

4-27-2017

## Role of habitat and predators in maintaining functional diversity of estuarine bivalves

Cassandra N. Glaspie  
*Virginia Institute of Marine Science*

Rochell D. Seitz  
*Virginia Institute of Marine Science*

Follow this and additional works at: <https://scholarworks.wm.edu/vimsarticles>



Part of the [Marine Biology Commons](#)

---

### Recommended Citation

Glaspie, Cassandra N. and Seitz, Rochell D., Role of habitat and predators in maintaining functional diversity of estuarine bivalves (2017). *Marine Ecology Progress Series*, 570, 113-125.  
doi: 0.3354/meps12103

This Article is brought to you for free and open access by the Virginia Institute of Marine Science at W&M ScholarWorks. It has been accepted for inclusion in VIMS Articles by an authorized administrator of W&M ScholarWorks. For more information, please contact [scholarworks@wm.edu](mailto:scholarworks@wm.edu).

# Role of habitat and predators in maintaining functional diversity of estuarine bivalves

Cassandra N. Glaspie<sup>1,2,\*</sup>, Rochelle D. Seitz<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, Virginia Institute of Marine Science, Gloucester Point, VA 23062, USA

<sup>2</sup>Present address: Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97731, USA

**ABSTRACT:** Habitat loss is occurring rapidly in coastal systems worldwide. In Chesapeake Bay, USA, most historical oyster reefs have been decimated, and seagrass loss is expected to worsen due to climate warming and nutrient pollution. This loss of habitat may result in declining diversity, but whether diversity loss will equate to loss in ecosystem function is unknown. A bivalve survey was conducted in a variety of habitat types (seagrass, oyster shell, shell hash, coarse sand, detrital mud) in 3 lower Chesapeake Bay sub-estuaries from spring 2012 through summer 2013 to examine the correlation between bivalve densities, habitat type, habitat volume (of material retained on 3 mm mesh), and predator density. Bivalves were analyzed as functional groups based on feeding mode, living position, and predator defense strategy. On average, seagrass supported one additional functional group, and diversity was increased 68–94%, in seagrass compared to the other habitats examined. Species richness and functional group richness were positively correlated with habitat volume. The greatest densities of deposit-feeding bivalves were in detrital mud habitats, the greatest densities of thin-shelled and surface-dwelling bivalves were in seagrass habitats, and the greatest densities of armored bivalves were in oyster shell habitats. Small, thin-shelled bivalves were negatively correlated with densities of predators, including blue crabs *Callinectes sapidus* and cownose rays *Rhinoptera bonasus*. Overall, bivalve diversity was associated with habitat type, habitat volume, and predator densities. These results suggest that all habitats, and particularly seagrass, play a role in maximizing bivalve functional diversity in Chesapeake Bay.

**KEY WORDS:** Chesapeake Bay · Seagrass · Habitat loss · Ecosystem services · Oyster

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

The effect of habitat loss on ecosystem functioning is an important issue in marine ecology due to the rapid rate at which species such as seagrass, mangroves, corals, and oysters are being lost from coastal waters (Duarte et al. 2008). These species promote diversity and stability of associated communities by providing structure for attachment, ameliorating environmental stressors, and protecting organisms from predation (Orth et al. 1984, Bertness & Callaway 1994, Stachowicz 2001). Loss of such species and the habitat they provide will inevitably lead to declines

in dependent species and diversity, but the degree to which such declines in diversity will equate to a loss of ecosystem integrity is unclear.

In benthic environments in Chesapeake Bay, complexity is provided by biogenic habitats such as seagrass and oyster reefs, along with non-biogenic habitats such as coarse sediments. In a region dominated by vast expanses of homogenous mud and sand, seagrass beds, oyster shell, shell hash, and pockets of coarse sand and gravel tend to have high species diversity (Orth et al. 1984, Gray 2002, Gutiérrez et al. 2003, Hewitt et al. 2005, Commito et al. 2008). In contrast, habitats with greater amounts of organic matter

\*Corresponding author: glaspiec@oregonstate.edu

(detrital muds) tend to be dominated by one or a few species, and thus support less diverse communities of organisms (Gray 2002, Fitch & Crowe 2012).

Some habitats in Chesapeake Bay are sensitive to climate change and coastal development. Eelgrass *Zostera marina* has been declining since the 1930s, when there was a massive die-off due to eelgrass wasting disease and hurricanes (Orth & Moore 1983, Orth et al. 2006). In the past several years, seagrass die-offs induced by extreme high temperatures in Chesapeake Bay have resulted in the prediction that *Z. marina* may disappear from the Bay entirely (Moore & Jarvis 2008). The eastern oyster *Crassostrea virginica* has experienced declines since the early 1900s, and still remains in the Bay at historically low levels (Rothschild et al. 1994). Nutrient enrichment, land clearing, and urban development alter the composition and quality of organic matter and detritus in rivers and nearshore sediments (Wang et al. 2013, Prater et al. 2015), which can affect habitat quality.

Changes in the quality and quantity of habitats in Chesapeake Bay will impact the associated communities of organisms. Many marine organisms, including fish, crustaceans, and bivalves use habitat for predator avoidance. The complexity offered by habitats such as seagrass and oyster shell may be beneficial for prey species because it interferes with detection and capture of prey by predators, which promotes high prey survival, especially for infaunal organisms such as bivalve mollusks (Peterson 1982, Heck & Thoman 1984, Orth et al. 1984). Some habitats such as shell hash facilitate colonization of epifaunal bivalves like mussels (Bertness & Grosholz 1985), while other habitats such as dense root mats or shell material may inhibit recruitment of large bivalves (Brenchley 1982, Fiori & Carcedo 2015). Entire bivalve feeding groups may be associated with certain habitats; more suspension feeders and fewer deposit feeders are typically associated with complex shell hash habitats (Hily 1991), oyster reefs (Rodney & Paynter 2006), and seagrass (Stoner 1980) than with less-complex habitats such as mud or sand. This may be due to the tendency of complex habitat to slow passing currents, allowing particles to settle out and enhancing food resources for suspension feeders (Peterson et al. 1984).

The link between habitat and bivalve distribution is important to understand, as bivalve diversity promotes ecosystem functioning because bivalves with different feeding and burrowing behaviors have different impacts on their environment (Biles et al. 2002). Specifically, bivalve feeding and burrowing activities influence nitrogen cycling, organic matter deposition, mineralization, silica flux, and sedimen-

tation (Covich et al. 1999, Norkko et al. 2001, Biles et al. 2002, Marinelli & Williams 2003, Welsh 2003). Suspension-feeding bivalves perform an important ecosystem service by filtering phytoplankton out of the water column (Grizzle et al. 2008), and in high densities, bivalves are able to control algal blooms and promote water clarity (Cohen et al. 1984). Similarly, deposit-feeding bivalves serve an important role in the ecosystem by mixing oxygen deeper into the sediment through their feeding and bioturbation (Levinton 1995), allowing for increases in microbial metabolism and influencing nutrient cycling (Biles et al. 2002). Thus, changes in the diversity of the bivalve community may alter the functioning of coastal marine ecosystems.

In addition to their role in cycling and storage of material in marine environments, bivalves also serve an important role in the food web. Bivalve morphology and living position with respect to the sediment surface can provide clues regarding the specifics of that role. In benthic marine ecosystems, predator-prey interactions are a key determinant of the distribution and abundance patterns of fauna (though food availability and abiotic factors such as currents and salinity are also important; see Eggleston et al. 1992, Seitz et al. 2001). To deal with predation pressure, bivalve mollusks exhibit a number of morphological and behavioral characteristics that defend them against predators, allowing these prey species to coexist with their predators and persist through time (Vermeij 1987). Some examples include maximizing burial depth (Blundon & Kennedy 1982a) or armor (Bertness & Grosholz 1985). These defenses define predator-prey interactions for a given species. For example, few marine predators can consume clams that burrow to 40 cm or more, such as the soft-shell clam *Mya arenaria*, which as an adult is only available as prey to excavating predators such as cownose rays *Rhinoptera bonasus* (Blundon & Kennedy 1982a, Fisher 2010).

