauns, M., Garcia, X.F., Walz, N., Pusch, M.T., 2007. Effects of human shoreline development on littoral macroinvertebrates in lowland lakes. J. Appl. Ecol. 44, 1138–1144.

Bulleri, F., Airoldi, L., 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. J. Appl. Ecol. 42, 1063–1072.

Bulleri, F., Chapman, M.G., 2010. The introduction of coastal infrastructure as a driver of change in marine environments. J. Appl. Ecol. 47, 26–35.

Bulleri, F., Abbiati, M., Airoldi, L., 2006. The colonisation of humanmade structures by the invasive alga *Codium fragile* ssp. *tomentosoides* in the north Adriatic Sea (NE Mediterranean). Hydrobiol. (Sofia) 555, 263–269.

Burke, R.P., 2010. Alternative Substrates as a Native Oyster (*Crassostrea virginica*) Reef Restoration Strategy in Chesapeake Bay. PhD Dissertation. College of William & Mary.

Büttger, H., Nehls, G., Witte, S., 2011. High mortality of pacific oysters in a cold winter in the north-Frisian wadden sea. Helgol. Mar. Res. 65, 525–532.

Chapman, M.G., Underwood, A.J., 2011. Evaluation of ecological engineering of "armoured" shorelines to improve their value as habitat. J. Exp. Mar. Biol. Ecol. 400, 302–313.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6. User Manual PRIMER-E, Plymouth, UK.

Coen, L.D., Brumbaugh, R.D., Bushek, D., Grizzle, R., Luckenbach, M.W., Posey, M.H., Powers, S.P., Tolley, S.G., 2007. Ecosystem services related to oyster restoration. Mar. Ecol. Prog. Ser. 341, 303–307.

Connell, J.H., 1972. Community interactions on marine rocky intertidal shores. Annu. Rev. Ecol. Systemat. 3, 169–192.

Costanza, R., 1992. Toward an operational definition of ecosystem health. Ecosyst. Health: N. Goals Environ. Manag. 1992, 239–256.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., Van Den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–261.

Currin, C.A., Chappell, W.S., Deaton, A., 2010. Developing alternative shoreline armoring strategies: the living shoreline approach in North Carolina. In: Shipman, H., Dethier, M.N., Glefenbaum, G., Fresh, K.L., Dinicola, R.S. (Eds.), Puget Sound Shorelines and the Impacts of Armoring – Proceedings of the State of the Science Workshop, May 2009: United States Geological Survey Scientific Investigations Report 2010-5254. Reston, VA, pp. 91–102.

Cusson, M., Bourget, E., 2005. Global patterns of macroinvertebrate production in marine benthic habitats. Mar. Ecol. Prog. Ser. 297, 1–14.

Davenport, T.M., Seitz, R.D., Knick, K.E., Jackson, N., 2018. Living shorelines support nearshore benthic communities in upper and lower Chesapeake Bay. Estuar. Coasts 41, 197–206. https://doi.org/10.1007/s12237-017-0361-8.

Davis, J.L.D., Takacs, R.L., Schnabel, R., 2006. Evaluating ecological impacts of living shorelines and shoreline habitat elements: an example from the upper western Chesapeake Bay. In: Erdle, S.Y., Davis, J.L., Sellner, K.G. (Eds.), Management Policy, Science and Engineering of Nonstructural Erosion Control in the Chesapeake Bay: Proceedings of the 2006 Living Shoreline Summit. CRC Publ. 08-164. CRC Press, Annapolis, MD, pp. 55–61.

D'Elia, C.F., Boynton, W.R., Sanders, J.G., 2003. A watershed perspective on nutrient enrichment, science, and policy in the Patuxent River, Maryland: 1960–2000. Estuaries 26, 171–185.

