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Loss of seagrass results in changes to benthic infaunal community structure and decreased secondary production

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ABSTRACT.—Seagrass beds have decreased in abundance and areal coverage over the past several decades. Although previous studies have examined the importance of seagrass for benthic community assemblages and abundances, the effect of seagrass on deep-dwelling, large (high-biomass) infauna and the importance for benthic secondary production in Chesapeake Bay have not been addressed. Using benthic suction and push cores, we compared density, diversity, and secondary productivity of benthic communities in seagrass to those in other shallow-water habitats and estimated benthic secondary productivity lost in the York River due to loss of seagrass from 1971 to 2016. We examined four habitat types in the York River: unvegetated, *Gracilaria* spp., mixed seagrass (multiple seagrass species), and *Zostera marina* L. seagrass. Physical characteristics of habitat types and biomass of organisms were assessed, and annual secondary productivity was calculated using biomass and production-to-biomass ratios. Benthic density, diversity, secondary productivity, sedimentary chlorophyll *a*, and percent sand were all highest in seagrass beds with *Z. marina* alone. Approximately 35% of benthic secondary productivity, or 1.51×10^8 g C yr⁻¹, was lost in the York River in 1971–2016 due to the loss of seagrass beds to unvegetated substrate. The loss of seagrass in the York River over time and the associated decrease in benthic secondary productivity that we estimated could have negative consequences for the productivity of epibenthic predators. Our data emphasize the importance of conservation and restoration of seagrass.

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Seagrasses, including eelgrass, *Zostera marina* L. (hereafter referred to as *Zostera*), and widgeon grass, *Ruppia maritima* L. (hereafter referred to as *Ruppia*), serve important ecological functions and provide critical ecosystem services (Costanza et al. 1997), such as habitat provisioning (Orth et al. 1984, Heck et al. 2003), nutrient cycling (Wigand et al. 2001, Romero et al. 2006), sediment stabilization (Bos et al. 2007), and wave baffling (Peterson et al. 2004, Gruber et al. 2011). A major ecological function of seagrass is as a nursery habitat (Heck and Thoman 1984, Heck et al. 2003), particularly for epibenthic predators, such as blue crabs, *Callinectes sapidus* Rathbun, 1896 (Beck et al. 2001, Lipcius et al. 2007, Jones 2014). Seagrass abundance

and diversity have declined globally over the long term (Orth et al. 2010), and ecosystem services, such as provision of habitat, are concurrently lost (Waycott et al. 2009, Short et al. 2011).

In Chesapeake Bay over the last 100 yrs, seagrass beds have been affected by multiple stressors, including disease, storms, and eutrophication (Lefcheck et al. 2017). In the 1930s, eelgrass wasting disease caused a dramatic decline in seagrass areal coverage (Orth and Moore 1984), and it rebounded in the 1960s (Lefcheck et al. 2017). Eelgrass declined by >50% with the passage of Tropical Storm Agnes in 1972 (Orth and Moore 1983, Orth et al. 2010, Lefcheck et al. 2017), and it never recovered. With the constant pressures of global environmental change, seagrass has been further decimated by additional stressors, including increased temperatures (Moore and Jarvis 2008) and eutrophication, that has decreased water clarity (Orth et al. 2010, Patrick and Weller 2015). Over the past decades, high-salinity, polyhaline regions in Chesapeake Bay have experienced decreases in seagrass density, areal coverage, and the depth at which seagrass can grow (Orth and Moore 1988, Moore et al. 1997, 2014, Orth et al. 2010). Turbidity and nutrient levels in the Chesapeake Bay are the main factors affecting seagrass survival in this system (Moore et al. 1997, Moore et al. 2001, Orth et al. 2010). An overall increase in turbidity and nutrients have caused light attenuation, epiphyte growth, and phytoplankton blooms, which have decreased the abundance of seagrass (Jernakoff et al. 1996, Duffy et al. 2001, 2003, Moore et al. 2012). Recently, nutrient reductions have led to seagrass recovery in Chesapeake Bay (Lefcheck et al. 2018).

Along with the decrease in seagrass in Chesapeake Bay, there has been a spread of the exotic macroalga *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Thomsen et al. 2006b). This species is potentially replacing some of the ecological functions of seagrass, such as providing structure for juvenile blue crabs (Johnston and Lipcius 2012). There are both native and exotic species of *Gracilaria* in Chesapeake Bay; the two native species are *Gracilaria tikvahiae* McLachlan (formerly *Gracilaria foliifera* var. *angustissima*), and *Gracilariopsis longissima* (S.G. Gmelin) M.Steentoft, L.M.Irvine and W.F.Farnham, 1995 (formerly *Gracilaria verrucosa*), and the exotic species is *G. vermiculophylla* (Thomsen et al. 2006b). *Gracilaria* spores attach to benthic substrates (such as pieces of shell or worm tubes) and the species can form large, dense beds in shallow habitats (Bellorin et al. 2004, Freshwater et al. 2006). At intermediate levels of algal biomass, *Gracilaria* may add structural complexity that supports faunal communities (Thomsen et al. 2006a, 2009, Byers et al. 2012). It appears that increases in algal biomass in Chesapeake Bay are due to the non-native species of *G. vermiculophylla* (hereafter *Gracilaria*), as has occurred in other systems (Ramus et al. 2017, Wood 2017). The ability of this new habitat to also support infaunal benthic communities in Chesapeake Bay remains untested.