The degree to which bivalve diversity would have to decrease for any effect on ecosystem function or on trophic dynamics to be seen is unknown. The redundancy hypothesis states that some species may not be necessary for ecosystem functioning (Lawton & Brown 1993, Ehrlich & Walker 1998). Many studies have examined the relationship between species richness and habitat type (Airoldi et al. 2008). However, species richness does not account for functional redundancy. Calculating functional diversity involves grouping organisms based on traits that represent their function in the environment to understand communities and ecosystems based on what organisms do, rather than

on their evolutionary history (Petchey & Gaston 2006). This approach, commonly used for terrestrial plants, has relatively recently been used to describe diversity of benthic macrobenthos (Bazairi et al. 2005, Savage et al. 2012, van der Zee et al. 2015), and the impact of habitat on functional diversity of marine organisms has been identified as a research need (Airoldi et al. 2008). In addition, although species are often grouped based on trophic position, most studies relate functional diversity only to bottom-up processes, omitting top-down processes that are likely to influence distribution and diversity of marine prey (though see Griffin et al. 2008, Clemente et al. 2010, Gauzens et al. 2016). Here, we define functional diversity as it relates to functional groupings of bivalves as consumers (feeding mode) and as prey (living position and predator defense strategy), and our study is one of the first to examine the effect of both habitat and predators on functional diversity in marine benthic communities. We thus can gain a better understanding of how habitat loss may alter ecosystem functioning.

### Objectives

The purpose of this study was to survey bivalves in lower Chesapeake Bay to determine the degree to which habitat type, habitat volume in the sample (as determined by water displacement), and predator density impact bivalve species diversity and functional diversity. Specifically, we examined (1) bivalve species diversity and species richness, (2) density of bivalves separated into functional groups based on feeding mode, living position, and predator defense strategy, and (3) bivalve functional diversity and functional richness.

### Hypotheses

1. Bivalve species diversity and functional diversity metrics are positively correlated with habitat volume, and bivalve communities are more diverse in more complex habitats, such as seagrass and oyster shell, than in less complex habitat, such as detrital mud.

2. Functional groups exhibit the following habitat preferences: higher densities of thin-shelled, suspension-feeding bivalves are associated with more complex habitats (seagrass and oyster shell) than with less complex habitats (detrital mud); the highest densities of armored bivalves are found in/on oyster shell; higher densities of deposit-feeding bivalves are found in detrital mud habitat than any other habitats.

3. Densities of bivalve groups with predominately thin-shelled species are negatively correlated with predator density, with the exception of deep-burrowing bivalves, which achieve a spatial refuge from predation.

## MATERIALS AND METHODS

### Study system

Lower Chesapeake Bay encompasses the Virginia portion of Chesapeake Bay. This portion of the Bay is mostly polyhaline (except in the upper reaches of the tributaries). Sediments in the lower Bay range from fine muds to coarse sand and gravel. Sediments often contain woody debris, marsh detritus, fossilized shell, oyster shell, or shell material from other mollusks. The lower Bay from south of the Potomac River through to the mouth of the Bay supports stands of mixed eelgrass *Zostera marina* and widgeongrass *Ruppia maritima*, although *Z. marina* has been eliminated from more than half of its pre-1976 range in Chesapeake Bay (Orth et al. 2010).

The most abundant demersal and epibenthic predators on benthos in Chesapeake Bay are spot *Leiostomus xanthurus*, Atlantic croaker *Micropogonius undulatus*, hogchoker *Trinectes maculatus*, and blue crab *Callinectes sapidus* (Hines et al. 1990). High predation rates on infauna are also associated with seasonal migratory behavior of the cownose ray *Rhinoptera bonasus* (Blaylock 1993), which is able to consume bivalves that would otherwise be nearly immune to predation due to burrowing behavior, heavy armor, and/or size refuge (Fisher 2010). While blue crabs are generalist predators, adult crabs show a preference for infaunal bivalves (Hines et al. 1990, Lipcius et al. 2007). Fish consume small infaunal clams and may consume the siphons of larger clams (Peterson & Skilleter 1994), but they are rarely responsible for mortality of adult, large-bodied clams (Hines et al. 1990, Eggleston et al. 1992).

### Survey design

A bivalve survey was completed in the following seasons and years: spring, summer, and fall 2012, and spring and summer 2013. Each season, bivalves were collected from 3 sub-estuaries of lower Chesapeake Bay (Lynnhaven River system, York River, and Mobjack Bay), 4 sites within each sub-estuary, and 3 replicate samples from each site (Fig. 1; GPS coordinates provided in Supplement 1 at [www.int-res.com/](http://www.int-res.com/)

[articles/suppl/m570p113\\_supp1.zip](#)). All sites were sampled in each season/year for a total of 180 samples, with 4 to 6 sampling dates in each season. All sampling was completed within 2 wk in each season except for fall 2012 (33 d) and summer 2012 (24 d), when weather prevented more efficient sampling (sample dates provided in Supplement 1). Sites were chosen based on knowledge of benthic habitat composition. Sites often contained a mix of different habitat types, and not all habitats were found in each site. At each site, the locations for the 3 replicate samples within each site were haphazardly selected by throwing a suction ring (0.11 m<sup>2</sup> area PVC tube) from the boat in shallow water of 1.5 to 2 m depth mean high water. Bivalves within the suction ring and to 40 cm depth were collected using a suction sampling device, and samples were sieved through 3 mm mesh. In the laboratory, all bivalves in the 3 mm samples were identified to species and counted. This mesh size (3 mm) is larger than that used in some bivalve studies (Seitz et al. 2016), but was chosen because the literature suggests that intense predation by small crustaceans on bivalve recruits does not occur until clams reach 1.5–2.0 mm in shell length (van der Veer et al. 1998), indicating clams much smaller than the 3 mm mesh would not be interacting with the crab and fish predators we examined in this study.

For all suction samples, we examined the substrate retained on the 3 mm mesh to assign a habitat type to each sample. The habitat category that made up the

majority of the material by volume on the mesh (assessed by eye) was designated as the habitat type for the sample. Habitat categories were detrital mud (which included woody debris or marsh detritus), coarse sand (which included pebbles or gravel), shell hash (which included fossilized shell and crushed or whole bivalve shells), oyster shell (both articulated and crushed shells which were associated with larger reefs and were thicker and larger than shell hash), or seagrass (any species). We calculated the total volume of habitat retained on a 3 mm sieve by water displacement.

Blue crab density at each site was quantified using 6 replicate 20 m tows with a modified commercial crab scrape (usually used for harvesting soft shell peeler crabs in seagrass in lower Chesapeake Bay) with an opening 1 m wide, a 6 mm mesh net, and a tickler chain to increase capture of small crabs (Seitz et al. 2008). Tows were completed on the same day as bivalve sampling or within a few days of sampling. All blue crabs were measured to the nearest 0.1 mm. In addition, any fish caught in tows were identified, measured to the nearest 1 mm and released. At each site, the number of ray pits within 1 m to either side of a 50 m transect were counted and are treated as a proxy of cownose ray *R. bonasus* density (Hines et al. 1997). Ray pits were about 0.3 m in diameter and 10 cm deep, and could be easily seen in good visibility or detected by sweeping the sediment with hands in poor visibility.