Diaz, R.J., Fredette, T., 1982. Secondary production of some dominant macroinvertebrate species inhabiting a bed of submerged vegetation in the lower Chesapeake Bay, SRAMSOE 267. In: Orth, R.J., van Montfrans, J. (Eds.), Structural and Functional Aspects of the Biology of Submerged Aquatic Macrophyte Communities in the Lower Chesapeake Bay, Volume III. Interactions of Resident Consumers in a Temperate Estuarine Seagrass Community: Vaucluse Shores, Virginia. Virginia Institute of Marine Science, Gloucester Point, VA, pp. 95–123.

Diaz, R.J., Schaffner, L.C., 1990. The functional role of estuarine benthos. In: Haire, M., Krone, E.C. (Eds.), Perspectives on the Chesapeake Bay 1990. Chesapeake Research Consortium, Gloucester Point, Virginia, pp. 25–56.

Diaz, R.J., Markwith, G., Orth, R.J., Rizzo, W., Wetzel, R., 1982. Examination of Tidal Flats, vol. 1 FHWA/RD-80/181, Washington, DC.

Dolbeth, M., Lillebo, A.I., Cardoso, P.G., Ferreira, S.M., Pardal, M.A., 2005. Annual production of estuarine fauna in different environmental conditions: an evaluation of the estimation methods. J. Exp. Mar. Biol. Ecol. 326, 115–127.

Douglass, S.L., Pickel, B.H., 1999. The tide doesn't go out anymore - the effect of bulkheads on urban shorelines. Shore Beach 67, 19–25.

Dugan, J.E., Airoldi, L., Chapman, M.G., Walker, S.J., Schlacher, T., 2011. Estuarine and coastal structures: environmental effects, A focus on shore and nearshore structures. In: Wolanski, E., McLusky, D. (Eds.), Treatise on Estuarine and Coastal Science. Academic Press, Waltham, MA, pp. 17–41.

Edgar, G.J., 1990. The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. J. Exp. Mar. Biol. Ecol. 137, 215–240.

Edgar, G.J., Barrett, N.S., 2002. Benthic macrofauna in Tasmanian estuaries: scales of distribution and relationships with environmental variables. J. Exp. Mar. Biol. Ecol. 270, 1–24.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Systemat. 34, 487–515.

Firth, L.B., Crowe, T.P., Moore, P., Thompson, R.C., Hawkins, S.J., 2009. Predicting impacts of climate-induced range expansion: an experimental framework and a test involving key grazers on temperate rocky shores. Glob. Chang. Biol. 15, 1413–1422.

Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airoldi, L., Bouma, T.J., Bozzeda, F., Ceccherelli, V.U., Colangelo, M.A., Evans, A., Ferrario, F., Hanley, M.E., Hinz, H., Hoggart, S.P.G., Jackson, J.E., Moore, P., Morgan, E.H., Perkol-Finkel, S., Skov, M.W., Strain, E.M., Hawkins, S.J., 2014. Between a rock and a hard place: environmental and engineering considerations when designing coastal defence structures. Coast Eng. 87, 122–135.

Folk, R.L., 1980. Petrology of Sedimentary Rocks. Hemphill Publishing, Austin, TX.

French McCay, D.P., Rowe, J.J., 2003. Habitat restoration as mitigation for lost production at multiple trophic levels. Mar. Ecol. Prog. Ser. 264, 233–247.

Geraldi, N.R., Smyth, A.R., Piehler, M.F., Peterson, C.H., 2014. Artificial substrates enhance non-native macroalga and N_2 production. Biol. Invasions 16, 1819–1831. https://doi.org/10.1007/s10530-013-0629-2.

Gittman, R.K., Scyphers, S.B., Smith, C.S., Neylan, I.P., Grabowski, J.H., 2016a. Ecological consequences of shoreline hardening: a meta-analysis. Bioscience 66, 763–773. https://doi.org/10.1093/biosci/biw091.

