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Marine benthic predator-prey interactions and global change.

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Marine benthic predator-prey interactions and global change

A Dissertation

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In Partial Fulfillment

of the Requirements for the Degree of

Doctor of Philosophy

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by

Cassandra N. Glaspie

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

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DISSERTATION ABSTRACT

Anthropogenic stressors such as habitat loss, extreme weather events, and acidification can change predator-prey interactions. An understanding of the mechanisms by which these stressors impact predator-prey interactions may elucidate the fate of bivalves in the face of global change. My dissertation research informs management of marine resources in Chesapeake Bay, which has experienced substantial seagrass and oyster reef loss, increased storm activity, and combined estuarine and atmospheric CO_2 acidification. In my dissertation, I used field survey data, field caging experiments, laboratory mesocosm experiments, time-series analysis, and density-dependent mathematical models to assess the role of habitat, major storm events, acidification, and predators on bivalve distribution in lower Chesapeake Bay, with a special focus on the commercially important, thin-shelled clam species *Mya arenaria*, which has declined significantly in the past few decades.

In field surveys, seagrass supported one additional bivalve functional group (based on bivalve morphology and feeding mode) than all other habitat types, and bivalve diversity was 27-54% higher in seagrass than in shell hash, oyster shell, coarse sand, and detrital mud habitats. The odds of finding *M. arenaria* were higher in seagrass than in all other habitats. Predators likely consumed seasonal pulses of juveniles each year. In field caging experiments, blue crabs *Callinectes sapidus* were likely responsible for most of the mortality of juvenile *M. arenaria*, which was 76.6% higher for caged juveniles than for uncaged individuals over 5 d. In mesocosm feeding trials, *M. arenaria* maintained a low-density refuge from predation by blue crabs, and had higher survival in oyster shell or shell habitats as compared to sand or seagrass habitats. Time series analysis suggested *M. arenaria* was subjected to a storm-driven phase shift to low abundance in 1972, which has been maintained by blue crab predation. Density-dependent predator-prey models parameterized with data from laboratory and field experiments confirmed the presence of a coexistence steady state at low densities of *M. arenaria*, providing the theoretical proof-of-concept that *M. arenaria* can exist in a low-density stable state in the face of blue crab predation. Acidification altered behavior of both predator (*C. sapidus*) and prey (*M. arenaria*), resulting in no net change in proportional mortality of clams between acidified and control feeding trials.

My dissertation examined multiple lines of evidence to address the importance of structured habitat, extreme weather events, and acidification in the mediation of predator-prey dynamics. For the crab-bivalve predator-prey interactions examined here, predation exacerbated the effects of some anthropogenic stressors (habitat loss, extreme weather events) and ameliorated the impacts of other stressors (acidification) on bivalve prey. An understanding of density-dependent predation is a necessary component of an adaptive management strategy that can cope with climate change.

AUTHOR'S NOTE

The chapters of this dissertation were written as manuscripts for publication in scientific journals. Each chapter is written in the third person, references my co-authors, and is formatted according to the guidelines of the journal to which it will be submitted. Citations for individual chapters (at the time of writing) are listed below:

CHAPTER 2

Glaspie, C. N. and Seitz, R. D. *In prep.* Habitat and predators drive functional diversity of estuarine bivalves. For submission to *Functional Ecology.*

*This manuscript comprises only a portion of Chapter 2

CHAPTER 3

Glaspie, C. N. and Seitz, R. D. *In prep.* Habitat complexity mediates benthic predator-prey interactions in Chesapeake Bay. For submission to *Ecological Monographs.*

CHAPTER 4

Glaspie, C. N., Seitz, R. D., and Lipcius, R. N. *In prep.* The perfect storm: Extreme weather and predators drive phase shift in dominant Chesapeake Bay bivalve. For submission to *Nature.*

CHAPTER 5

Glaspie, C. N., Longmire, K., and Seitz, R. D. *In prep.* Acidification alters predator-prey interactions of blue crab *Callinectes sapidus* and soft-shell clam *Mya arenaria.* For submission to *Marine Ecology Progress Series.*

CHAPTER 6

Glaspie, C. N. *In prep.* Density-dependent predation and climate change in marine environments. For submission to *Frontiers in Ecology and the Environment.*

Marine benthic predator-prey interactions and global change

CHAPTER 1

Dissertation Introduction

Humans have drastically altered coastal marine environments through pollution and unsustainable harvesting practices. Anthropogenic CO_2 emissions have resulted in global climate change, including ocean warming (Solomon et al. 2007) and an increase the intensity and frequency of extreme events such as storms (Handmer et al. 2012, Settele et al. 2014). Atmospheric CO_2 pollution along with coastal eutrophication (and resultant changes to ecosystem metabolism) have led to acidification in near-shore environments (Orr et al. 2005, Feely et al. 2010, Duarte et al. 2013). Warming and increases in turbidity due to nutrient pollution have caused losses of vegetated habitats in coastal waters (Walker & McComb 1992, Nielsen et al. 2002, Hagy et al. 2004, Kemp et al. 2004, Moore & Jarvis 2008). Overfishing or destructive fishing methods have reduced structured habits such as oyster reefs (Rothschild et al. 1994).