Seagrass beds are also important as benthic habitats that provide primary production by autotrophs and secondary production by infaunal and epifaunal benthos, which support higher trophic levels. The combination of phytoplankton, seagrass, macroalgae, epiphytic algae attached to seagrass leaves, and benthic microalgae living in the surficial sediments enrich sediments, making seagrass beds habitats of high primary productivity (Orth et al. 1984, Valentine et al. 2002). The epifaunal and infaunal organisms supported by this productivity allow fish and crab predators to use the seagrass beds as foraging sites where they can feed on seagrass inhabitants (Heck and Thoman 1984, Bell and Westoby 1987, Fredette et al. 1990). Density of

infauna and epifauna is higher in seagrass than unvegetated habitats in many systems (Orth et al. 1984 and references therein, Edgar 1990, Boström and Bonsdorff 1997), as roots, rhizomes, and shoots of seagrass plants provide some protection from predation (Orth et al. 1984, Seitz et al. 2001). They also stabilize the sediment, increasing food availability, and reduce wave action (Fonseca et al. 1982, Lewis 1984). Previous studies examining infauna and epifauna were conducted using methods that only collect organisms within approximately the upper 12 cm of the sediment column (e.g., Stoner 1980, Wong et al. 2011). Larger infauna, such as some bivalves, tend to reside deeper in the sediment (Hines and Comtois 1985) and may not have been accounted for by previous sampling. These larger infauna serve as important food sources for many epibenthic-feeding predators (Laughlin 1982, Hines et al. 1990, Mansour 1992). Therefore, the effects of seagrass on deep-dwelling benthic organisms and their contribution to secondary production need to be adequately assessed to fully understand food-web dynamics in seagrass beds and potential impacts of seagrass loss.

Annual secondary production ($\text{g C m}^{-2} \text{ yr}^{-1}$) of benthic organisms is important because it represents the amount of food available to higher trophic levels, and it can reflect habitat quality and ecosystem functioning (Wilber and Clarke 1998, Dolbeth et al. 2005). Importantly, secondary production is also a valuable metric because many ecosystem services scale to biological production; it integrates over time and space, it synthesizes contributions to food resources, and it accounts for benefits of habitat structure. However, direct estimations of secondary productivity can be labor intensive and cost prohibitive (Wilber and Clarke 1998). Estimation of secondary production using biomass and published production:biomass (i.e., P:B) ratios provides a relatively simple and standard method that can be employed in comparisons within and among ecosystems (Banse and Mosher 1980, Wong et al. 2011). By estimating productivity, one can determine the energy budget of a system, as well as predict potential yields for fishery species (Cowley and Whitfield 2002).

Many studies have documented that seagrass presence can influence the abundance of benthic organisms (Stoner 1980, Orth et al. 1984, Fredette et al. 1990, Boström and Bonsdorff 1997), and some have examined benthic secondary production in adjacent seagrass and unvegetated habitats in other ecosystems (e.g., Gulf of Mexico, Valentine and Heck 1993, Bologna and Heck 2002; New England, Heck et al. 1995; Southeastern US, Wong et al. 2011; Australia, Edgar 1990). Yet previous studies have not examined the importance of deep-dwelling infauna to secondary production in seagrass, algal, and unvegetated habitats. In addition to vegetation type, other characteristics of the benthic habitat can influence secondary production, and they should be accounted for when elucidating the impacts of vegetation on infaunal production. In general, benthic secondary production is higher in mixed and sandy sediments than in muddy sediments, and varies with salinity and temperature (Diaz and Schaffner 1990). Little information exists on benthic secondary production in various structured habitats in Chesapeake Bay.

In the present study, we focused on density, diversity, and secondary productivity of benthic organisms in seagrass habitats as compared to other shallow-water habitats, and we estimated secondary production lost due to seagrass decline in the York River, Chesapeake Bay. Although we have data on seagrass loss for the entire bay, the benthic productivity measurements come from the York River estuary, so we are most confident in applying our estimates of ecosystem services lost to the York River

only. We examined secondary production ($\text{g C m}^{-2} \text{ yr}^{-1}$) by measuring biomass and using published P:B ratios for Chesapeake Bay organisms (Diaz and Schaffner 1990) to estimate total annual production, as done in previous studies (Diaz and Fredette 1982, Hagy 2002, Wong et al. 2011). Estimations of biomass allowed us to calculate productivity in each habitat type (Randall and Minns 2000). We hypothesized that density, diversity, and secondary production would be high in *Zostera* seagrass habitats as compared to other shallow-water habitat types. We used digitized seagrass maps to determine changes in areal coverage of seagrass beds from 1971 to 2016. These maps, in combination with our estimates of secondary productivity for each habitat type, were used to quantify productivity lost due to degradation of seagrass habitats in the York River, Chesapeake Bay, from 1971 to 2016.

METHODS

STUDY SITES.—Our studies were conducted in four shallow-water (<2 m depth) habitat types, all located adjacent to the mouth of the Perrin River, a tributary of the York River. The York River has seagrass beds in the mainstem that are primarily *Z. marina* and *R. maritima* (Moore et al. 2000), and there are also habitats with the exotic red macroalgae (*G. vermiculophylla*; Johnston and Lipcius 2012). Therefore, our experimental habitat types included unvegetated mud, mud with the red macroalgae (*Gracilaria*) attached to the bottom, mixed seagrass including *Zostera* and *Ruppia*, and *Zostera* seagrass (Fig. 1). The mixed seagrass habitat type consisted of an approximately equal amount of the seagrass *Z. marina* and *R. maritima* (a narrower blade, shorter seagrass plant; Moore et al. 2014). In summer of 2007, three replicate sampling locations were randomly chosen within each of the four habitat types. Seagrass patch size, shoot density, and depth were consistent among seagrass sampling locations. Though our study was conducted in a limited geographic region (Perrin River) and at one point in time, other analyses of seagrass-resident organisms have found this area to be similar to other regions of the York River Estuary, thus we are confident in extending our results to the York River Estuary in general (Pardieck et al. 1999, Ralph et al. 2013).

FIELD SAMPLING.—At each location, we characterized the sediment by measuring benthic chlorophyll *a* (methods modified from Lorenzen 1967), analyzing grain size (Plumb 1981), and measuring sedimentary carbon and nitrogen (to get organic content of the sediment) (CHN analysis in a Perkin Elmer 2400, Series 2 CHN S/O analyzer) to elucidate differences by habitat type. At each location, we took two types of samples to examine the benthos: (1) a suction sample for deep-dwelling benthos; and (2) a push-core sample for shallow-dwelling, smaller benthos. For the suction sample, a 0.11 m² PVC core was pushed into the sediment to approximately 40 cm depth. A suction apparatus was then used to vacuum the sediment within the cylinder into a coarse mesh bag (3 mm) to sample organisms that dwell deep in the sediment or are sparsely distributed, such as large bivalves (Eggleston et al. 1992). This methodology also collects some epifauna, though it is not designed for their collection. For the push-core sampling, we used a 10-cm diameter core (0.008 m²) that was pushed 15 cm into the sediment, and contents were sieved through a 500- μm mesh to collect smaller organisms that dwell closer to the surface.