Gittman, R.K., Peterson, C.H., Currin, C.A., Fodrie, F.J., Piehler, M.F., Bruno, J.F., 2016b. Living shorelines can enhance the nursery role of threatened estuarine habitats. Ecol. Appl. 26, 249–263. https://doi.org/10.1890/14-0716.

Gittman, R.K., Fodrie, F.J., Popowich, A.M., Keller, D.A., Bruno, J.F., Currin, C.A., Peterson, C.H., Piehler, M.F., 2015. Engineering away our natural defenses: an analysis of shoreline hardening in the US. Front. Ecol. Environ. 13, 301–307.

Glasby, T.M., Connell, S.D., 1999. Urban structures as marine habitats. Ambio 28, 595–598.

Glasby, T.M., Connell, S.D., Holloway, M.G., Hewitt, C.L., 2007. Nonindigenous biota on artificial structures: could creation facilitate biological invasions? Mar. Biol. 151, 887–895.

Goodsell, P.J., Chapman, M.G., Underwood, A.J., 2007. Differences between biota in anthropogenically fragmented habitats and in naturally patchy habitats. Mar. Ecol. Prog. Ser. 351, 15–23.

Grizzle, R.E., Greene, J.K., Coen, L.D., 2008. Seston removal by natural and constructed intertidal eastern oyster (*Crassostrea virginica*) reefs: a comparison with previous laboratory studies, and the value of in situ methods. Estuar. Coasts 31, 1208–1220.

Guidetti, P., Bussotti, S., Boero, F., 2005. Evaluating the effects of protection on fish predators and sea urchins in shallow artificial rocky habitats: a case study in the northern Adriatic Sea. Mar. Environ. Res. 59, 333–348.

Gutiérrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101, 79–90.

Hagy, J.D., 2002. Eutrophication, Hypoxia, and Trophic Transfer Efficiency in Chesapeake Bay. PhD dissertation. University of Maryland, Center for Environmental Science, Solomons, MD.

Hartzell, J.L., Jordan, T.E., Cornwell, J.C., 2010. Phosphorus burial in sediments along the salinity gradient of the Patuxent River, a subestuary of the Chesapeake Bay (USA). Estuar. Coasts 33, 92–106.

Hobbs, R.J., Higgs, E., Harris, J.A., 2009. Novel ecosystems: implications for conservation and restoration. Trends Ecol. Evol. 24, 599–605.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A.G., Epstein, P.R., Ewel, J.J., Klink, C.A.G., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vila, M., Zamora, R., Zobel, M., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Glob. Ecol. Biogeogr. 15, 1–7.

Hummel, H., Amiard-Triquet, C., Bachelet, G., Desprez, M., Marchand, J., Sylvand, B., Amiard, J.C., Rybarczyk, H., Bogaards, R.H., Sinke, J., De Wit, Y., 1996. Sensitivity to stress of the estuarine bivalve *Macoma balthica* from areas between The Netherlands and its southern limits (Gironde). J. Sea Res. 35, 315–321.

IPCC 2014, Team, C.W., Pachauri, R.K., Meyer, L.A., 2014. IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland, pp. 151. http://ipcc.ch/pdf/assessment-report/ar5/syr/AR5_SYR_FINAL_SPM.pdf.

Jackson, A.C., Chapman, M.G., Underwood, A.J., 2008. Ecological interactions in the provision of habitat by urban development: whelks and engineering by oysters on artificial seawalls. Austral Ecol. 33, 307–316.

Karp, M.A., Seitz, R.D., Fabrizio, M.C., 2018. Faunal communities on restored oyster reefs: effects of habitat complexity and environmental conditions. Mar. Ecol. Prog. Ser. 590, 35–51. https://doi.org/10.3354/meps12470.

Kennish, M.J., 2001. Coastal salt marsh systems in the US: a review of anthropogenic impacts. J. Coast. Res. 17, 731–748.

Kennish, M.J., 2002. Environmental threats and environmental future of estuaries. Environ. Conserv. 29, 78–107.