Anthropogenic stressors such as habitat loss, extreme weather events, and acidification can change predator-prey interactions in coastal systems. Habitat features such as seagrass beds interfere with predator detection and capture of prey, which promotes high prey survival (Orth et al. 1984, Stoner 2009); when structured habitat is lost, entire trophic levels may decline resulting in sudden changes in ecosystem state (Jansson & Dahlberg 1999, Rafaelli 1999, Thomson et al. 2015). Similarly, severe weather events such as storms may cause mass mortality of one or a few species with low tolerance to fluctuations in salinity or sedimentation (Vaselli et al. 2008, Perkol-Finkel & Airoldi 2010, Gera et al. 2014). Such declines in abundance of one or a few species may lead to an alternative stable state (Mumby et al. 2007, Byrnes et al. 2011). Acidification is expected to result in malformation of bivalve shells (Beniash et al. 2010, Amaral et al. 2012a), which may alter bivalve defenses from predation and fundamentally alter predator-prey interactions (Gazeau et al. 2007, Amaral et al. 2012b). An understanding of the mechanisms by which stressors alter predator-prey interactions may elucidate the fate of bivalves in the face of global change.

I used shallow, benthic environments in Chesapeake Bay as a model system to demonstrate the interaction between trophic dynamics and large-scale anthropogenic stressors. In lower Chesapeake Bay, the blue crab *Callinectes sapidus* is a generalist predator that alters its feeding efficiency depending on prey density and habitat (Hines et al. 1990, Eggleston et al. 1992, Seitz et al. 2001). Chesapeake Bay also supports several bivalve species that exhibit different predator defense mechanisms: thin-shelled and deep-burrowing *Mya arenaria* and *Tagelus plebeius*; shallow-burrowing and armored *Mercenaria mercenaria*; and armored, aggregative *Geukensia demissa*. These species provide a model system to conduct field and laboratory experiments with the goal of understanding the ways global change will alter predator-prey interactions in coastal environments. This model system can be used to make predictions about how predator-prey interactions are expected to change with seagrass loss, extreme storm events, and acidification.

The following chapters focus on a commercially important thin-shelled species, *M. arenaria*, which has experienced major declines in Chesapeake Bay. *Mya arenaria* was once harvested in Chesapeake Bay but has been in decline since the early 1970s and now exists in Chesapeake Bay at low densities (Dungan et al. 2002, Homer et al. 2011). Tropical Storm Agnes, a 100-year storm that drastically reduced salinities and increased sedimentation throughout Chesapeake Bay (Hyer & Ruzecki 1976, Schubel 1976, Schubel et al. 1976), caused mass mortality for *M. arenaria* (Cory & Redding 1976). I examine several factors that have been blamed for the inability of *M. arenaria* to recover from Tropical Storm Agnes and that are keeping this species at low densities in an effort to inform restoration and management initiatives that aim to conserve this species in Chesapeake Bay.

This dissertation builds upon current research by examining multiple lines of evidence (field, laboratory, and modeling studies) to address the role of predator-prey dynamics in shaping ecosystem response to three aspects of global change: habitat loss, extreme weather events, and acidification. In Chapter 2, I related bivalve distribution and functional diversity to predator abundance and habitat complexity with a focus on two commercially important, large-bodied, burrowing bivalves, the soft-shell clam *Mya arenaria* and the stout razor clam *Tagelus plebeius*. In Chapter 3, I examined natural predation of juvenile *M. arenaria* in different habitat types in a field caging study. Field observations of predation were compared to specific mechanisms of density-dependent predation by blue crabs *Callinectes sapidus* in different habitat types in a laboratory mesocosm experiment. In Chapter 4, I chronicled the impact of one of the most extreme storms to impact Chesapeake Bay watershed, Tropical Storm Agnes (1972), on the decline of *M. arenaria*. I also examined the evidence for a storm-induced phase shift maintained by density-dependent predation by blue crabs. In Chapter 5, I present a laboratory experiment that determined the impact of CO_2 acidification on a predator-prey system including *C. sapidus* and *M. arenaria*. In Chapter 6, I reviewed the impact of climate warming, extreme weather, habitat loss, hypoxia, and acidification on density-dependent predation in marine environments, and provided recommendations for future research that will inform conservation of marine resources. Ecosystem managers should consider density-dependent predation to give threatened or exploited species the best chance of overcoming stressors related to global change.

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CHAPTER 2

Habitat and predators drive distribution and persistence of estuarine bivalves

ABSTRACT

Habitat loss is occurring rapidly in coastal systems around the world. In Chesapeake Bay, seagrass loss is expected to worsen due to warming and nutrient pollution. This loss of habitat will result in declines in diversity and loss of commercial species that depend on seagrass, but whether diversity loss will equate to loss in ecosystem services is unknown. A bivalve survey was conducted in a variety of habitat types (seagrass, oyster shell, shell hash, coarse sand, and detrital mud) in three lower Chesapeake Bay subestuaries from fall 2011 through summer 2013 to examine trends between bivalve densities (including the commercially important bivalves *Mya arenaria* and *Tagelus plebeius*) and habitat quality (type, relative amount of mineral material) and quantity (volume), predator density, and environmental variables. To assess the role of the above factors in structuring functional diversity, bivalves were assigned to functional groups based on feeding mode, living position, and predator defense strategy. On average, seagrass supported one additional functional group than all other habitat types, and diversity was increased 27-54% in seagrass compared to the other habitats examined. The odds of finding *M. arenaria* and *T. plebeius* were higher in seagrass than any other habitat type. Pulses of recruitment in *M. arenaria* were attenuated through the summer months when predators are most active, indicating predators likely influence temporal dynamics in this species. Overall, habitat quality, habitat quantity, and predator abundance drive patterns of bivalve diversity and influence population dynamics of commercially important bivalve species. These results suggest that a loss of seagrass in Chesapeake Bay will impact ecosystem services and alter trophic dynamics.

INTRODUCTION

The role of habitat and predators in structuring bivalve functional diversity

The effect of habitat loss on ecosystem functioning is an important issue in marine ecology due to the fast rate at which foundation habitat species such as seagrass, mangroves, corals, and oysters are being lost from coastal waters (Duarte *et al.* 2008). These foundation 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 foundation 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.