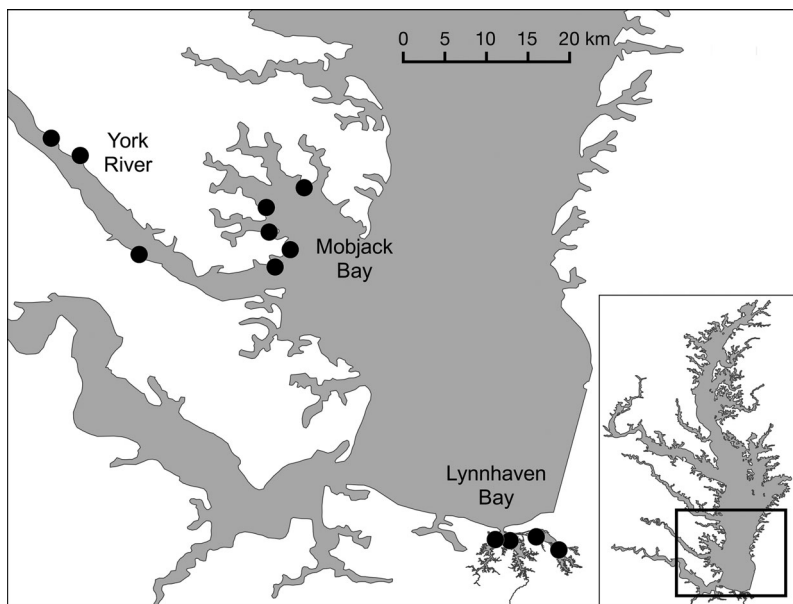


Fig. 1. Sampling sites in lower Chesapeake Bay, VA, USA (inset). Samples were collected in 3 sub-estuaries: Mobjack Bay, the York River, and Lynnhaven; 4 sites were sampled in each sub-estuary

### Statistical analysis

Species diversity was calculated as the Gini-Simpson index of diversity, or the probability that 2 randomly selected individuals will be of different species. The Gini-Simpson index,  $\lambda$ , is calculated as  $1 - \text{Simpson's index}$ , where Simpson's index =  $\sum_{i=1}^R p_i^2$ , in which  $p_i$  = the proportional abundance of the  $i^{\text{th}}$  species. The Gini-Simpson index ranges from 0 to 1, with larger values representing higher diversity. Species richness was calculated as the number of species present in each sample, and total bivalve density was also calculated for each sample. To account for bias in species richness associated with variability in the number of individuals collected in a given sample, we calculated rarefied species



richness using fixed-coverage subsampling (Chao & Jost 2012) using the iNEXT package in R (Hsieh et al. 2016).

For each sample, bivalves were assigned to functional groupings based on 3 categories summarizing their life history and trophic niche: armor (thin-shelled or armored), feeding mode (deposit feeding or suspension feeding), and living position (deep burrowing or shallow/surface dwelling; Fig. 2). These groupings included (1) facultative deposit-feeding (DF) bivalves, (2) deep-burrowing suspension-feeding (DBSF) bivalves, (3) thin-shelled surface-dwelling (TSSD) bivalves (which included both shallow-burrowing bivalves such as *Gemma gemma* and epifaunal bivalves such as the paper mussel *Arcuatula papyria*), and (4) armored bivalves (ARM; see Table 1). Bivalves were considered armored if they had thicker or stronger shells than other bivalves in their size range (Blundon & Kennedy 1982b). Bivalves were considered deep-burrowing if adults of the species burrowed to depths of 15 cm or more (Fraser 1967, Alexander et al. 1993). The only exception was *Limecola balthica* which, despite the ability to burrow deeply in the sediment as an adult, was included as a deposit feeder (Blundon & Kennedy 1982a) because the majority of the individuals collected were small. Functional richness was calculated as the number of functional groups represented in the sample, and functional diversity was calculated as the Gini-Simpson's diversity index of bivalve functional groups for the sample (Schleuter et al. 2010).

Gini-Simpson's index of species diversity, species richness, functional group richness and functional diversity were analyzed using a generalized linear model with a Gaussian distribution and an identity

link function. Densities for the 4 functional bivalve groupings were analyzed with generalized linear models with a quasi-Poisson distribution and a log link function. Generalized linear models contained the following predictor variables as fixed effects: year (2 levels), season (3 levels), sub-estuary (3 levels), site (4 levels, nested within sub-estuary), habitat (5 levels), habitat volume (ml), blue crab density ( $m^{-2}$ ), fish density ( $m^{-2}$ ), and ray pit density ( $m^{-2}$ ). McFadden's  $R^2$  (also known as rho-squared) was calculated as a measure of fit for all generalized linear models of density data (McFadden 1974). Confidence intervals (95%) were calculated for coefficients within the model and for best-fit lines, and are presented back-transformed to the original scale.

All variables were examined for multicollinearity with scatter plots before inclusion in the model. In addition, assumptions of generalized linear models were examined using quantile-quantile plots and residual plots. All models met the assumptions of normality and homogeneity of variance except models for TSSD and DF bivalve groups. These groups were examined further using zero-inflated Poisson models. However, zero-inflated models provided no improvement in ability to meet assumptions, and resulted in more extreme residuals than quasi-Poisson models. Analyses proceeded using quasi-Poisson generalized linear models for both TSSD and DF bivalves, and any conclusions should be treated with caution due to the deviance from assumptions.

For multiple comparisons, significant difference was determined using non-parametric bootstrap hypothesis testing with 10 000 simulations and  $\alpha = 0.05$  (Efron & Tibshirani 1993) because many response variables deviated from the assumptions of parametric methods. Bootstrap hypothesis testing is a more powerful alternative to traditional hypothesis testing on transformed data (Russell & Dean 2000). Contrasts proceeded as follows: the category with the largest value of the response was compared with the category with the lowest value. If this comparison was significant at  $\alpha = 0.05$ , the category with the largest response was compared to the category with the next lowest value, and so on until the result was not significant at  $\alpha = 0.05$ . This procedure was then repeated for the category with the second largest response. For each response variable, p-values were corrected for multiple comparisons using the Bonferroni method. Cohen's  $d$  was calculated as a measure of effect size for all 2-group comparisons. All analyses were completed using R statistical software (R Core Team 2016), and code and data files are provided in Supplement 1.

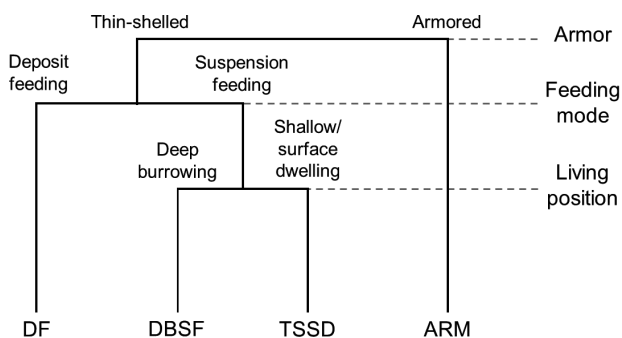


Fig. 2. Functional dendrogram of the relationships between functional groupings. Based on these groupings, bivalves were assigned into 4 functional groups: facultative deposit-feeding (DF), deep-burrowing suspension-feeding (DBSF), thin-shelled surface-dwelling (TSSD), and armored (ARM) bivalves

## RESULTS

In all, 2871 bivalves representing 17 species were collected in the survey (Table 1). The maximum density observed for a single species was 2082 m<sup>-2</sup> *Limecola balthica* in the York River in spring 2013. After *L. balthica* (with 1250 total individuals collected), the most commonly encountered bivalves were, in descending order, the stout razor clam *Tagelus plebeius* (312 collected), *Ameritella mitchelli* (299 collected), and *Kelliopsis elevata* (287 collected).

Average overall sample Gini-Simpson diversity index and rarefied species richness were 0.37 and 8.44, respectively. Rarefied species richness was significantly greater in seagrass than in detrital mud ( $d = 0.08$ ,  $p = 0.04$ ; Fig. 3a), and functional richness was greater in seagrass than in oyster shell ( $d = 0.07$ ,  $p = 0.04$ ), shell hash ( $d = 0.08$ ,  $p = 0.007$ ), and detrital mud ( $d = 0.08$ ,  $p = 0.05$ ; Fig. 3b). Trends in the Gini-Simpson diversity index and functional diversity were both very similar to trends in species richness, and results are included in Fig. S1 and Table S1 in Supplement 2 at [www.int-res.com/articles/suppl/m570p113\\_supp2.pdf](http://www.int-res.com/articles/suppl/m570p113_supp2.pdf).