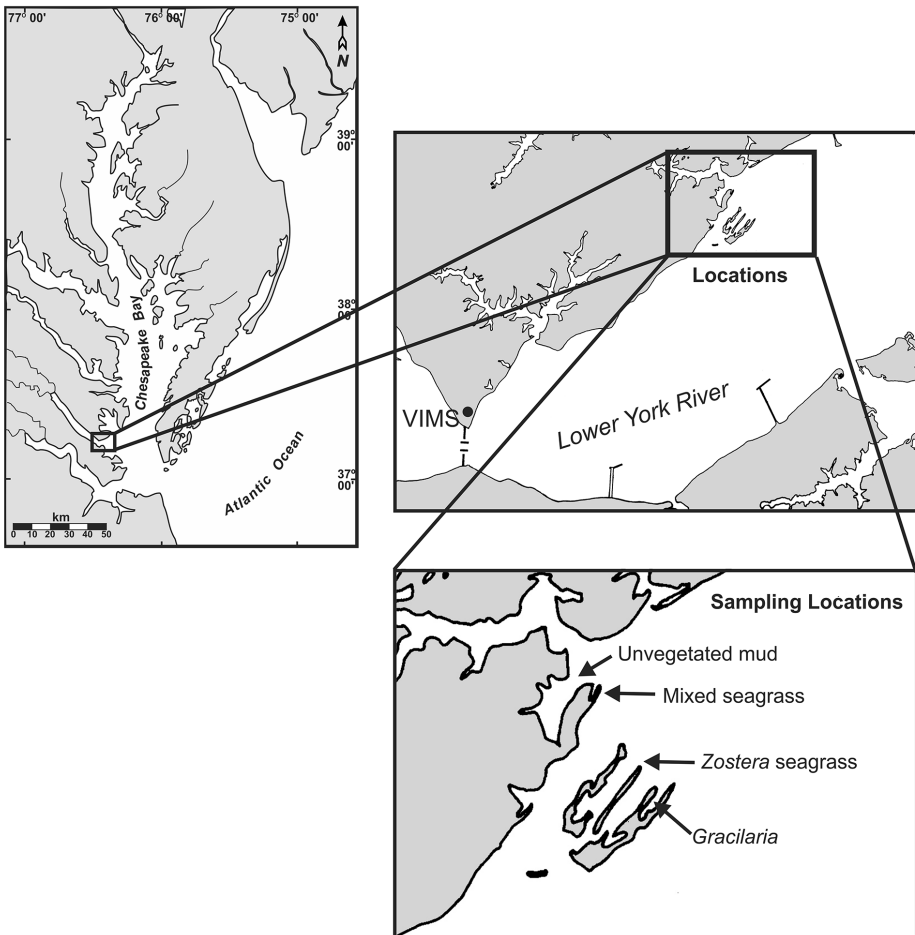


Figure 1. Chesapeake Bay (top left panel), Lower York River (top right panel), and Sampling Locations of various habitat types (bottom right panel). Location of the Virginia Institute of Marine Science (VIMS) indicated.

LABORATORY METHODS.—Contents of all suction samples were identified to the lowest possible taxonomic level (usually species), dried for 48 hrs at 60 °C, and combusted for 4 hrs at 550 °C to obtain ash-free-dry-weight (AFDW) biomass (Diaz and Schaffner 1990). We also assessed Shannon-Wiener (H') diversity using PRIMER v5.2.9 (Clarke and Gorley 2001, Clarke and Warwick 2001). Of the three 500- μm samples taken in each habitat type, one sample was used to identify organisms to the lowest possible taxonomic level (usually species) and counts of individuals were made. In remaining samples, major taxonomic groups [crustaceans, polychaetes nemerteans, bivalves, and “others” (e.g., oligochaetes)] were separated out, bivalves were identified to species, organisms were dried for 48 hrs, and organisms were combusted to obtain AFDW biomass for each habitat type (Diaz and Schaffner 1990). Polychaetes, nemerteans, and other vermiforms (e.g., phoronids, nematodes, oligochaetes) were combusted together, as the same P:B ratio was used for all of them. No echinoderms were collected by either sampling method, and no gastropods were collected in 500- μm samples.

PRODUCTION CALCULATIONS AND STATISTICAL ANALYSES.—Using these biomass estimates, we calculated production for each taxonomic group at each location using P:B ratios [Diaz and Schaffner 1990; crustaceans: 5.7; polychaetes, nemerteans, and other vermiforms (e.g., phoronids, nematodes, oligochaetes): 4.9; bivalves: 2.9]. These data were used to estimate the annual secondary productivity of each habitat type per m^2 . The temperatures at our sites (25–27 °C) and body sizes of animals in our study were from a similar system and were comparable to those analyzed in Diaz and Schaffner (1990). Thus, the Diaz and Schaffner (1990) P:B ratios account for annual temperature variations for calculations of production in our study as well. Sediment characteristics, benthic density, diversity, and secondary production were compared across habitat types using analysis of variance (ANOVA), Tukey multiple comparison tests, and non-metric multidimensional scaling (nMDS). Data were examined using Levene's test to determine whether they met the assumptions of ANOVA and were log transformed when necessary to homogenize variances (necessary only for percent sand). Also, to examine the relative importance of habitat type in comparison to physical factors of the environment [sediment type, chlorophyll *a*, total organic carbon (TOC)], we used general linear models (GLM) with different combinations of factors and compared models using Akaike's information criteria (AIC) to determine which factors had most influence on response variables by selecting the model that best explained the data. We first tested for collinearity for models using a cross-correlation matrix in R and eliminated factors that were highly linearly correlated ($r > 0.50$). Models with the factors habitat, sediment type (percent sand), chl *a*, and TOC (highly correlated with total nitrogen; $r = 0.97$) together and alone were run and tested against each other. We used individuals m^{-2} in 3-mm samples, and production in 3-mm samples to show the typical patterns for response variables, though results for all response variables were similar (AIC resulted in the habitat only model as the best). Models with $\Delta\text{AICc} < 4$ and probability (w_i) > 0.1 were considered "probable." We also examined goodness-of-fit for each model with R^2 (calculated as $1 - \text{residual deviance}/\text{null deviance}$) (Burnham et al. 2011).