Seagrass habitats are sensitive to climate change and coastal development (Orth *et al.* 2006). Chesapeake Bay 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) . The severe and persistent declines of seagrass in the recent past have mostly been attributed to anthropogenic nutrient and sediment pollution (Kemp *et al.* 2004). Humans have increased nitrogen and phosphorus loading into Chesapeake Bay by a factor of three, as compared to pre-industrial times (Hagy *et al.* 2004). Total nitrogen concentration in coastal waters is highly correlated with turbidity (Nielsen *et al.* 2002), and in very turbid waters, such as those of Chesapeake Bay, light no longer penetrates to the bottom of the water column due to a combination of nutrient-related phytoplankton, epiphytic growth, and high suspended sediment concentrations (Cerco & Moore 2001; Kemp *et al.* 2004), and subsequent seagrass losses occur (Walker & McComb 1992). 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).

Seagrass loss in Chesapeake Bay will impact the communities of organisms associated with seagrass and organisms that depend on seagrass for protection from predators. Many marine organisms, including fish, crustaceans, and bivalves, use habitat for predator avoidance. Increased habitat complexity allows species to avoid predators more efficiently by reducing the effectiveness of certain predator foraging behaviors or strategies (Sih *et al.* 1985; Sponaugle & Lawton 1990; Seitz *et al.* 2001; Stoner 2009). The habitat complexity offered by seagrass may be beneficial for prey because it interferes with predator detection and capture of prey, which promotes high prey survival, especially for infaunal organisms such as bivalve mollusks (Peterson 1982; Heck & Thoman 1984; Orth *et al.* 1984).

Bivalve mollusks play a key ecological and economic role in marine coastal systems. Bivalves are commercially valuable organisms (Cooley & Doney 2009), with oysters, scallops, and clams comprising three of the top ten US domestic fisheries groups landed in 2014 and valued at $1.3 billion dollars (NMFS 2015). Bivalves serve as prey for many other commercially important species (Yeager & Layman 2011), and link benthic and pelagic food webs (Nielsen & Maar 2007; Basen *et al.* 2013). In addition, bivalves influence the exchange of nutrients, organic material, and inorganic material between the sediment and the water column (Norkko *et al.* 2001; Marinelli & Williams

2003). Specifically, bivalve feeding and burrowing activities contribute to nitrogen cycling (Covich *et al.* 1999; Biles *et al.* 2002); organic matter deposition and mineralization (Welsh 2003); the flux of minerals such as silica (Marinelli & Williams 2003); and sedimentation rates (Norkko *et al.* 2001).

Bivalve diversity promotes ecosystem functioning, because bivalves with different feeding and burrowing behaviors have different impacts on their environment (Biles *et al.* 2002). Ecosystem functioning, as defined by Hooper et al. (2005), encompasses ecosystem properties related to cycling and storage of material, and the ecosystem goods and services to which humans attach value. 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 (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 will likely alter functioning of coastal marine ecosystems.

The degree to which bivalve diversity would have to decrease to see any effect on biogeochemical cycling is unknown. The redundancy hypothesis states that some species may not be necessary for ecosystem functioning (Lawton & Brown 1993; Ehrlich & Walker 1998). However, the study of functional diversity, as defined by Petchey & Gaston (2006), is a desire to understand communities and ecosystems based on what organisms do, rather than on their evolutionary history. Grouping organisms based on their function in the environment allows predictions to be made regarding the impact of biodiversity loss on ecosystem function.

A functional group, as defined by Hooper et al. (2005), is a set of species that have similar effects on a specific ecosystem process or similar responses to environmental conditions. A bivalve's feeding mode is an important determinant of its role in ecosystem functioning. In addition, bivalve morphology and living position in respect to the sediment surface can provide clues regarding a bivalve's role in the food web. 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 prey 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). This study uses functional traits that relate to bivalves as consumers (deposit versus suspension feeders) and as prey (living position and shell strength) to examine the effect of habitat on functional diversity, in an effort to gain a better understanding of how habitat loss may alter ecosystem functioning.

Spatial and temporal trends in commercially important thin-shelled species

The soft-shell clam *Mya arenaria* is a long-lived, large-bodied, deep-burrowing bivalve that supports a large commercial fishery in the U.S. and accounted for 12% of commercial bivalve dollar value in 2014 (NMFS 2015). In Chesapeake Bay, this species has supported a commercial hydraulic dredge fishery in Maryland waters since the early 1950s. Historically, *M. arenaria* served an important role as a biomass dominant that contributed substantially to the food web of Chesapeake Bay (Abraham & Dillon 1986; Eggleston *et al.* 1992; Seitz *et al.* 2001).

In Chesapeake Bay, *M. arenaria* has been in decline since the early 1970s, with more pronounced declines in the 1990s, and this species now exists in Chesapeake Bay at record low levels (Figure 1). Declines after 1972 are attributed to Tropical Storm Agnes, a 100-year storm that drastically reduced salinities and increased sedimentation throughout Chesapeake Bay (Hyer & Ruzecki 1976; Schubel 1976; Schubel *et al.* 1976), which resulted in a mass mortality event for *M. arenaria* (Cory & Redding 1976). Due to this storm, a large-scale hydraulic dredge fishery for *M. arenaria* was never established in the Virginia portion of the Bay (though it was considered prior to Agnes; Haven 1970). More recent (post-1990) declines in abundance of *M. arenaria* have resulted in a cessation of the commercial fishery in Maryland waters due to lack of profitability (Dungan *et al.* 2002; Homer *et al.* 2011). Since 1980, commercial clammers have gradually switched to harvest of the stout razor clam *Tagelus plebeius*, which is harvested for eel and crab bait (Dungan *et al.* 2002; Homer *et al.* 2011). *Tagelus plebeius* is a large-bodied clam that is found in similar habitats and occupies a similar trophic niche as *M. arenaria*. Like *M. arenaria*, stout razor clams have experienced a decline in recent years, which was first documented in 2003 and resulted in the loss of 70-80% of the population in Maryland (Homer *et al.* 2011). There are no historical landings records or long-term time series of *T. plebeius* abundance, so the history of decline and potential mechanisms for decline in this species are largely unknown.