Detrital mud supported higher densities of the facultative DF *L. balthica* and *A. mitchelli* than seagrass ( $d = 0.15$ ,  $p = 0.0006$ ; Fig. 4a). DBSF bivalves, such as *T. plebeius*, *Ensis directus*, *Mya arenaria*, *Petricolaria*

Table 1. Bivalve species and functional groups encountered during a survey of lower Chesapeake Bay. Bivalve species presented in order of cumulative total number of individuals collected over the course of the study (total collected). Maximum densities (m<sup>-2</sup>) are the maximum observed in one sample. Bivalves were grouped into 4 functional groups: facultative deposit-feeding (DF), deep-burrowing suspension-feeding (DBSF), thin-shelled surface-dwelling (TSSD), and armored (ARM) bivalves

Species	Total collected	Maximum density	DF	DBSF	TSSD	ARM
<i>Limecola balthica</i>	1250	2082	X			
<i>Tagelus plebeius</i>	312	218		X		
<i>Ameritella mitchelli</i>	299	327	X			
<i>Kelliopsis elevata</i>	287	345			X	
<i>Arcuatula papyria</i>	233	527			X	
<i>Ensis directus</i>	90	136		X		
<i>Mulinia lateralis</i>	88	91				X
<i>Mya arenaria</i>	79	191		X		
<i>Mercenaria mercenaria</i>	64	73				X
<i>Parvilucina crenella</i>	45	218			X	
<i>Gemma gemma</i>	31	45			X	
<i>Petricolaria pholadiformis</i>	29	173		X		
<i>Tagelus divisus</i>	26	55		X		
<i>Geukensia demissa</i>	21	118				X
<i>Lyonsia hyalina</i>	8	18			X	
<i>Modiolus modiolus</i>	7	27				X
<i>Noetia ponderosa</i>	2	9				X

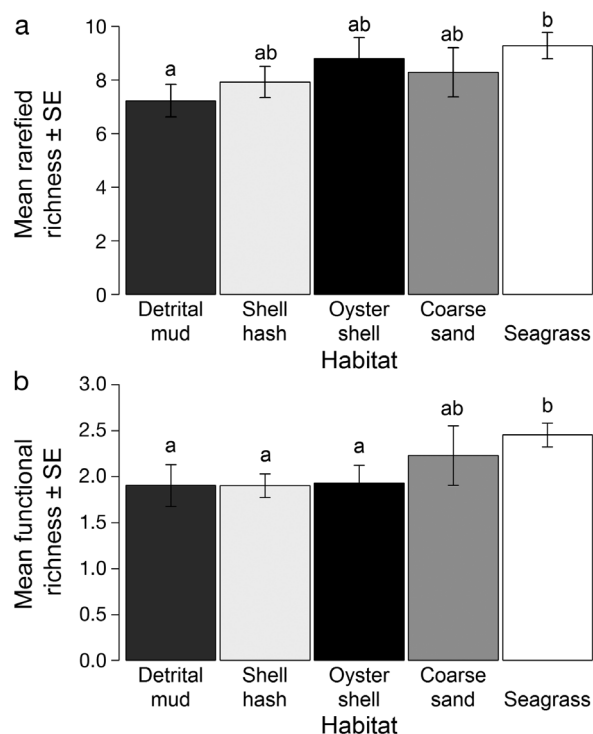


Fig. 3. Bivalve diversity in different habitats. Means  $\pm$  1 SE for (a) rarefied species richness and (b) functional richness in different habitat types in lower Chesapeake Bay. Samples were collected in detrital mud ( $n = 21$ ), shell hash ( $n = 61$ ), oyster shell ( $n = 30$ ), coarse sand ( $n = 13$ ), and seagrass ( $n = 55$ ). Letters denote significant differences at  $\alpha = 0.05$

*pholadiformis*, and *Tagelus divisus* (Table 1), had similar densities in all habitats (Fig. 4b). TSSD bivalves, such as *K. elevata* and *Arcuatula papyria* (Table 1), had higher densities in seagrass habitat than detrital mud ( $d = 0.06$ ,  $p = 0.05$ ), or shell hash ( $d = 0.04$ ,  $p = 0.04$ ; Fig. 4c). ARM bivalves, such as *Geukensia demissa*, *Mercenaria mercenaria*, *Mulinia lateralis*, *Noetia ponderosa*, and *Modiolus modiolus* (Table 1), had the highest densities in oyster shell, and densities of ARM bivalves were significantly higher in oyster shell than in detrital mud ( $d = 0.09$ ,  $p = 0.04$ ) or shell hash ( $d = 0.07$ ,  $p = 0.03$ ; Fig. 4d).

In generalized linear models, species diversity, functional diversity, species richness, and functional richness were all positively associated with presence of seagrass (Tables S2–S5 in Supplement 2). In comparison with detrital mud (the habitat with

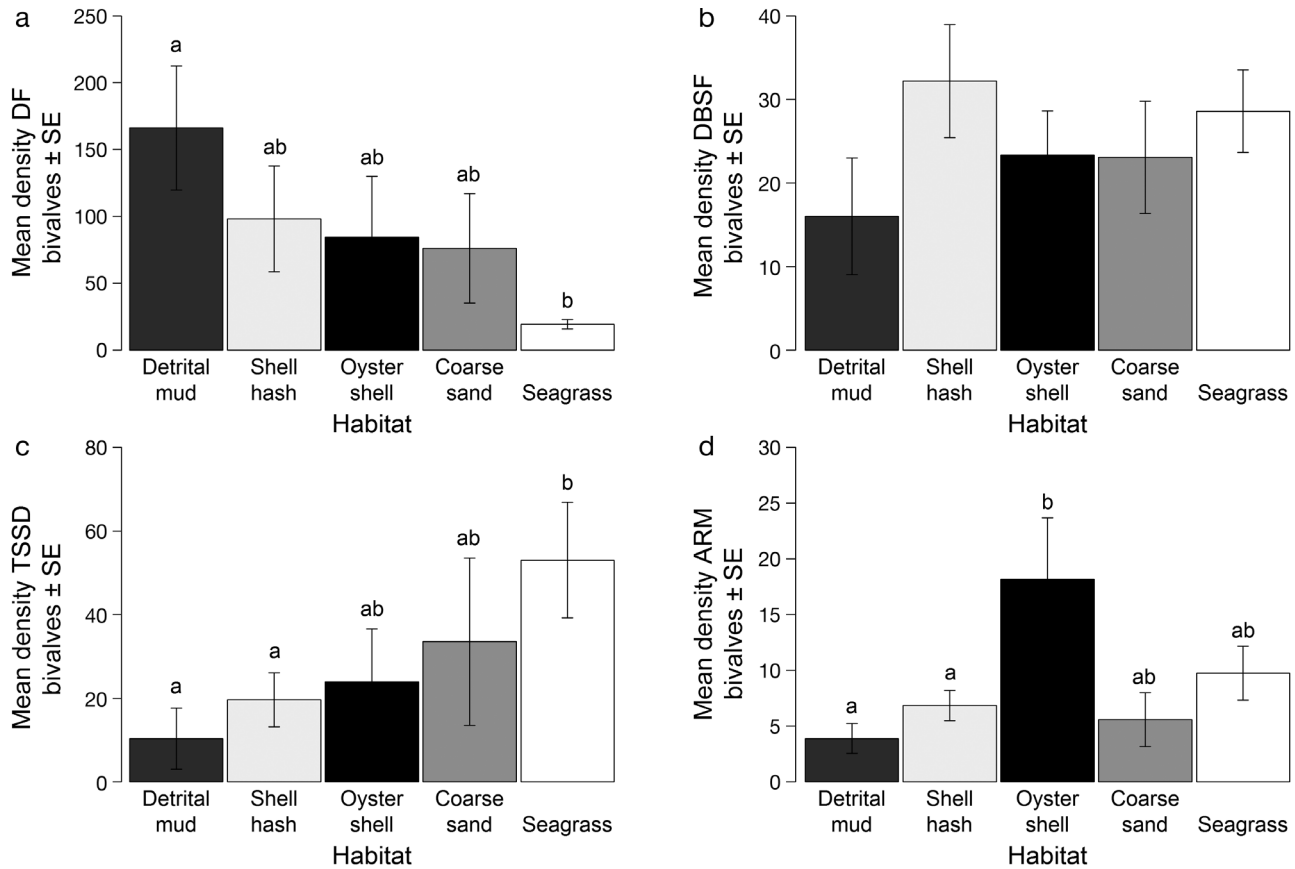


Fig. 4. Bivalve functional group densities (m<sup>-2</sup>) in different habitats. Means ± 1 SE for densities of (a) facultative deposit-feeding (DF) bivalves, (b) deep-burrowing suspension-feeding (DBSF) bivalves, (c) thin-shelled surface-dwelling (TSSD) bivalves, and (d) armored (ARM) bivalves in different habitat types in lower Chesapeake Bay. Samples were collected in detrital mud (n = 21), shell hash (n = 61), oyster shell (n = 30), coarse sand (n = 13), and seagrass (n = 55). Letters denote significant differences at  $\alpha = 0.05$