A nMDS analysis from a Bray-Curtis similarity matrix was performed on 3 mm infauna and epifauna to summarize patterns of benthic assemblages by the factor habitat type using Primer v5.2.9 (Clarke and Gorley 2001, Clarke and Warwick 2001). We created nMDS plots to examine similarities among communities and used bubbles to indicate abundance within each sample for a dominant bivalve, *Limecola balthica* (Linnaeus, 1758) (formerly *Macoma balthica*). We ran an analysis of similarity (ANOSIM) to determine differences in community composition among habitat types and ran a similarity percentages (SIMPER) analysis to determine which species were contributing to any dissimilarity among communities.

SEAGRASS AREAL COVERAGE ESTIMATIONS.—To compare areal coverage of seagrass beds between 1971 (the earliest year of areal seagrass coverage available) and 2016 (the most recent year of areal seagrass coverage currently available), we downloaded data for areal coverage of seagrass of the York River that was calculated using digital maps from the Seagrass Mapping Group at the Virginia Institute of Marine Science (VIMS) and the VIMS Seagrass Mapping website (<http://web.vims.edu/bio/sav/SegmentAreaTable.htm>). Aerial surveys do not discern between different seagrass types or seagrass vs *Gracilaria*. The information on seagrass coverage, along with our estimations of benthic secondary production in experimental *Zostera*,

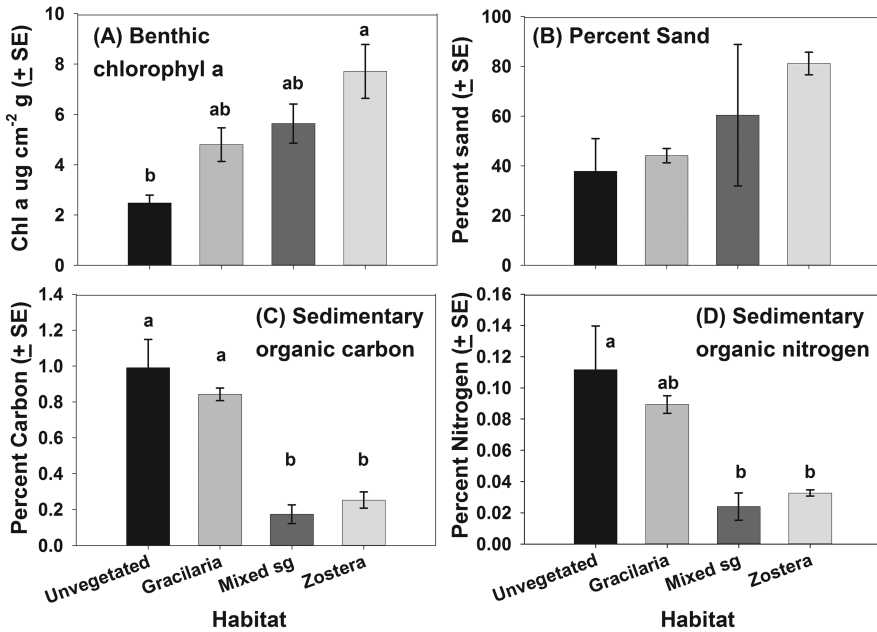


Figure 2. Physical characteristics of the habitats including (A) benthic chlorophyll *a*; (B) percent sand; (C) sedimentary total organic carbon; and (D) sedimentary total organic nitrogen for the four habitat types, unvegetated, *Gracilaria* spp. (*Gracilaria*), mixed seagrass (Mixed sg) and *Zostera marina* (*Zostera*). Different letters above bars indicate significant differences (Tukey test).

mixed seagrass, *Gracilaria*, and unvegetated habitat types allowed us to estimate the amount of secondary productivity lost in seagrass habitats of the York River from 1971 to 2016 due to the loss of seagrass and consequent conversion of seagrass beds to unvegetated habitat (since this absolute distinction is the only one discernable from the seagrass areal coverage data). For those calculations, we converted total hectares of habitat in York River in each year to m² area × proportion of a particular habitat × estimated annual productivity per m² of habitat (g C m⁻² yr⁻¹). This resulted in the estimated production throughout that habitat (g C yr⁻¹). We used the following calculations:

Estimated production per habitat was calculated as: HA × 10,000 m² ha⁻¹ × PH × PR, where: HA = Ha of habitat in York River in each yr, PH = proportion of a particular habitat, and PR = estimated annual productivity of habitat.

RESULTS

SEDIMENT CHARACTERISTICS.—Benthic sedimentary chlorophyll *a* levels were significantly higher in the *Zostera* than in the unvegetated habitat type, and the other two habitat types were intermediate (Fig. 2A, Table 1). Sediment composition of the seagrass beds was mostly sand, and the difference in sediment among habitats was not significant (Fig. 2B, Table 1). Nutrient levels of both sedimentary carbon and nitrogen were relatively low in both the mixed seagrass and *Zostera* only habitat

Table 1. Statistical results for analysis of variance for physical and biological variables by habitat type [unvegetated (Unveg), *Gracilaria* (Grac), mixed seagrass (Mix), *Zostera* seagrass (Zost)]. Bold *P* values indicate significant differences at alpha = 0.05. Tukey test results for significant differences. Adj MS = adjusted mean square terms.

Variable	Source of variation				F	<i>P</i>	Tukey test
	Habitat		Error				
	df	Adj MS	df	Adj MS			
Benthic chlorophyll <i>a</i>	3	14.02	8	1.73	8.13	0.008	Unveg < Zost
Percent sand	3	1,123.00	8	758.00	1.48	0.291	Unveg = Grac = Mix = Zost
Sedimentary carbon	3	0.51	8	0.02	22.09	<0.005	Unveg = Grac > Mix = Zost
Sedimentary nitrogen	3	0.01	8	<0.01	8.75	0.007	Unveg = Grac > Mix = Zost
Total 3-mm individuals m ²	3	1,268.00	8	183.00	6.92	0.013	Unveg = Grac = Mix < Zost
Species richness 3 mm	3	66.33	8	7.58	8.75	0.007	Unveg < Zost
Diversity (H') 3 mm	3	1.91	8	0.22	8.64	0.007	Unveg < Grac = Mix = Zost
2° production (3 mm)	3	3,222.00	8	218.00	14.75	0.001	Unveg = Grac = Mix < Zost
2° production (500 µm)	3	458.00	6	465.00	0.99	0.460	Unveg = Grac = Mix = Zost
Total 2° production (3 mm + 500 µm)	3	4,181.00	8	917.00	4.56	0.038	Unveg < Zost

types and were significantly higher in the unvegetated and *Gracilaria* habitat types (Fig. 2C, D, Table 1).