Multiple factors have been blamed for the inability of *M. arenaria* to recover from Tropical Storm Agnes and the recent declines in *M. arenaria* and *T. plebeius*, including overfishing, disease, rising temperatures, low recruitment, habitat loss, and predation. In lower Chesapeake Bay, these species have not been fished commercially since the closure of the hydraulic dredge fishery in the 1970s. The major disease of concern in *M. arenaria* and *T. plebeius* is the parasitic protist *Perkinsus chesapeaki* (Reece *et al.* 2008); however, incidence of infection in lower Chesapeake Bay remains low (Seitz et al. *in prep*). The cancer 'disseminated neoplasia' also causes mortality of *M. arenaria*, but this disease does not affect *T. plebeius* (Dungan *et al.* 2002), and thus is not likely the sole causative agent in the concurrent decline of both species. Similarly, high temperatures cannot explain declines in both species; while *M. arenaria* is at the southern end of its range in Virginia and is believed to be sensitive to heat waves, *T. plebeius* is distributed into South America (Abrahao *et al.* 2010). Recruitment of *M. arenaria* remains high in several tributaries of Chesapeake Bay (Bradley 2011), though these individuals rarely survive to adulthood, except in habitats with sufficient structure to allow protection from predators (Seitz *et al.* 2005). Given this evidence regarding potential drivers for the declines in *M. arenaria* and *T. plebeius*, this study examines the effects of predation, structured habitat, and environmental variables such as temperature on the distribution and persistence of these commercially important bivalve species.

Objectives

The purpose of this study is to survey bivalves in lower Chesapeake Bay to determine the degree to which habitat (type, quantity, and quality), predators (abundance and average size), and environmental variables (temperature, salinity, and dissolved oxygen) impact bivalve diversity and biomass. Specifically, we examined 1) bivalve species diversity, species richness, and total density; 2) density of bivalves separated into functional groups based on predator defense strategy and feeding mode; 3) bivalve functional diversity and functional richness; and 4) biomass of the commercially important thin-shelled species the soft-shell clam *Mya arenaria* and the stout razor clam *Tagelus plebeius*.

Hypotheses

1. Species diversity and functional diversity metrics will be positively correlated with habitat quantity, and bivalve communities will be more diverse in more complex habitats such as seagrass and oyster shell than in less complex habitat such as detrital mud.
2. Functional groups will exhibit the following habitat preferences: more deep-burrowing and suspension-feeding bivalves will be found associated with more complex habitats (seagrass and oyster shell) than in less complex habitats (detrital mud); hard-shelled bivalves will be most abundant on oyster shell, due to habitat

preferences of mussels; more deposit-feeding bivalves will be found in detrital mud habitat than any other habitats.

3. Bivalve groups with predominately thin-shelled species will be negatively correlated with predator abundance and size.
4. Biomass of *M. arenaria* will be positively associated with seagrass presence, negatively correlated with temperature, and negatively correlated with blue crab and ray abundance. Biomass of *T. plebeius* will also be positively correlated with seagrass and negatively correlated with predator abundance, but will not be dependent on temperature.

MATERIALS AND METHODS

Study system

Lower Chesapeake Bay encompasses the Virginia portion of Chesapeake Bay estuary, the largest estuary in the United States. This portion of the Bay is mostly polyhaline (except in the upper reaches of the tributaries) and experiences seasonal hypoxia from May to September in the main stem, with frequent advection of hypoxic water into the tributaries and shallows (Sturdivant *et al.* 2014). 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*, though *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 *Leiostous xanthurus,* Atlantic croaker *Micropogonus undulatus*, hogchoker *Trinectes maculatus*, and the blue crab *Callinectes sapidus* (Hines *et al.* 1990). High predation rates on infauna are also associated with seasonal migratory behavior of 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, they 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 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 for fall 2011, spring/summer and fall of 2012, and spring/summer of 2013. Bivalves were collected from three subestuaries of lower Chesapeake Bay (Lynnhaven River system, York River, and Mobjack Bay), four sites within each subestuary, and three replicate samples from each site (Figure 2). Sites were chosen haphazardly from areas of known substrate composition (including sediment type and presence of other structure such as shell material or seagrass), to achieve a relatively equal number of sites with substrates or habitats representative of the area. Samples were collected in shallow water of 1.5-2 m depth mean high water. At each site, a YSI (Model 85, Yellow Springs Instruments) was deployed prior to sampling to take measurements of dissolved oxygen, temperature, and salinity. At each sampling period, bivalves were collected using a suction sampling device that collects samples of 0.11 m^2 area and 40 cm depth, and samples were sieved through 3-mm mesh. In the laboratory, all bivalves in the 3-mm samples were identified to species and counted; *M. arenaria* and *T. plebeius* were also dried in a drying oven for 24 hours and ashed in a muffle furnace at 550 °C for 5 hours. The ash-free dry weight (dry weight minus ash weight) was calculated for *M. arenaria* and *T. plebeius* as a measure of biomass.

For all suction samples, we examined the substrate retained on 3-mm mesh to assign a substrate type to each sample. Any sample that contained seagrass (of any species) was characterized as seagrass substrate; otherwise, the substrate category that made up the majority of the material on the mesh was designated as the substrate type for the sample. Substrate 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), or oyster shell (which included live or dead oysters, both articulated and crushed). We calculated the volume of substrate retained on a 3-mm sieve by water displacement, and a representative sample of the substrate was used to calculate ash weight of substrate. Percent ash weight is an index of the contribution of mineral matter to the substrate, and was calculated as the proportion of the dry weight that was composed of "ash" (or the carbon material left behind after ashing) reported as a percentage (0-100%).