lowest diversity), seagrass had 0.19–0.55 units higher Gini-Simpson diversity index, 0.18–0.51 units higher functional diversity index, and supported 4.11–9.65 more species (95% CIs). On average, seagrass supported 0.74–2.20 more functional groups than detrital mud, 0.41–1.96 more than coarse sand, 0.56–1.93 more than oyster shell, and 0.53–1.64 more than shell hash (95% CIs).

Indices of diversity were influenced by both habitat and predators, although the influence of predators was not necessarily negative. Gini-Simpson diversity index and functional diversity were both positively correlated with the index of ray density (no. ray pits m<sup>-2</sup>; Tables S2 & S3). An increase of 1 ray pit m<sup>-2</sup> resulted in a 0.19–1.34 unit increase in the Gini-Simpson diversity index and a 0.31–1.37 unit increase in functional diversity (95% CIs; Fig. 5a,b). Both rarefied species richness and functional richness were positively correlated with habitat volume; an increase of 1 l habitat volume was associated with an increase in rarefied species richness of 0.03–1.50,

and an increase in functional richness of 0.02–0.41 (Fig. 5c,d; Tables S4 & S5).

Predator density was identified as one of the major factors associated with DF bivalve distribution; DF bivalves were negatively correlated with blue crab density (Fig. 5e), and negatively correlated with ray pit density (Fig. 5f; Table S6 in Supplement 2). DBSF bivalves were mainly associated with high habitat volume (Fig. 5g; Table S7). TSSD bivalves tended to be positively correlated with habitat volume (Fig. 5h) and negatively correlated with blue crab density (Fig. 5i). These predictors were significant at  $\alpha = 0.10$ , and there were no predictors significant at  $\alpha = 0.05$  for TSSD bivalves (Table S8). ARM bivalves were significantly more abundant in oyster shell than in detrital mud, coarse sand, or shell hash habitats, and ARM bivalve density was positively correlated with habitat volume (Fig. 5j; Table S9). Bivalve densities were not correlated with fish densities for any bivalve functional group (Tables S2–S9).



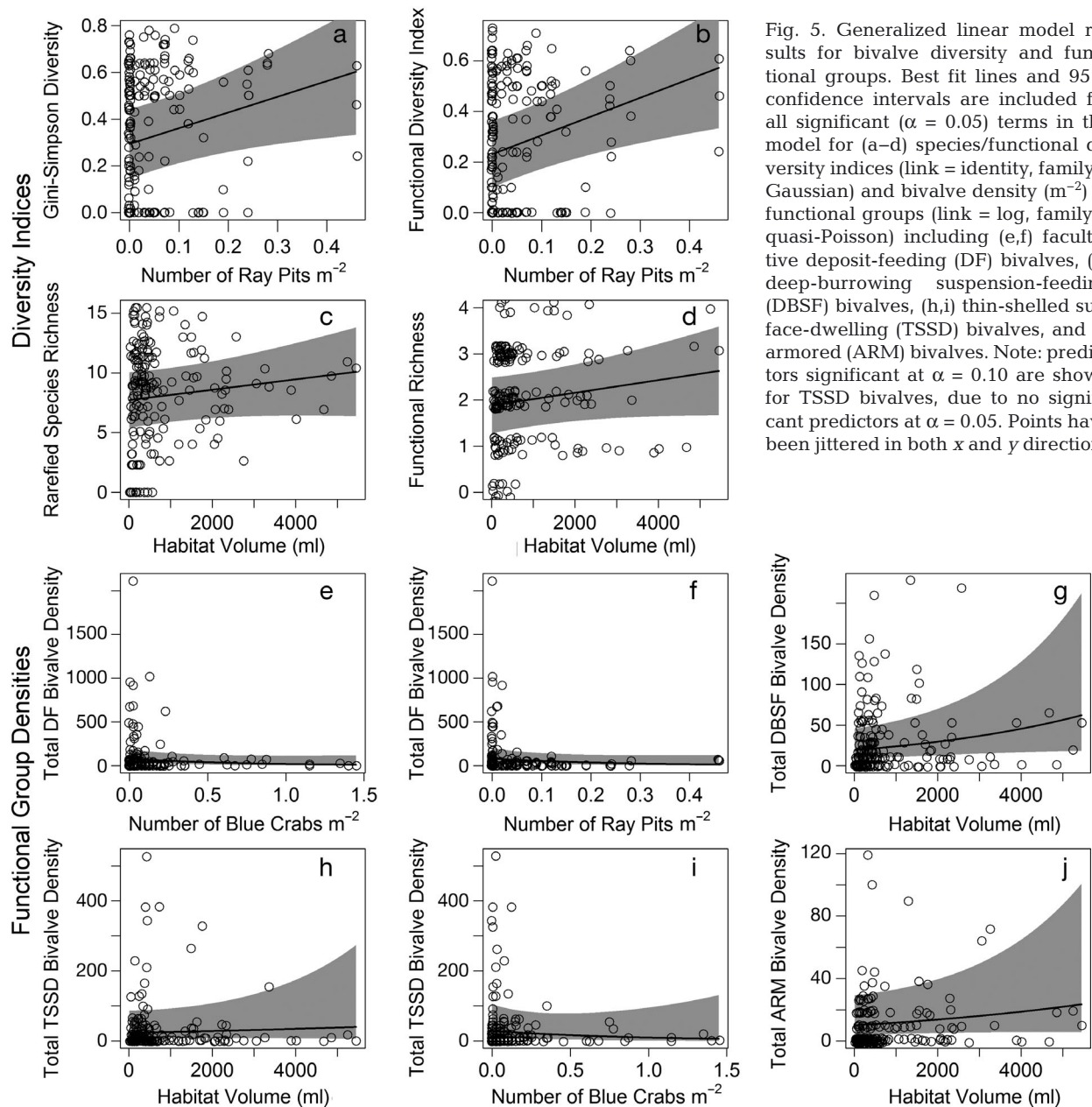


Fig. 5. Generalized linear model results for bivalve diversity and functional groups. Best fit lines and 95% confidence intervals are included for all significant ( $\alpha = 0.05$ ) terms in the model for (a–d) species/functional diversity indices (link = identity, family = Gaussian) and bivalve density ( $m^{-2}$ ) in functional groups (link = log, family = quasi-Poisson) including (e,f) facultative deposit-feeding (DF) bivalves, (g) deep-burrowing suspension-feeding (DBSF) bivalves, (h,i) thin-shelled surface-dwelling (TSSD) bivalves, and (j) armored (ARM) bivalves. Note: predictors significant at  $\alpha = 0.10$  are shown for TSSD bivalves, due to no significant predictors at  $\alpha = 0.05$ . Points have been jittered in both x and y directions

## DISCUSSION

Habitat appears to be an important factor in bivalve community structure and distribution in lower Chesapeake Bay, consistent with our hypotheses. Bivalve species diversity and functional diversity metrics were positively correlated with habitat volume, and bivalve communities were more diverse in seagrass than in less complex habitats. Seagrass increased bivalve diversity by 68, 76, 87, and 94% when compared to oyster shell, detrital mud, coarse sand, and shell hash habitats, respectively, in models. Seagrass had one additional bivalve functional group

compared to the other habitats (out of 4 total functional groupings).