King, R.S., Hines, A.H., Craige, F.D., Grap, S., 2005. Regional, watershed and local correlates of blue crab and bivalve abundances in subestuaries of Chesapeake Bay, USA. J. Exp. Mar. Biol. Ecol. 319, 101–116.

Kohler, K.E., Gill, S.M., 2006. Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Comput. Geosci. 32, 1259–1269. https://doi.org/10.1016/j.cageo.2005.11.009.

Krebs, C.J., 1989. Ecological Methodology. No. QH541. 15. S72. K74 1999. Harper and Row, New York, NY.

Lenihan, H.S., Micheli, F., 2001. Soft-sediment communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), Marine Community Ecology. Sinauer Associates, Inc, Sunderland, MA, pp. 253–287.

Lipcius, R.N., Burke, R.P., 2018. Successful recruitment, survival and long-term persistence of eastern oyster and hooked mussel on a subtidal, artificial restoration reef system in Chesapeake Bay. PLoS One 13 (10), e0204329. https://doi.org/10.1371/journal.pone.0204329.

Liversage, K., Chapman, M.G., 2018. Coastal ecological engineering and habitat restoration: incorporating biologically diverse boulder habitat. Mar. Ecol. Prog. Ser. 593, 173–185.

Living Shoreline Summit Steering Committee, 2006. Preface. In: Proceedings of the 2006 Living Shoreline Summit, Chesapeake Bay. CRC Publ. No. 08–164, Annapolis, MD.

Long, W.C., Seitz, R.D., 2009. Hypoxia in Chesapeake Bay tributaries: worsening effects of hypoxia on macrobenthic community structure in Chesapeake Bay tributaries. Estuar. Coasts 32, 287–297.

Lovall, C.D., Seitz, R.D., Knick, K.E., 2017. Benthic communities and trophic structure at altered shorelines in a depauperate estuary. Bull. Mar. Sci. 93 (3), 715–741.

Magurran, A.E., 2004. Measuring Biological Diversity. Chapter 4, an Index of Diversity. Blackwell Science Ltd, Oxford, UK.

Marris, E., 2009. Ragamuffin earth. Nature 460, 450–453.

McCann, K.S., 2000. The diversity-stability debate. Nature 405, 223–233.

Menge, B.A., Branch, M.A., 2001. Rocky intertidal communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), Marine Community Ecology. Sinauer Associates.

Menge, B.A., Sutherland, J.P., 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am. Nat. 110, 351–369.

Menge, B.A., Sutherland, J.P., 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. 130, 730–757.

Milton, S.J., 2003. 'Emerging ecosystems': a washing-stone for ecologists, economists and sociologists? South Afr. J. Sci. 99, 404–406.

Nuzzo, R., 2014. Scientific method: statistical errors. Nat. News 506 (7487), 150.

Ouboter, M.R.L., Van Eck, B.T.M., Van Gils, J.A.G., Sweerts, J.P., Villars, M.T., 1998. Water quality modeling of the western Scheldt estuary. Hydrobiologia 366, 129–142.

Paine, R.T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65–75.

Peterson, C.H., Kneib, R.T., Manen, C.A., 2003. Scaling restoration actions in the marine environment to meet quantitative targets of enhanced ecosystems services. Mar. Ecol. Prog. Ser. 264, 173–175.

Pianka, E.R., 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat. 33–46.

Piazza, B.P., Banks, P.D., La Peyre, M.K., 2005. The potential for created oyster shell reefs as a sustainable shoreline protection strategy in Louisiana. Restor. Ecol. 13, 499–506.

Pister, B., 2009. Urban marine ecology in southern California: the ability of riprap structures to serve as rocky intertidal habitat. Mar. Biol. 156, 861–873.