Blue crab abundance at each site was quantified using six replicate 20-m tows of a modified crab scrape (1 m width). 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 (*Rhinoptera bonasus*) abundance. Due to logistical constraints, predator and environmental data are missing from some samples. These samples were not included in analyses that depended on predator or environmental data.

Statistical analysis

Community structure and diversity

Species diversity was calculated as the Gini-Simpson index of diversity, or the probability that two randomly selected individuals will be from different species, which can be calculated as follows:

$$Gini - Simpson\ index = 1 - \lambda = 1 - \sum_{i=1}^{R} {p_i}^2$$

where λ = the Simpson's diversity index and p_i = the proportional abundance of the i^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.

For each sample, bivalves were assigned to functional groupings based on life history and trophic niche. These groupings included (1) deep-burrowing suspension-feeding (DBSF) bivalves, (2) facultative deposit-feeding (DF) 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 *Amygdalum papyrium*), and (4) hard-shelled bivalves (HS; Table 1). Bivalves were considered deep-burrowing if adults of the species burrowed to depths of 15 cm or more. Bivalves belonged to only one group; for example, *Macoma balthica* is a facultative deposit feeder, and thus is included in the DF functional group and not the DBSF group, despite the ability to suspension feed and burrow deeply in the sediment. 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 general linear model with the following predictor variables: year (categorical, 3 levels), season (categorical, 3 levels), river (categorical, 3 levels), substrate (categorical, 5 levels), substrate volume (mL), substrate percent ash weight, number of fish (per 20 m^2 tow), average fish length (mm), number of crabs (per 20 m^2 tow), average crab shell length (mm), number of ray pits (per transect, which covered 100 m^2), temperature (°C), salinity, and dissolved oxygen (mg L^{-1}). Total bivalve density and densities for the four functional bivalve groupings were analyzed with generalized linear models with a Poisson distribution and a log link function. All variables were examined for multicollinearity with draftsmen's plots before inclusion in the model. One large model (global) was created with all significant terms at the alpha = 0.20 level. McFadden's R-squared (also known as rho-squared) was calculated as a measure fit for all generalized linear models of density data (McFadden 1974). Confidence intervals (95%) were calculated for coefficients within the model and are presented back-transformed to the original scale.

In graphs showing multiple comparisons using letters over bars, significant difference was determined with bootstrap hypothesis testing. 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 the $\alpha = 0.05$ level. Then this procedure was repeated for the category with the second largest response. At most, this resulted in six comparisons for any one variable.

Spatial and temporal trends in commercial species

Spatial autocorrelation

To determine the degree to which biomass of *T. plebeius* and *M. arenaria* were spatially autocorrelated, a variogram for each species was constructed of combined log-transformed biomass data from all sampling periods and examined for visual evidence of spatial correlation. The following ANOVAs were constructed to test for additive or interactive effects of latitude and longitude on clam biomass: biomass as a function of longitude, biomass as a function of latitude, biomass as a function of longitude and latitude (additive), biomass as a function of latitude and longitude (interaction), and biomass as a function of latitude and longitude (interaction) with either a nonlinear latitude term or a nonlinear longitude term. Each model was compared to a less-complicated model by computing an ANOVA table of linear model fits. If there was evidence of spatial autocorrelation (i.e. variograms exhibiting linear trends in semivariance at low distances and significantly better fit of a model taking into account spatial structure at the $\alpha = 0.05$ level), these trends were removed by taking the residuals of the best model as identified by AIC.

Zero-inflated modeling

Biomass of the commercially important species *T. plebeius* and *M. arenaria* were examined separately. Densities were also calculated for both species; however, trends in density were very similar to trends in biomass, so only biomass data are presented here. Both species exhibited a patchy distribution (many instances of zero catch), so two models were used to analyze the data: presence/absence was modeled with a binomial generalized linear model (logit link), and non-zero biomass was modeled with a Gaussian generalized linear model (log link).

Presence/absence generalized linear models were examined first with the full suite of predictors including: year (categorical, 3 levels), season (categorical, 3 levels), river (categorical, 3 levels), substrate (categorical, 5 levels), substrate volume (mL), substrate percent ash weight, number of fish (per 20 m^2 tow), average fish length (mm), number of crabs (per 20 m^2 tow), average crab shell length (mm), number of ray pits per transect covering 100 m^2), temperature (°C), salinity, and dissolved oxygen (mg L^{-1}). The model was examined for any significance (at the alpha = 0.20 level) in the following predictor variables: temperature, salinity, dissolved oxygen, crab abundance, fish abundance, crab length, and fish length. If environmental variables or variables relating to predators were all not significant, they were all removed from the model to allow the models to include more data. Confidence intervals (95%) were calculated for coefficients within the model and were back-transformed to odds.

Non-zero data were log transformed and examined first using a general linear model with the following predictor variables: year (categorical, 3 levels), season (categorical, 3 levels), river (categorical, 3 levels), substrate (categorical, 5 levels), substrate volume (mL), substrate percent ash weight, number of fish, average fish length (mm), number of crabs, average crab shell length (mm), number of ray pits, temperature (°C), salinity, and dissolved oxygen (mg L^{-1}). All variables were examined for multicollinearity with draftsmen's plots before inclusion in the model. One large linear model (global) was created with all significant terms at the alpha = 0.20 level. Subsequent models contained a subset of variables from this longer model. Between 3 and 7 models were created. AICc was used to select the model with the most support out of the candidate set of models. Generalized linear models with a Gaussian distribution and a log link function were used to analyze the best model as identified by AICc. McFadden's R-squared (also known as rho-squared) was calculated as a measure fit (McFadden 1974). Confidence intervals (95%) were calculated for coefficients within the model and were back-transformed to the original scale.