FAUNAL COMPOSITION.—We collected a total of 26 species in the 3-mm samples and 47 species in the 500-µm samples (see Online Table A1). In the 3-mm mesh samples, infaunal densities were significantly higher in *Zostera* than in the other habitat types, while the other three habitat types were similar to one another (Fig. 3A, Tables 1, 2). The differences were mostly due to the clams *L. balthica* and *Mya arenaria* Linnaeus, 1758, polychaetes, and crustaceans. In the 500-µm mesh samples, highest densities were again in the *Zostera* habitat type, where densities were about nine times greater than in the unvegetated habitat type. This was mostly due to polychaetes and crustaceans (Fig. 3B, Online Table A1). In AIC analysis of models using the factors habitat, sediment type (percent sand), chlorophyll *a*, and TOC together and alone, the model with habitat alone had the lowest AIC, had a high probability of support, and was the best model to describe the data (Online Tables A2 and A3).

In the 3-mm mesh samples, species richness in the *Zostera* habitat type was significantly different and approximately five times higher than that in the unvegetated habitat type, while the other two habitat types were intermediate and similar to one another (Fig. 3C, Table 1). Shannon-Wiener (H') diversity was highest in *Zostera*, was also high in *Gracilaria* and mixed seagrass habitat types (similar to that in *Zostera*), but was significantly lower in the unvegetated habitat type (Fig. 3D, Table 1).

nMDS plots showed a clear separation in community assemblages among habitat types, with *Zostera* and unvegetated widely separated from other habitat types (Fig. 4A; stress = 0.08). There was a high global R (ANOSIM global R = 0.823, *P* = 0.002), suggesting that habitat type (or a factor covarying with habitat type) had a great influence on community assemblages. The differences among habitat types were apparent in some of the key bivalves, including *L. balthica*, where the highest densities were in the unvegetated habitat type (Fig. 4B). Other bivalves, such as *Ameritella mitchelli* (Dall, 1895), had higher densities in unvegetated, *Gracilaria*, and mixed seagrass than in *Zostera* (Online Table A1), and the bivalve *Kelliopsis elevata* (Stimpson, 1851) had higher densities in *Gracilaria* and mixed seagrass than in *Zostera* (Online Table

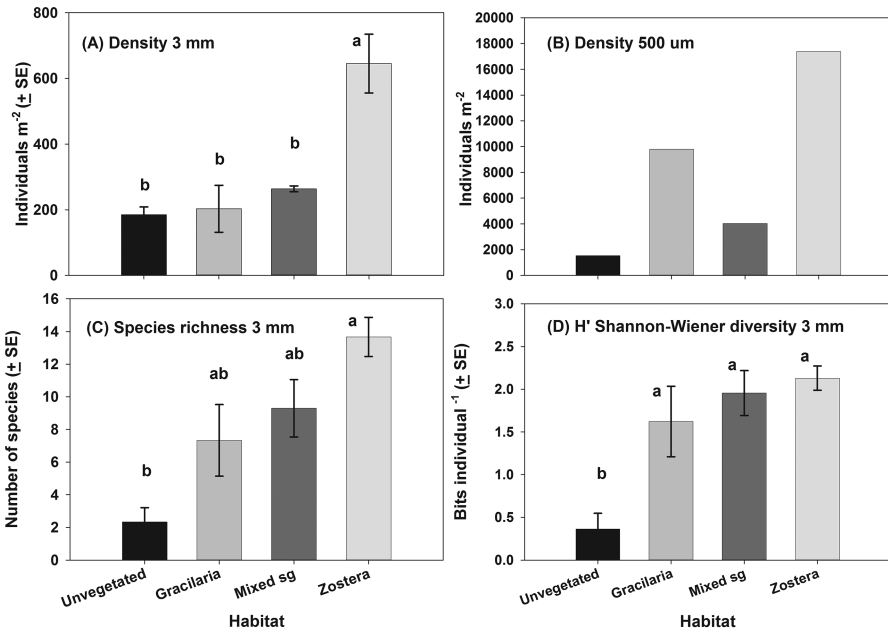


Figure 3. Biological characteristics of the four habitat types, unvegetated, *Gracilaria* spp. (*Gracilaria*), mixed seagrass (Mixed sg) and *Zostera marina* (*Zostera*) including (A) density of 3-mm samples, (B) density of 500- μ m samples, (C) species richness, (D) Shannon-Wiener H' diversity in 3-mm samples. Different letters above bars indicate significant differences (Tukey test).

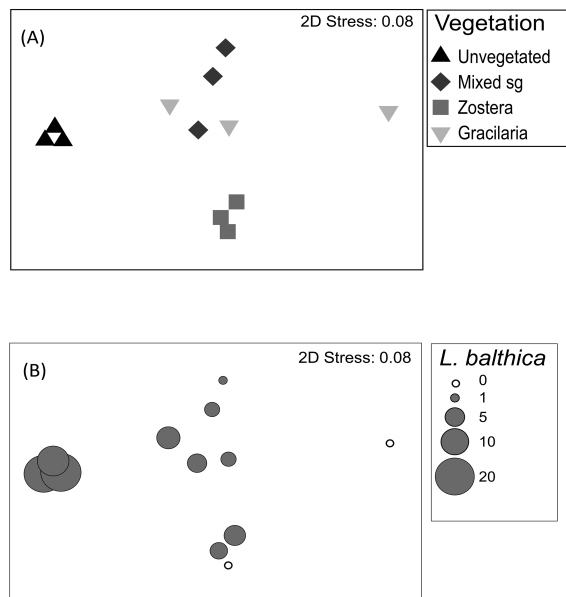


Figure 4. (A) nMDS plot of benthic community assemblages among habitats (vegetation type) for 3-mm benthic samples. (B) nMDS plot of densities (per m²) of the bivalve *Limecola balthica* (formerly *Macoma*) *balthica* among the locations shown in Figure 4A. Notice high densities in unvegetated habitats on left of plot.