Plumb Jr., R.H., 1981. Procedures for Handling and Chemical Analysis of Sediment and Water Samples. Environmental Laboratory, US Army Waterways Experiment Station, Vicksburg, MS Technical Report EPA/CE-81-1. Prepared by Great Lakes Laboratory, State University College at Buffalo, Buffalo, NY for the US Environmental Protection Agency/Corps of Engineers Technical Committee on Criteria for Dredged and Filled Material.

Powell, E.N., Kraeuter, J.N., Ashton-Alcox, K.A., 2006. How long does oyster shell last on an oyster reef? Estuarine. Coast Shelf Sci. 69, 531–542.

Rapport, D.J., Costanza, R., McMichael, A.J., 1998. Assessing ecosystem health. Trends Ecol. Evol. 13 (10), 397–402.

Rebele, F., 1994. Urban ecology and special features of urban ecosystems. Glob. Ecol. Biogeogr. 4, 173–187.

Sammarco, P.W., Atchison, A.D., Boland, G.S., 2004. Expansion of coral communities within the Northern Gulf of Mexico via offshore oil and gas platforms. Mar. Ecol. Prog. Ser. 280, 129–143.

Sandstrom, U.G., Angelstam, P., Khakee, A., 2006. Urban comprehensive planning – identifying barriers for the maintenance of functional habitat networks. Landsc. Urban Plan. 75, 43–57.

Savard, J.P.L., Clergeau, P., Mennechez, G., 2000. Biodiversity concepts and urban ecosystems. Landsc. Urban Plan. 48, 131–142.

Scavia, D., Field, J.C., Boesch, D.F., Buddermeier, R.W., Burkett, V., Cayan, D.R., Fogarty, M., Harewell, M.A., Howarth, R.W., Mason, C., Reed, D.J., Royer, T.C., Sallenger, A.H., Titus, J.G., 2002. Climate change impacts on U.S. coastal and marine ecosystems. Estuaries 25, 149–164.

Schaeffer, D.J., Herricks, E.E., Kerster, H.W., 1988. Ecosystem health: I. Measuring ecosystem health. Environ. Manag. 12, 445–455.

Schleupner, C., 2008. Evaluation of coastal squeeze and its consequences for the Caribbean island Martinique. Ocean Coast Manag. 51, 383–390.

Scyphers, S.B., Powers, S.P., Heck Jr., K.L., Byron, D., 2011. Oyster reefs as natural breakwaters mitigate shoreline loss and facilitate fisheries. PLoS One 6 (8), e22396. https://doi.org/10.1371/journal.pone.0022396.

Seitz, R.D., Lawless, A., 2008. Landscape-level impacts of shoreline development upon Chesapeake Bay benthos and their predators. In: Erdle, S.Y., Davis, J.L., Sellner, K.G. (Eds.), Management Policy, Science and Engineering of Nonstructural Erosion Control in the Chesapeake Bay: Proceedings of the 2006 Living Shoreline Summit. CRC Publ. 08–164. CRC Press, Annapolis, MD, pp. 63–70.

Seitz, R.D., Dauer, D.M., Llansó, R.J., Long, W.C., 2009. Broad-scale effects of hypoxia on benthic community structure in Chesapeake Bay, USA. J. Exp. Mar. Biol. Ecol. 381, S4–S12. https://doi.org/10.1016/j.jembe.2009.07.004.

Seitz, R.D., Knick, K.E., Davenport, T.M., Saluta, G.S., 2018. Human influence at the coast: upland and shoreline stressors affect coastal macrofauna and are mediated by salinity. Estuar. Coasts 41, 114–130. https://doi.org/10.1007/s12237-017-0347-6.

Seitz, R.D., Lipcius, R.N., Olmstead, N.H., Seebo, M.S., Lambert, D.M., 2006. Influence of shallow-water habitats and shoreline development on abundance, biomass, and diversity of benthic prey and predators in Chesapeake Bay. Mar. Ecol. Prog. Ser. 326, 11–27.