RESULTS

The role of habitat and predators in structuring bivalve functional diversity

In all, 3,141 bivalves representing 17 species were collected in the survey (Table 1). The maximum density observed for a single species was 2,082 m^{-2} *Macoma balthica* in the York River in spring 2013. After *M. balthica* (with 1,252 total individuals collected), the most commonly encountered bivalves were, in order, the stout razor clam *Tagelus plebeius* (394 collected), *Macoma mitchelli* (375 collected), and *Aligena elevata* (354 collected).

Average sample Gini-Simpson diversity index and species richness were 0.37 and 2.64, respectively. The Gini-Simpson diversity index was significantly greater in seagrass than in detrital mud (p = 0.0003), shell hash (p = 0.0001), coarse sand (p = 0.03), or oyster shell (p = 0.003; Figure 3a). Species richness was significantly greater in seagrass than in detrital mud (p = 0.008), shell hash (p = 0.0002), and oyster shell (p = 0.03; Figure 3b). Mean bivalve density was greatest in detrital mud, and significantly lower in seagrass than in detrital mud (Figure 3c).

Deep-burrowing suspension-feeding (DBSF) bivalves such as *Tagelus plebeius, Ensis directus, Mya arenaria, Petricola pholadiformis,* and *Tagelus divisus* (Fraser 1967, Alexander *et al.* 1993; Table 1) had similar densities in all habitats, with a trend towards higher densities in seagrass than in detrital mud (p = 0.07; Figure 4a). Thin-shelled and surface-dwelling (TSSD) bivalves such as *Aligena elevata* and *Amygdalum papyrium*

(Table 1) had higher densities in seagrass habitat than detrital mud (p = 0.02) or shell hash (p = 0.007, Figure 4b). Detrital mud habitat supported higher densities of the facultative deposit feeders (DF) *Macoma balthica* and *Macoma mitchelli* than seagrass (p = 0.004, Figure 4c). Hard-shelled (HS) bivalves such as mussels, *Mercenaria mercenaria*, ark clams, and *Mulinia lateralis* (Blundon & Kennedy 1982a; Table 1) had the highest densities in oyster shell, and densities of HS bivalves were significantly lower in detrital mud than in oyster shell (p = 0.01) or seagrass (p = 0.05, Figure 4d).

Presence of seagrass was positively associated with diversity and species richness (Table 2). While total bivalve density increased with presence of oyster shell, this effect was in part ameliorated by a negative relationship between density and substrate percent ash weight, such that for a unit increase in percent ash weight (which was higher in areas with a lot of shell), bivalve density decreased by on average 2.65% (Table 2). Salinity was the only environmental variable to appear consistently in models of Gini-Simpson diversity, species richness, and total bivalve density; it was significantly negatively correlated with total bivalve density and species richness such that for every unit increase in salinity, there was a 12.35% mean decrease in bivalve density and a mean decrease of 0.07 in species richness (Table 2). The index of ray abundance (number of ray pits per 100 m^2) was also included consistently in models of Gini-Simpson diversity, species richness, and total bivalve density. The number of ray pits was positively correlated with the Gini-Simpson diversity index such that an increase of one ray pit per 100 m^2 resulted in a 0.05 unit increase in the diversity index, on average. There was a tendency for species richness to increase with number of ray pits, though this was not significant in the model (Table 2). Total bivalve density was negatively correlated with number of ray pits (7.74% mean decrease per ray pit; Table 2).

Seagrass and oyster shell supported higher densities of bivalves from all functional groups except DF bivalves, which were negatively associated with seagrass (Table 2). Instances of relatively high volume of substrate retained on a 3-mm mesh (2000-5500 mL) were observed for all substrate types except seagrass, which had a maximum volume of 660 mL. Volume of substrate was positively correlated with bivalve densities in three out of the four functional groups (DBSF, DF, and HS; Table 2). Crab abundance was negatively correlated with density of bivalves from all functional groups except HS bivalves (Table 2). There was a significant negative relationship between ray pits and bivalve density for DBSF bivalves (5.21% decrease per ray pit) and the DF group (10.52% decrease per ray pit; Table 2).

Functional diversity and richness were both greater in seagrass than in detrital mud, oyster shell, and shell hash (Figure 5a,b). On average, seagrass supported 1.14 more functional groups than detrital mud (SE = 0.28), 1.25 more than oyster shell (SE = 0.28), and 1.22 more than shell hash (SE = 0.21). Functional richness was positively correlated with substrate volume and negatively correlated with salinity (Table 2). Number of ray pits was included in the best models for functional richness and functional diversity; however, the term was only significant in the model for functional diversity, where an increase of one ray pit per 100 m^2 resulted in an increase in the functional diversity index of 0.05, on average (Table 2). Even though ray pit number was not significant in the model for functional richness, it tended towards a positive correlation ($p = 0.09$; Table 2). For full summary tables of generalized linear models examining the impact of environmental, substrate-related, and predator-related predictors on species richness, Gini-Simpson's diversity index, total density of bivalves, bivalve functional groups, functional richness, and functional diversity, see Supplementary Tables 1-9.