Table 2. SIMPER analysis for dissimilarity between 3-mm *Zostera* (Zost) habitat compared to unvegetated (Unveg) habitat. Total average dissimilarity = 91.86. Average abundance (No individuals per sample) for each habitat. Percent species contribution and percent cumulative contribution to the dissimilarity for each of the top six most important species. Taxonomic group for each species indicated after the species name: M = Mollusca, P = Polychaeta, C = Crustacea.

Species	Average abundance		Average dissimilarity (SD)	Species contribution (%)	Cumulative contribution (%)
	Unveg	Zost			
<i>Limecola balthica</i> (M)	18.00	3.33	16.67 (2.56)	18.15	18.15
<i>Clymenella torquata</i> (P)	0.00	14.67	14.29 (1.09)	15.56	33.71
<i>Alitta succinea</i> (P)	0.33	13.00	14.23 (2.31)	15.50	49.20
<i>Erichsonella attenuata</i> (C)	0.00	13.00	13.88 (2.36)	15.11	64.31
<i>Leitoscoloplos</i> sp. (P)	0.00	5.67	6.89 (1.30)	7.50	71.81
<i>Mya arenaria</i> (M)	0.00	4.67	5.26 (3.59)	5.72	77.54

A1). In the SIMPER analysis, the top six species contributing to the dissimilarity of *Zostera* compared to other communities accounted for 77% of the total dissimilarity and included the polychaetes, *Alitta succinea* (Leuckart, 1847), *Clymenella torquata* (Leidy, 1855), and *Leitoscoloplos* sp., the crustacean *Erichsonella attenuata* (Harger, 1873), and the bivalves *L. balthica* and *M. arenaria* (Table 2).

In the 3-mm mesh samples, secondary productivity in *Zostera* was significantly different and three times higher than that in the unvegetated habitat type, and *Gracilaria* and mixed seagrass were low, similar to the unvegetated habitat type (Fig. 5A, Table 1). Variance in productivity of the 500- μm samples was high and habitat types did not differ significantly (Fig. 5B, Table 1). The relative biomass and secondary productivity of large-bodied infauna (from 3-mm mesh samples) was much greater than that from 500- μm mesh samples in unvegetated and *Zostera* habitat types, but production tended to be greater in 500- μm mesh samples than in 3-mm mesh samples for *Gracilaria* and mixed seagrass habitat types (Fig. 5A, B). Total secondary productivity (3-mm and 500- μm combined) ranged from a minimum of 40 g C m⁻² yr⁻¹ in unvegetated to a maximum of 120 g C m⁻² yr⁻¹ in *Zostera* and was significantly different between the two habitat types (Table 1). Total productivity in *Zostera* was about three times higher than that in unvegetated, and this was driven by large-bodied organisms, whereas total secondary productivity was highly variable and intermediate in *Gracilaria* and mixed seagrass habitat types (Fig. 5C).

SEAGRASS AND HABITAT LOSS ESTIMATIONS.—Areal coverage of submerged aquatic vegetation (SAV) in the York River changed substantially over time (Fig. 6); the passage of Tropical Storm Agnes in 1972 was associated with a >50% decline in *Zostera* (Orth and Moore 1983, Orth et al. 2010, Lefcheck et al. 2017), and by 1974 the lower York River (polyhaline section) had already declined to 90 ha, or almost half of the total remaining in 2016. Some of this was re-established in the early 2000s and subsequently declined. By 1978, all seagrass was lost from the upper York River (mesohaline section) and it never returned. Data from 1971 and 2016 were used as endpoints of the available data to calculate secondary productivity lost from past to present (Table 3). Though we do not have data on the relative proportions of mixed seagrass vs *Zostera* alone in the York River, using depth distributions of the various species, we can make some assumptions about this. On the western shore of Chesapeake Bay, *Zostera* grows to approximately 1 m below mean low water (MLW), whereas *Ruppia* grows shallower, to approximately 25 cm below MLW (Orth and

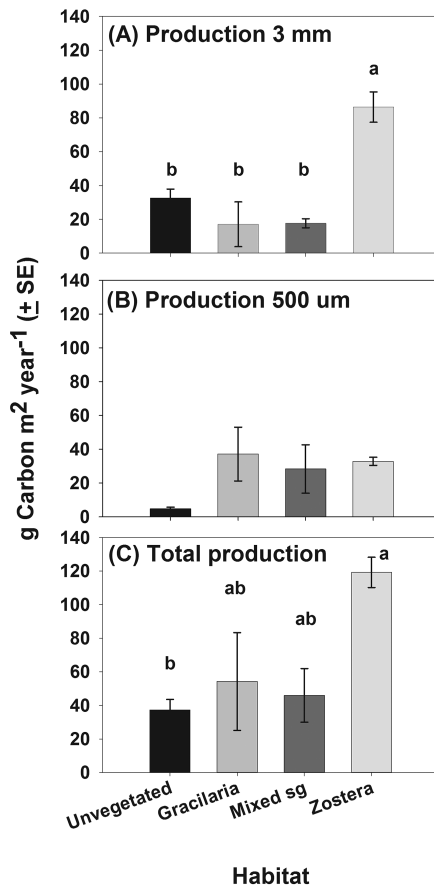


Figure 5. Mean annual secondary production for the four habitat types, unvegetated, *Gracilaria* spp. (*Gracilaria*), mixed seagrass (Mixed sg) and *Zostera marina* (*Zostera*) for (A) 3-mm samples; (B) 500- μ m samples; and (C) total from 3-mm and 500- μ m samples combined. Different letters above bars indicate significant differences (Tukey test).