The functional group that was consistently found in seagrass, and relatively rarely found in other habitat types, was the TSSD group that included the species *Kelliopsis elevata*, *Arcuatula papyria*, *Parvilucina crenella*, *Gemma gemma*, and *Lyonsia hyalina*. Two of these species, *A. papyria* (epifaunal) and *L. hyalina* (infaunal) were nearly exclusively found in seagrass habitats. In contrast to other high complexity habitats such as oyster shell and shell hash, seagrass provides both aboveground and belowground structure, offering protection for infaunal and epifaunal bivalves

(Orth et al. 1984). This characteristic of seagrass habitat may make it possible for TSSD bivalves, which do not have many defenses from predators, to persist in seagrass. Seagrass may also indirectly facilitate TSSD bivalves in ways unrelated to the functional groupings used in this study (e.g. protection from predation or feeding mode). For example, seagrass blades may increase rates of larval settlement by baffling water currents (Heiss et al. 2000). More research is needed to determine the exact mechanism behind the association between seagrass and TSSD bivalves.

The functional groupings in this study represent the role of bivalves in trophic interactions; thus, loss of seagrass habitat, and the concurrent loss of an entire functional group, may impact ecosystem function. Impacts of the loss of a functional group of bivalves will ultimately be determined by the ability of other groups to fill the role of the lost species. For example, the role of oysters in the Chesapeake Bay was at least partially filled by zooplankton, planktivorous fish, suspension-feeding polychaetes, and clams (Baird & Ulonowicz 1989, Thompson & Schaffner 2001). However, despite these functional replacements, the loss of oysters still had massive implications for water quality and ecosystem function in the Chesapeake Bay (Rothschild et al. 1994). This indicates that when a functional group is lost, complete functional replacement by other species may be unlikely in the Chesapeake Bay.

Consistent with our hypotheses, functional groups exhibited the following habitat preferences: the greatest densities of DF bivalves were in detrital mud habitats, the greatest densities of TSSD bivalves were in seagrass habitats, and the greatest densities of ARM bivalves were in oyster shell habitats. These results confirm that the functional groupings of bivalves used in this study represent realized niches driven by bivalve morphology and feeding mode. To allow all of the functional groups to persist in the Bay, all of the habitats must be maintained, with a special focus on seagrass, the presence of which is a major factor in both species and functional diversity. Amount of habitat also matters: habitat volume was correlated with density of all suspension-feeding bivalve groups (DBSF, TSSD, and ARM bivalves). The ecological consequence of these results is that maintaining diverse habitats is important for sustaining full functionality in lower Chesapeake Bay.

In disagreement with our hypotheses, DBSF bivalves did not have higher densities in more complex habitats. Sediment penetrability in complex habitats is often very low, preventing burrowing behaviors and prohibiting some of the deep-burrowing species

from colonizing these areas (Fiori & Carcedo 2015). A few of the DBSF species found in the samples, including *Ensis directus* and *Petricola pholadiformes*, are sensitive to sediment texture and are unable to burrow efficiently when sediment particles exceed an optimal range (Alexander et al. 1993), and this may be why these habitat types were not particularly advantageous to DBSF species.

As we hypothesized, densities of 2 functional groups that contained thin-shelled bivalves that were not deep burrowing were either negatively associated (DF) or tended towards a negative relationship (TSSD) with blue crab density. There was also evidence that DF bivalves were negatively associated with ray pits, which corresponds to evidence that cownose rays *Rhinoptera bonasus* prey heavily on *Limecola balthica*, the dominant DF species (Fisher 2010). These groups do not exhibit armor or deep-burrowing behavior, and are presumably more susceptible to predation (i.e. top-down control). These results are opposite of what was seen in some studies demonstrating bottom-up control of bivalves on crabs (Seitz & Lipcius 2001, Seitz et al. 2003, 2016). However in these studies, top-down control became more apparent at smaller spatial scales (Seitz & Lipcius 2001, Seitz et al. 2016). The current study was conducted at a small spatial scale, where predators do not move among habitats that differ greatly in food availability, so top-down control was more evident in the current results.

Predators, specifically rays, had an unexpected positive effect on bivalve diversity. There was a positive correlation between ray pit density and bivalve diversity/functional diversity. Ray pits may serve as a disturbance that promotes diversity of bivalves by interrupting succession (Sousa 1979) and decreasing the abundance of competitive dominants (Menge & Sutherland 1987). In otherwise homogenous environments like sand and mud flats, where rays often feed, ray feeding activity may serve to structure communities of bivalves.

Declines in ecosystem function due to the loss of invertebrate groups has led to unpredictable and serious consequences in other regions of the world (Goedkoop & Johnson 1996, Lodge et al. 1998). When seagrasses and other complex macrophytes were lost in Scotland, the Baltic, and Western Australia, the result was a truncation of the food web and a loss of many important fish and bird species (Jansson & Dahlberg 1999, Rafaelli 1999, Thomson et al. 2015). In Chesapeake Bay, the dominant seagrass species (eelgrass *Zostera marina*) is near its upper thermal tolerance limit, so extreme and frequent seagrass

die-backs are expected in the future as global temperatures warm (Moore & Jarvis 2008). Thus, based on lessons from other regions, and due to bivalves' importance for ecosystem functioning, seagrass loss in Chesapeake Bay may be associated with a loss in functionality.

This study is one of the first to examine the impact of predator density and habitat (although see Duffy et al. 2001) on functional diversity and individual functional groups in marine benthic communities. With declines in top predators worldwide, and in particular in many of the same ecosystems experiencing habitat loss (Jackson et al. 2001), it is important to understand the combined effect of predators and habitat on bivalve functional diversity and ultimately ecosystem function. In addition, restoration efforts targeting maximized ecosystem function may find this information useful, as habitat restoration and predator management are both key components in bivalve restoration (Brumbaugh et al. 2006). If the goal of restoration is to maximize functional diversity, blue crab density should be taken into consideration to encourage survival of thin-shelled bivalves.

Future research should focus on the impact of the loss of seagrass and other habitats on benthic–pelagic coupling in Chesapeake Bay, including both direct links between habitat loss and biogeochemical cycling as well as indirect effects that are mediated by concurrent losses in bivalve functional diversity. This research should include an examination of quantitative bivalve functional traits related to feeding preferences and predator avoidance, and experimental designs that document shifts in these traits when habitat is lost from embayments and tributaries in the Bay. An interdisciplinary approach is necessary to understand how loss of bivalve functional diversity in Chesapeake Bay will alter the geology, chemistry, and biology of this highly productive estuary. For example, little is known regarding the degree to which loss of seagrass in particular will alter the volume and quality of organic matter in the Bay, and the degree to which changes in organic matter due to seagrass loss will impact biogeochemical cycling directly (Eyre et al. 2013) or indirectly through changes in bivalve distribution and feeding modes (Caliman et al. 2007). These lines of inquiry can inform models that will lead to predictions for the future of biogeochemical cycling in Chesapeake Bay as seagrass continues to decline. Considering the consequences of shifts in benthic community structure in other estuaries (Petersen et al. 2008, Kristensen et al. 2014), these steps are necessary to ensure Chesapeake Bay will continue to provide ecosystem goods and services for future generations.

## CONCLUSIONS

Chesapeake Bay bivalves interacted with habitat and predators differently depending on the bivalves' feeding mode, predator defense strategy, and living position. Bivalve species diversity and functional diversity were positively associated with complex habitats and quantity (volume) of habitat. Bivalve functional groups exhibited habitat preferences based on feeding mode and susceptibility to predators. Densities of bivalves in functional groups that were expected to be most susceptible to predation were negatively related to predator densities. Loss of structured habitat may lead to loss of functional groups of bivalves in Chesapeake Bay. The group that is most at risk contains thin-shelled suspension-feeding bivalves that live near the sediment surface, either as shallow-burrowing infauna or epifauna. Complex habitat such as seagrass may provide these bivalves with protection from predation, especially by the dominant epibenthic predator in Chesapeake Bay, the blue crab *Callinectes sapidus*. Through an examination of functional diversity of bivalves in Chesapeake Bay habitats, this study has identified a potential mechanism by which habitat loss may lead to a decrease in ecosystem functioning in Chesapeake Bay: by removing entire groups of bivalves that contribute to nutrient cycling and trophic dynamics.