Spatial and temporal trends in commercial species

Spatial autocorrelation

Variograms of biomass for *M. arenaria* and *T. plebeius* were scattered and showed no clear linear trends. For both clam species, the intercept only model was not significantly different from the model containing longitude (*M. arenaria*: $F_1 = 3.21$, $p = 0.08$; *T. plebeius*: $F_1 = 1.17$, $p = 0.28$) or latitude (*M. arenaria*: $F_1 = 3.21$, $p = 0.08$; *T. plebeius*: $F_1 = 0.24$, $p = 0.62$). Although models containing longitude or latitude neared the $\alpha = 0.05$ significance level for *M. arenaria*, residuals of these models showed almost no differences when viewed as variograms. We suspect that these trends were an artifact of the large number of zeros in the data, since these trends disappeared when zero data were removed and the analysis was repeated (longitude: $F_1 = 0.01$, $p = 0.95$; latitude: $F_1 = 0.21$, $p = 0.65$). We concluded there was a lack of spatial autocorrelation among the samples, and no spatial trends were removed from the data.

Zero-inflated modeling

For *T. plebeius* presence/absence data, temperature, salinity, dissolved oxygen, and all variables related to predators were not significant in the model, so these were removed from analysis. Of the remaining variables in the model (year, season, river, substrate type, substrate volume, and substrate percent ash), only substrate type was significant. The odds of finding *T. plebeius* in seagrass were: 3.11 – 38.92 times greater than in detrital mud, 1.19 – 17.79 times greater than in oyster shell, and 1.91 – 16.51 times greater than in shell hash (95% confidence intervals). The odds of finding *T. plebeius* in seagrass were not significantly different from the odds of finding them in coarse sand (95% CI [0.82, 20.34]). When *T. plebeius* was present, the model that best explained clam biomass included temperature, salinity, and dissolved oxygen (AICc weight = 0.73, pseudo-R^2 = 0.07). Of these variables, only dissolved oxygen was significant in the model, and it was negatively correlated with *T. plebeius* biomass such that a 1-mg L^{-1} increase in dissolved oxygen led to, on average, a 20% reduction in *T. plebeius* biomass (95% CI [0.04, 0.36]).

For *M. arenaria* presence/absence data, all variables related to predators were not significant in the model, so these were removed from analysis. The inclusion of season resulted in perfect separation of the response variable, so similar low summer and fall biomass were combined together for analysis. Of the remaining variables in the model (year, season, river, substrate type, substrate volume, substrate percent ash, temperature, salinity, and dissolved oxygen), substrate type and dissolved oxygen were significant. The odds of finding *M. arenaria* in seagrass were at least 4.91 times greater than in detrital mud, and at least 1.93 times greater than in shell hash (lower 95% CI limit). For every unit increase in dissolved oxygen, the odds of finding *M. arenaria* decreased by a factor of 0.47 (95% CI [0.23, 0.71]).

Only 22 samples contained one or more *M. arenaria*. For non-zero biomass analysis, summer and fall biomass were again lumped into one category. Fish abundance and length were also removed from analysis due to low significance in the full model. The model that best explained *M. arenaria* biomass (AICc weight = 0.83, pseudo R^2 = 0.72) contained river, substrate type, substrate volume, substrate percent ash weight, crab abundance, and crab length; however, none of the variables in the model were significant. The second best model (AICc weight = 0.17, pseudo R^2 = 0.66) contained all of the same variables except river and substrate type, and among the significant variables in this reduced model were: substrate volume, which for a mL increase in volume increased *M. arenaria* biomass by 0.16% (95% CI [0.05%, 0.26%]); substrate percent ash weight, which for a unit increase in percent ash decreased *M. arenaria* biomass by 7.64% (95% CI [1.77%, 13.50%]); and crab length, which for every 1-mm increase in average crab size decreased *M. arenaria* biomass by 4.71% (95% CI [1.11%, 8.31%]).

In seasonal trends for both years, *M. arenaria* had the greatest biomass in the spring, with declining biomass through the fall (Figure 6a). Only two individuals were captured in the fall, and both were in 2011. *Tagelus plebeius* biomass was similar throughout the seasons, with a tendency for lower biomass in the fall and increasing biomass through the spring and possibly into the summer (Figure 6b). Within each season, there were no significant differences in *M. arenaria* biomass among substrates; however, *M. arenaria* were never found in coarse sand, were only found in detrital mud in the spring, and had consistent presence in oyster shell and seagrass throughout the seasons (Figure 7a). In the summer, *M. arenaria* were only found in seagrass or (rarely) in oyster shell (Figure 7a). *Tagelus plebeius* was found in all substrates in all seasons, with no significant differences in biomass among seasons (Figure 7b). Within each season, there were no significant differences in *T. plebeius* biomass among substrates, and no clear trends emerged in *T. plebeius* biomass in different substrates through the seasons (Figure 7b). For full summary tables of generalized linear models, presence/absence models, and AIC tables see Supplementary Tables 10-15.

DISCUSSION

The role of habitat and predators in structuring bivalve functional diversity

Habitat appears to be an important driving factor in bivalve community structure and distribution in lower Chesapeake Bay, consistent with our hypotheses. Seagrass presence equated to higher diversity of bivalves. In addition, total bivalve density and functional group richness were positively correlated with habitat quantity (volume of substrate retained on 3-mm mesh), indicating that both habitat quality and quantity matter in promoting bivalve diversity.

The greatest densities of deep-burrowing and suspension-feeding (DBSF) bivalves were found in seagrass habitats, the greatest densities of hard-shelled (HS) bivalves were found in oyster shell habitats, and the greatest densities of deposit-feeding (DF) bivalves were found in detrital mud habitats. These results were consistent with our hypotheses on functional group habitat preferences, and confirm that the functional groupings of bivalves used in this study represent realized niches driven by bivalve morphology and feeding mode. The ecological consequence of these results is that maintaining diverse habitats is important for sustaining full functionality in lower Chesapeake Bay, because different bivalve functional groups have their greatest densities in different habitats. 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 driving both species and functional diversity.