Moore 1988, Pardieck et al. 1999; K Moore, Virginia Institute of Marine Science, pers comm). Thus, a mixture of *Zostera* and *Ruppia* seagrass would be about one-quarter of the SAV beds, and *Zostera* alone would be the other three-quarters. For our calculations, we assumed that the SAV beds in the York River historically were composed of 75% *Zostera* and 25% mixed seagrass, and later some vegetated areas were converted to unvegetated habitat as seagrass was lost. Aerial images give no indication of *Gracilaria* extent, and only indicate a total of mixed seagrass (possibly including some *Gracilaria* in later years) vs unvegetated habitats.

Total production for each time frame was calculated. For 1971 as: sum of production from *Zostera* + mixed seagrass. For 2017 as: sum of production of *Zostera* + mixed seagrass + unvegetated (Table 4). Productivity lost was calculated as: total productivity in 1971 minus total productivity in 2017, or: 4.33×10^8 g C yr⁻¹ (1971) – 2.82×10^8 g C yr⁻¹ (2016) = 1.51×10^8 g C yr⁻¹ lost (or 34.87%).

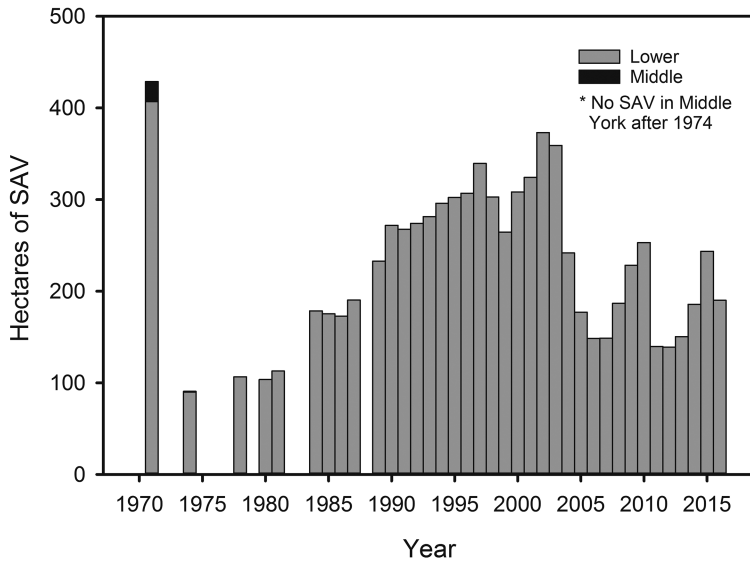


Figure 6. Hectares of submerged aquatic vegetation (SAV) in the Lower and Middle York River (and stacked Total) over time for the years when areal coverage data were available (note that some consecutive years are missing between 1971 and 1989). VIMS SAV Mapping Laboratory: <http://web.vims.edu/bio/sav/SegmentAreaTable.htm>

DISCUSSION

Density, diversity, and annual secondary production of benthic infauna and epifauna were all significantly higher in *Zostera* seagrass as compared to unvegetated habitat types, and some metrics were significantly higher in *Zostera* than mixed seagrass and *Gracilaria*. Though increased densities in vegetated vs unvegetated habitats have been documented previously (Orth et al. 1984, Edgar 1990), and high secondary productivity in seagrass has been documented in other systems (Edgar 1990, Wong et al. 2011), the high benthic productivity including deep-dwelling infauna in Chesapeake Bay seagrass is novel. This high productivity resulted from a preponderance of deep-dwelling bivalves (e.g., *M. arenaria*) and large polychaetes (e.g., *C. torquata*), as was seen in Harker's Island natural habitats (marsh and seagrass) in North Carolina (Wong et al. 2011). Bivalves and polychaetes are important food sources for predators such as blue crabs (Lipcius et al. 2007), thus suggesting the importance of these vegetated habitats for higher trophic levels. Our estimates of secondary production of over $120 \text{ g C m}^{-2} \text{ yr}^{-1}$ in *Zostera* seagrass was much higher than that in *Posidonia* seagrass in Australia ($47 \text{ g C m}^{-2} \text{ yr}^{-1}$; Edgar 1990), but

Table 3. Hectares of historical (1971) and present (2016) submerged aquatic vegetation (SAV) in the York River. Data from the Virginia Institute of Marine Science SAV Mapping Laboratory, available from: <http://web.vims.edu/bio/sav/SegmentAreaTable.htm>

Segment of bay	Historical SAV (ha)	2016 SAV (ha)	SAV remaining in 2016
York River (Polyhaline)	406.86	190.16	46.74%
York River (Mesohaline)	21.97	0.00	0.00%
Total York River	428.72	190.16	44.35%

Table 4. Calculations for estimated seagrass and unvegetated habitat secondary productivity from 1971 to 2016. Habitat types: unvegetated (Unveg), mixed seagrass (Mix), *Zostera* seagrass (Zost). Total YR = total York River area, na = not applicable.

Year	Habitat	Total YR habitat (ha)	Proportion seagrass	Annual productivity (g C m ⁻² yr ⁻¹)	Production in habitat (g C yr ⁻¹)
1971	Zost	428.72	0.75	119.24	3.83 × 10 ⁸
1971	Mix	428.72	0.25	45.97	0.49 × 10 ⁸
1971	Zost + mix				4.33 × 10 ⁸
2016	Zost	190.16	0.75	119.24	1.70 × 10 ⁸
2016	Mix	190.16	0.25	45.97	0.22 × 10 ⁸
2016	Unveg	238.56	na	37.90	0.90 × 10 ⁸
2016	Zost + mix + unveg				2.82 × 10 ⁸

equivalent to that in *Zostera* seagrass in North Carolina (Wong et al. 2011). Though some deep-dwelling, high-production clam species, such as *M. arenaria*, were only present in *Zostera*, other clam species, such as *L. balthica*, were more abundant in the unvegetated habitat types. *Zostera* also had a higher abundance of worms and crustaceans than the other habitat types, leading to the overall high secondary productivity. The patterns we observed must be interpreted cautiously considering that the study was a snapshot in the summer. However, this time frame is optimal to observe habitat differences since it is after spring benthic recruitment, and after predators have entered Chesapeake Bay and have been feeding on the benthos. Benthic community assemblages among habitats are likely to remain distinct, though densities may change based on recruitment and predation events through the seasons (Bologna and Heck 2002). Keeping in mind that shallow, benthic habitats can show variation over small temporal and spatial scales (Boström and Bonsdorff 1997), caution should be used in extrapolating results to other locations and time periods.