*Acknowledgements.* We gratefully acknowledge the assistance given by the students and staff of the Community Ecology and Marine Conservation Biology labs at the Virginia Institute of Marine Science. Dr. Jon Lefcheck provided valuable comments on an earlier draft of the manuscript. This material is based upon work supported by the National Oceanic and Atmospheric Administration grant number NA11NMF4570218, the Environmental Protection Agency EPA STAR Fellowship under grant number FP91767501, and the National Science Foundation Administration GK-12 program under grant number DGE-0840804. This paper is contribution number 3619 from the Virginia Institute of Marine Science, College of William & Mary. All data files and R scripts associated with this analysis have been uploaded as supporting information.

## LITERATURE CITED

- ✦ Airolidi L, Balata D, Beck MW (2008) The gray zone: relationships between habitat loss and marine diversity and their applications in conservation. *J Exp Mar Biol Ecol* 366:8–15
- ✦ Alexander RR, Stanton RJ, Dodd JR (1993) Influence of sediment grain size on the burrowing of bivalves: correlation with distribution and stratigraphic persistence of selected Neogene clams. *Palaios* 8:289–303
- ✦ Baird D, Ulonowicz RE (1989) The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol Monogr* 59:329–364

- ✦ Bazairi H, Bayed A, Hily C (2005) Structure and bioassessment of benthic communities of a lagoonal ecosystem of the Atlantic Moroccan coast. *C R Biol* 328:977–990
- ✦ Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193
- ✦ Bertness MD, Grosholz E (1985) Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. *Oecologia* 67:192–204
- ✦ Biles CL, Paterson DM, Ford RB, Solan M, Raffaelli DG (2002) Bioturbation, ecosystem functioning and community structure. *Hydrol Earth Syst Sci* 6:999–1005
- ✦ Blaylock RA (1993) Distribution and abundance of the cownose ray, *Rhinoptera bonasus*, in lower Chesapeake Bay. *Estuaries* 16:255–263
- ✦ Blundon JA, Kennedy VS (1982a) Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *J Exp Mar Biol Ecol* 65:67–81
- ✦ Blundon JA, Kennedy VS (1982b) Mechanical and behavioral aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. *J Exp Mar Biol Ecol* 65:47–65
- ✦ Brenchley GA (1982) Mechanisms of spatial competition in marine soft-sediment communities. *J Exp Mar Biol Ecol* 60:17–33
- Brumbaugh RD, Beck MW, Coen LD, Craig I, Hicks P (2006) A practitioner's guide to the design and monitoring of shellfish restoration projects: an ecosystem services approach. The Nature Conservancy, Arlington, VA
- ✦ Caliman A, Leal JF, Esteves FA, Carneiro LS, Bozelli RL, Farjalla VF (2007) Functional bioturbator diversity enhances benthic–pelagic processes and properties in experimental microcosms. *J N Am Benthol Soc* 26:450–459
- ✦ Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93:2533–2547
- ✦ Clemente S, Hernández JC, Rodríguez A, Brito A (2010) Identifying keystone predators and the importance of preserving functional diversity in sublittoral rocky-bottom areas. *Mar Ecol Prog Ser* 413:55–67
- ✦ Cohen RRH, Dresler PV, Phillips EJP, Cory RL (1984) The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnol Oceanogr* 29:170–180
- ✦ Commito JA, Como S, Grupe BM, Dow WE (2008) Species diversity in the soft-bottom intertidal zone: biogenic structure, sediment, and macrofauna across mussel bed spatial scales. *J Exp Mar Biol Ecol* 366:70–81
- ✦ Covich AP, Palmer MA, Crowl TA (1999) The role of benthic invertebrate species in freshwater ecosystems: zoobenthic species influence energy flows and nutrient cycling. *Bioscience* 49:119–127
- ✦ Duarte CM, Dennison WC, Orth RJW, Carruthers TJB (2008) The charisma of coastal ecosystems: addressing the imbalance. *Estuaries Coasts* 31:233–238
- ✦ Duffy JE, Macdonald KS, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82:2417–2434
- Efron B, Tibshirani RJ (1993) An introduction to the bootstrap. Chapman & Hall, New York, NY
- ✦ Eggleston DB, Lipcius RN, Hines AH (1992) Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Mar Ecol Prog Ser* 85:55–68
- ✦ Ehrlich P, Walker B (1998) Rivets and redundancy. *Bio-science* 48:387
- ✦ Eyre BD, Maher DT, Squire P (2013) Quantity and quality of organic matter (detritus) drives N<sub>2</sub> effluxes (net denitrification) across seasons, benthic habitats, and estuaries. *Global Biogeochem Cycles* 27:1083–1095
- ✦ Fiori SM, Carcedo MC (2015) Influence of grain size on burrowing and alongshore distribution of the yellow clam (*Amarilladesma mactroides*). *J Shellfish Res* 34:785–789
- Fisher RA (2010) Life history, trophic ecology, and prey handling by cownose ray, *Rhinoptera bonasus*, from Chesapeake Bay. Virginia Institute of Marine Science, Gloucester Point, VA
- ✦ Fitch JE, Crowe TP (2012) Combined effects of inorganic nutrients and organic enrichment on intertidal benthic macrofauna: an experimental approach. *Mar Ecol Prog Ser* 461:59–70
- Fraser TH (1967) Contributions to the biology of *Tagelus divisus* (Tellinacea: Pelecypoda) in Biscayne (Florida). *Bull Mar Sci* 17:111–132
- ✦ Gauzens B, Legendre S, Lazzaro X, Lacroix G (2016) Intermediate predation pressure leads to maximal complexity in food webs. *Oikos* 125:595–603
- ✦ Goedkoop W, Johnson RK (1996) Pelagic-benthic coupling: profundal benthic community response to spring diatom deposition in mesotrophic Lake Erken. *Limnol Oceanogr* 41:636–647
- ✦ Gray JS (2002) Species richness of marine soft sediments. *Mar Ecol Prog Ser* 244:285–297
- ✦ Griffin JN, de la Haye KL, Hawkins SJ, Thompson RC, Jenkins SR (2008) Predator diversity and ecosystem functioning: density modifies the effect of resource partitioning. *Ecology* 89:298–305
- ✦ Grizzle RE, Greene JK, Coen LD (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. *Estuaries Coasts* 31:1208–1220
- ✦ Gutiérrez JL, Jones CG, Strayer DL, Iribarne OO (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* 101:79–90
- ✦ Heck KL, Thoman TA (1984) The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. *Estuaries* 7:70–92
- ✦ Heiss WM, Smith AM, Probert PK (2000) Influence of the small intertidal seagrass *Zostera novazelandica* on linear water flow and sediment texture. *N Z J Mar Freshw Res* 34:689–694
- ✦ Hewitt JE, Thrush SF, Halliday J, Duffy C (2005) The importance of small-scale habitat structure for maintaining beta diversity. *Ecology* 86:1619–1626
- ✦ Hily C (1991) Is the activity of benthic suspension feeders a factor controlling water quality in the Bay of Brest? *Mar Ecol Prog Ser* 69:179–188
- ✦ Hines A, Haddon A, Wiechert L (1990) Guild structure and foraging impact of blue crabs and epibenthic fish in a sub-estuary of Chesapeake Bay. *Mar Ecol Prog Ser* 67:105–126
- ✦ Hines AH, Whitlatch RB, Thrush SF, Hewitt JE, Cummings VJ, Dayton PK, Legendre P (1997) Nonlinear foraging response of a large marine predator to benthic prey: eagle ray pits and bivalves in a New Zealand sandflat. *J Exp Mar Biol Ecol* 216:191–210
- Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol Evol* 7:1451–1456