Shumway, S.E., 1996. Natural environmental factors. In: Kennedy, V.S., Newell, R.I.E., Eble, A.F. (Eds.), The Eastern Oyster *Crassostrea virginica*. Maryland Sea Grant College, College Park, MD, pp. 467–513.

Sisson, M., Wang, H., Li, Y., Shen, J., Kuo, A., Gong, W., Brush, M., Moore, K., 2010. Development of Hydrodynamic and Water Quality Models for the Lynnhaven River System. Final Report to the U. S. Army Corps of Engineers, Fort Norfolk Office and the City of Virginia Beach. Special Report in Applied Marine Science and Ocean Engineering No. 408. Virginia Institute of Marine Science, The College of William and

Mary, Gloucester Point, VA.

Soniat, T.M., Burton, G.M., 2005. A comparison of the effectiveness of sandstone and limestone as cultch for oysters, *Crassostrea virginica*. J. Shellfish Res. 24, 483–485.

Spellerberg, I.F., Fedor, P.J., 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. Glob. Ecol. Biogeogr. 12, 177–179.

Strain, E.M.A., Morris, R.L., Coleman, R.A., Figueira, W.F., Steinberg, P.D., Johnston, E.L., Bishop, M.J., 2018a. Increasing microhabitat complexity on seawalls can reduce fish predation on native oysters. Ecol. Eng. 120, 637–644. https://doi.org/10.1016/j.ecoleng.2017.05.030.

Strain, E.M., Olabarria, C., Mayer-Pinto, M., Cumbo, V., Morris, R.L., Bugnot, A.B., Dafforn, K.A., Heery, E., Firth, L.B., Brooks, P.R., Bishop, M.J., 2018. Eco-engineering urban infrastructure for marine and coastal biodiversity: which interventions have the greatest ecological benefit? J. Appl. Ecol. 55, 426–441.

Sturdivant, S.K., Díaz, R.J., Llansó, R., Dauer, D.M., 2014. Relationship between hypoxia and macrobenthic production in Chesapeake Bay. Estuar. Coasts 37, 1219–1232.

Theuerkauf, S.J., Burke, R.P., Lipcius, R.N., 2015. Settlement, growth and survival of eastern oysters on alternative reef substrates. J. Shellfish Res. 34, 241–250.

Tyrell, M., Byers, J., 2007. Do artificial substrates favor nonindigenous fouling species over native species? J. Exp. Mar. Biol. Ecol. 342, 54–60.

Underwood, A.J., 1997. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge, UK.

Underwood, A.J., Chapman, M.G., 1996. Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia 107, 212–224.

Vaselli, S., Bulleri, F., Benedetti-Cecchi, L., 2008. Hard coastal-defence structures as habitats for native and exotic rocky-bottom species. Mar. Environ. Res. 66, 395–403.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science 277, 494–499.

Warton, D.I., Duursma, R.A., Falster, D.S., Taskinen, S., 2012. SMATR 3 – an R package for estimation and inference about allometric lines. Methods Ecol. Evol. 3, 257–259. https://doi.org/10.1111/j.2041-210X.2011.00153.x.

Wethey, D.S., 1983. Geographic limits and local zonation: the barnacles *Semibalanus* (*Balanus*) and *Chthamalus* in new england. Biol. Bull. 165, 330–334.

Wethey, D.S., 2002. Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. Integr. Comp. Biol. 42, 872–880.

Wilbur, D., Clarke, D., 1998. Estimating secondary production and benthic consumption in monitoring studies: a case study of the impacts of dredged material disposal in Galveston Bay, Texas. Estuar. Coasts 21, 230–245.

Wilson Jr., W.H., 1989. Predation and the mediation of intraspecific competition in an infaunal community in the Bay of Fundy. J. Exp. Mar. Biol. Ecol. 132 (3), 221–245.

Wong, M.C., Peterson, C.H., Piehler, M.F., 2011. Evaluating estuarine habitats using secondary production as a proxy for food web support. Mar. Ecol. Prog. Ser. 440, 11–25.