Increased faunal abundance and diversity in seagrass as compared to other habitats has been attributed to a variety of mechanisms (Orth et al. 1984). The large amount of benthic algae (as seen with high chlorophyll *a*) in the seagrass habitats represents high food availability for deposit-feeding infauna (Diaz and Schaffner 1990) and may have had a positive effect on secondary productivity. One explanation for higher chlorophyll *a* in the seagrass habitat is stabilization of the sediments from seagrass roots reducing turbidity and allowing benthic microalgae to proliferate (Orth et al. 2010). Sediment type affects infauna present, and a high percentage of sand in the seagrass habitats can stabilize the habitat and increase oxygen availability, benefiting the diverse suite of organisms living there (Stoner 1980, Diaz and Schaffner 1990). However, sediment grain size did not differ significantly among our habitats (though sample size was low), but chlorophyll *a* was higher in *Zostera* habitats than in unvegetated habitats, therefore composition of the sediment could be partially driving the faunal differences we saw. It was somewhat surprising that the mixed seagrass habitat did not perform as well as the *Zostera* habitat (except for 3-mm diversity), especially given the similar sedimentary organic matter in the two habitats. The differences were driven by the large bivalves *M. arenaria* and *Tagelus plebeius* (Lightfoot, 1786) that were present in *Zostera* and not mixed seagrass (Online Table A1). The low levels of sediment organic matter found in both *Zostera* seagrass and mixed seagrass beds agrees with previous observations that seagrass often does not grow in sediment with high organic content (Moore et al. 2004); organic,

silty sediments can be easily resuspended causing turbidity in the water column, which inhibits plant growth. High organic content can also reduce sediment redox potential and increase sulfides and ammonium (DeLaune et al. 1983). Abundance and diversity of infauna and epifauna can also be affected by seagrass patch size and seagrass density (Bowden et al. 2001, Ralph et al. 2013), though these were held relatively constant in our study.

In previous studies, secondary productivity in spatially complex habitats has been high compared to other habitats (e.g., Orth et al. 1984, Pihl 1986). In our Chesapeake Bay study, the productivity from the large-mesh *Zostera* samples (which included large, deep-dwelling organisms) was 2–4 times higher than that in mixed seagrass sediments (see Diaz and Schaffner 1990), was higher than that in other types of seagrass (Edgar 1990), and was similar to that of *Zostera* in other systems (Wong et al. 2011). Because the majority of the biomass in our *Zostera* habitat came from large, infaunal *M. arenaria* clams, we hypothesize that the structure of the seagrass roots and the protection from predation that they provide may play an important role in influencing biomass and productivity of these suspension-feeding bivalves (Orth et al. 1984, Seitz et al. 2001, Glaspie and Seitz 2017). Though large, adult *M. arenaria* are deep dwelling and protected, smaller *M. arenaria* dwelling closer to the surface (Hines and Comtois 1985) are likely available to predators, leading to increased trophic transfer in habitats where these clam populations thrive (Glaspie and Seitz 2017). Alternatively, *L. balthica* are facultative deposit-feeding bivalves (Kamermans et al. 1992), which prefer muddy habitats where organic carbon is plentiful, where they can burrow deep, and they are precluded from penetrating stiff sediments with large grain size (Alexander et al. 1993). Furthermore, secondary production estimates that do not include deep-dwelling, large (high-biomass) organisms are likely vast underestimates of productivity. The importance of these seagrass habitats for large prey species that serve as food for epibenthic predators (Lipcius et al. 2007) suggests that conservation and restoration of these habitats is warranted; however, if warming conditions worsen, this may preclude *Zostera* establishment, even if restoration is undertaken (Moore and Jarvis 2008).

The decline of seagrass in the York River from 1971 to 2016 resulted in a nearly 35% loss of secondary productivity, which may dramatically affect higher trophic levels. Many epibenthic predators feed on benthic infauna (Hines et al. 1990, Lipcius et al. 2007), and their loss from the system could cause predators to depend on other food sources. Blue crabs are abundant in seagrass beds, feed on benthos in those habitats (Orth and van Montfrans 1990, Lipcius et al. 2007), and are likely to be greatly affected by loss of seagrass habitats. The presence of concurrent blue crab declines after *M. arenaria* declines in 1972 corroborate this contention (Miller et al. 2005, Glaspie et al. unpubl data). Our estimates of loss of benthic productivity could be overestimates if *Gracilaria* inhabits some of the habitats vacated by *Zostera*, which is expected to decline with temperature increases (Moore and Jarvis 2008). As a caveat, it is unknown exactly when *Gracilaria* invaded Chesapeake Bay, though some investigators document invasions throughout the East Coast (Thomsen et al. 2006a). *Gracilaria* may have been mistaken for seagrass in aerial surveys and thus aerial surveys might overestimate the abundance of seagrass in recent years (after the invasion). In addition, some of the loss in secondary production of *Zostera* habitats might be compensated for by increases in habitat value of *Gracilaria*, and the extent to which the benthic community changes in these various habitats is a subject

of recent studies (Wood 2017). Fine-scale studies of the extent of *Gracilaria* beds vs *Zostera* and mixed seagrass beds in Chesapeake Bay using satellite imagery are also underway (R Lipcius, Virginia Institute of Marine Science, pers comm). There has been substantial loss of *Zostera* seagrass throughout Chesapeake Bay (Orth et al. 2007, 2010), until recently (Lefcheck et al. 2018) thus, the losses estimated for the York River could be indicative of other losses throughout the bay. Though other seagrass species have been increasing over time in the upper Chesapeake Bay (e.g., the freshwater *Vallisneria americana* Michx.; Orth et al. 2010), the losses of *Zostera* will have dramatic effects on density, diversity, and secondary production of benthos. This could be particularly important in the polyhaline regions. Thus, restoration of *Zostera* habitats in lower Chesapeake Bay would benefit benthic prey resources and the predators that depend upon them. More research on the effects of seagrass loss, including patterns throughout the bay, comparisons between different types of seagrass habitats, different seasons, and the effects of seagrass loss on higher trophic levels would be beneficial.

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