- ✦ Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Jansson BO, Dahlberg K (1999) The environmental status of the Baltic Sea in the 1940s, today, and in the future. *Ambio* 28:312–319
- Kristensen E, Delefosse M, Quintana CO, Flindt MR, Valdemarsen T (2014) Influence of benthic macrofauna community shifts on ecosystem functioning in shallow estuaries. *Front Mar Sci* 1:1–14
- Lawton JH, Brown VK (1993) Redundancy in ecosystems. In: Schulze ED, Mooney HA (eds) *Biodiversity and ecosystem function*. Springer-Verlag, New York, NY, p 25–270
- Levinton J (1995) Bioturbators as ecosystem engineers: control of the sediment fabric, inter-individual interactions, and material fluxes. In: Jones CG, Lawton JH (eds) *Linking species & ecosystems*. Springer Science+Business Media, Dordrecht, p 29–36
- Lipcius RN, Eggleston DB, Heck KL, Seitz RD, van Monfrans J (2007) Post-settlement abundance, survival, and growth of postlarvae and young juvenile blue crabs in nursery habitats. In: Kennedy VS, Cronin LE (eds) *Biology and management of the blue crab*. University of Maryland Press, Baltimore, MD, p 535–565
- ✦ Lodge DM, Stein RA, Brown KM, Covich AP, Bronmark C, Garvey JE, Klosiewski SP (1998) Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. *Aust J Ecol* 23:53–67
- ✦ Marinelli RL, Williams TJ (2003) Evidence for density-dependent effects of infauna on sediment biogeochemistry and benthic-pelagic coupling in nearshore systems. *Estuar Coast Shelf Sci* 57:179–192
- McFadden D (1974) Conditional logit analysis of qualitative choice behavior. In: Zarembka P (ed) *Frontiers in econometrics*. Academic Press, New York, NY, p 105–142
- ✦ Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am Nat* 130:730–757
- ✦ Moore KA, Jarvis JC (2008) Environmental factors affecting recent summertime eelgrass diebacks in the lower Chesapeake Bay: implications for long-term persistence. *J Coast Res (Spec Issue)* 55:135–147
- ✦ Norkko A, Hewitt JE, Thrush SF, Funnell GA (2001) Benthic-pelagic coupling and suspension-feeding bivalves: linking site-specific sediment flux and biodeposition to benthic community structure. *Limnol Oceanogr* 46:2067–2072
- ✦ Orth RJ, Moore KA (1983) Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. *Science* 222:51–53
- ✦ Orth RJ, Heck KL Jr, van Montfrans J (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7:339–350
- ✦ Orth RJ, Carruthers TJB, Dennison WC, Duarte CM and others (2006) A global crisis for seagrass ecosystems. *BioScience* 56:987–996
- ✦ Orth RJ, Marion SR, Moore KA, Wilcox DJ (2010) Eelgrass (*Zostera marina* L.) in the Chesapeake Bay Region of mid-Atlantic coast of the USA: challenges in conservation and restoration. *Estuaries Coasts* 33:139–150
- ✦ Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. *Ecol Lett* 9:741–758
- ✦ Petersen JK, Hansen JW, Laursen MB, Clausen P, Carstensen J, Conley DJ (2008) Regime shift in a coastal marine ecosystem. *Ecol Appl* 18:497–510
- ✦ Peterson CH (1982) Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. *Mar Biol* 66:159–170
- ✦ Peterson CH, Skilleter GA (1994) Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica*, flow environment, and siphon-cropping fishes. *Oecologia* 100:256–267
- ✦ Peterson CH, Summerson HC, Duncan PB (1984) The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, *Mercenaria mercenaria*. *J Mar Res* 42:123–138
- ✦ Prater C, Norman EJ, Evans-White MA (2015) Relationships among nutrient enrichment, detritus quality and quantity, and large-bodied shredding insect community structure. *Hydrobiologia* 753:219–232
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Rafaelli D (1999) Impact of catchment land-use on an estuarine benthic food web. In: Gray JS, Ambrose W, Szaniawska A (eds) *Biogeochemical cycling and sediment ecology*. Springer, Dordrecht, p 161–171
- ✦ Rodney WS, Paynter KT (2006) Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland. *J Exp Mar Biol Ecol* 335:39–51
- ✦ Rothschild BJ, Ault JS, Gouletquer P, Héral M (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. *Mar Ecol Prog Ser* 111:29–39
- ✦ Russell CJ, Dean MA (2000) To log or not to log: bootstrap as an alternative to the parametric estimation of moderation effects in the presence of skewed dependent variables. *Organ Res Methods* 3:166–185
- ✦ Savage C, Thrush SF, Lohrer AM, Hewitt JE (2012) Ecosystem services transcend boundaries: estuaries provide resource subsidies and influence functional diversity in coastal benthic communities. *PLOS ONE* 7:e42708
- ✦ Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. *Ecol Monogr* 80:469–484
- ✦ Seitz R, Lipcius R (2001) Variation in top-down and bottom-up control of marine bivalves at differing spatial scales. *ICES J Mar Sci* 58:689–699
- ✦ Seitz RD, Lipcius RN, Hines AH, Eggleston DB (2001) Density-dependent predation, habitat variations, and the persistence of marine bivalve prey. *Ecology* 82:2435–2451
- Seitz RD, Lipcius RN, Stockhausen WT, Delano KA, Seebo MS, Gerdes PD (2003) Potential bottom-up control of blue crab distribution at various spatial scales. *Bull Mar Sci* 72:471–490
- ✦ Seitz RD, Lipcius RN, Knich KE, Seebo MS, Long WC, Brylawski BJ, Smith A (2008) Stock enhancement and carrying capacity of blue crab nursery habitats in Chesapeake Bay. *Rev Fish Sci* 16:329–337
- Seitz RD, Lipcius RN, Hines AH (2017) Consumer versus resource control and the importance of habitat heterogeneity for estuarine bivalves. *Oikos* 126:121–135
- ✦ Sousa WP (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225–1239
- ✦ Stachowicz JJ (2001) Mutualism, facilitation, and the structure of ecological communities. *Bioscience* 51:235–246



- Stoner AW (1980) The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bull Mar Sci* 30:537–551
- ✦ Thompson ML, Schaffner LC (2001) Population biology and secondary production of the suspension feeding polychaete *Chaetopterus* cf. *variopedatus*: implications for benthic-pelagic coupling in lower Chesapeake Bay. *Limnol Oceanogr* 46:1899–1907
- ✦ Thomson JA, Burkholder DA, Heithaus MR, Fourqurean JW, Fraser MW, Statton J, Kendrick GA (2015) Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. *Glob Change Biol* 21:1463–1474
- ✦ van der Veer HW, Feler RJ, Weber A, Witte JI (1998) Importance of predation by crustaceans upon bivalve spat in the intertidal zone of the Dutch Wadden Sea as revealed by immunological assays of gut contents. *J Exp Mar Biol Ecol* 231:139–157
- ✦ van der Zee EM, Tielens E, Holthuijsen S, Donaldi S and others (2015) Habitat modification drives benthic trophic diversity in an intertidal soft-bottom ecosystem. *J Exp Mar Biol Ecol* 465:41–48
- Vermeij GJ (1987) *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton, NJ
- ✦ Wang Y, Liu D, Richard P, Li X (2013) A geochemical record of environmental changes in sediments from Sishili Bay, northern Yellow Sea, China: anthropogenic influence on organic matter sources and composition over the last 100 years. *Mar Pollut Bull* 77:227–236
- ✦ Welsh DT (2003) It's a dirty job but someone has to do it: the role of marine benthic macrofauna in organic matter turnover and nutrient recycling to the water column. *Chem Ecol* 19:321–342

*Editorial responsibility: Paul Snelgrove,  
St. John's, Newfoundland and Labrador, Canada*

*Submitted: August 8, 2016; Accepted: February 27, 2017  
Proofs received from author(s): April 8, 2017*