All three functional groups that contained thin-shelled bivalves (DBSF, DF, and thin-shelled surface dwellers [TSSD]) were negatively associated with predator abundance. Furthermore, predator abundance was not included as a significant predictor in the model for HS bivalves. This evidence supports our hypothesis that thin-shelled species are negatively correlated with predator abundance, presumably because of direct effects of predation. However, all bivalve functional groups were positively correlated with crab size and/or fish size, which was contrary to our hypothesis. This association between predator size and bivalve densities may indicate that small predators are as efficient at limiting bivalve distribution and persistence as large predators, or that relative predator size is an indicator of overall ecosystem health. However, considering the majority of samples were taken in the relatively pristine habitats of the York River and Mobjack Bay, the former explanation is more likely.

A bivalve's dietary preferences, susceptibility to predators, and the interaction between these two factors and habitat type largely drive bivalve distribution patterns in Chesapeake Bay. The interaction between habitat and predators, specifically substrate penetrability and how that impacts predation risk for infaunal bivalves, has previously been cited as a mechanism explaining patterns in the distribution of several Chesapeake Bay bivalves, including *Mya arenaria* and *Mercenaria mercenaria* (Peterson 1982; Lipcius & Hines 1986; Seitz *et al.* 2001). For *M. arenaria*, the reduced penetrability of sand, together with the deep burrowing depth for the species, reduced encounters with blue crabs and promoted greater rates of survival as compared to mud (Lipcius & Hines 1986). In a study involving the hard clam *M. mercenaria*, seagrass root mats reduced penetrability by binding sediment and obstructing excavation by predatory whelks (Peterson 1982). These patterns are very similar to those observed in the current study, where DBSF bivalves such as *M. arenaria* and HS bivalves such as *M. mercenaria* were found more commonly in complex habitats such as seagrass and oyster shell, respectively, than in less complex habitats such as detrital mud. However, high levels of habitat complexity did not result in high densities for all bivalve functional groups: DF bivalves were found more commonly in detrital mud habitats, indicating a potential bottom-up mechanism controlling the distribution and density of this group. Considering the DF bivalves *Macoma balthica* and *Macoma mitchelli* are the dominant infaunal bivalve species in the soft sediment portions of the Bay (Seitz *et al.* 2008; Beukema *et al.* 2010), dietary preferences should not be ignored when interpreting patterns of clam density or biomass in Chesapeake Bay.

The increased diversity and density of bivalves within seagrass beds as compared to other habitat types implies that regions experiencing large-scale seagrass loss, such as the polyhaline region of Chesapeake Bay, may experience losses of ecosystem functioning. Seagrass increased bivalve diversity by 27%, 32%, 42%, and 54% when compared to shell hash, coarse sand, detrital mud, and oyster shell habitats, respectively.

Seagrass had an average of one additional bivalve functional group compared to most other habitats. The functional group that was consistently found in seagrass, and relatively rarely found in other habitat types, was the thin-shelled surface-dwelling group that included the species *Aligena elevata, Amygdalum papyrium, Parvilucina multilineata, Gemma gemma*, and *Lionsia hyalina*. Two of these species, *A. papyrium* and *L. hyalina*, were nearly exclusively found in seagrass habitats. 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, is likely to impact ecosystem function.

Spatial and temporal trends in commercial species

As we hypothesized, the provision of complex habitat impacts the distribution of thin-shelled commercial species *M. arenaria* and *T. plebeius*. There were increased odds of finding both *T. plebeius* and *M. arenaria* in the habitats with the highest degree of complexity (seagrass and oyster shell) as compared to some less complex habitats. Complex habitats may be more favorable for these species because they increase rates of larval settlement by baffling water currents (Heiss *et al.* 2010), provide increased food resources for both suspension and facultative deposit-feeding modes (Peterson *et al.* 1984), and provide refuge from predators (Orth *et al.* 1984). However, this also implies that habitat loss may be an important factor in the decline of *M. arenaria* and *T. plebeius*, as both seagrass and oyster reef habitats are declining in Chesapeake Bay (Orth & Moore 1983; Rothschild *et al.* 1994; Beck *et al.* 2011).

Contrary to our hypothesis, temperature was not included as a significant predictor in models of *M. arenaria* presence/absence or non-zero biomass. *Mya arenaria* is a cold-water species that is distributed from the sub-arctic regions to North Carolina (Abraham & Dillon 1986; Maximovich & Guerassimova 2003). Typically *M. arenaria* survives well in temperatures from 2 to 28°C (Cohen 2005), with mortality usually occurring above 30 °C (Kennedy & Mihursky 1971). It is expected that with global climate change, Chesapeake Bay may become inhospitable for this species. The upper tolerance range for *M. arenaria* is frequently surpassed in the summer in Chesapeake Bay, especially in shallow water where this sampling effort took place. In the current study, temperatures exceeding 28 °C were observed for 60 samples, which accounts for about 28% of all samples collected. However, effects of temperature were not apparent in this study, leaving us unable to conclude that high summer temperatures are a major factor in the decline of *M. arenaria* in lower Chesapeake Bay.

Hydrodynamics and sediment organic content may play a role in the distribution of large-bodied, thin-shelled bivalves in the Chesapeake Bay. The non-zero biomass of *T. plebeius* and the odds of finding *M. arenaria* were both negatively correlated with dissolved oxygen. However, sampling sites were all shallow and all oxygen values were normoxic. In this analysis, dissolved oxygen may be confounded with local hydrodynamics, such that flow rate could be positively correlated with dissolved oxygen and negatively correlated with *T. plebeius* biomass. Bivalve larvae accumulate in the layer of water closest to the sediment surface during periods of low flow, possibly increasing settlement (Knights *et al.* 2006). Alternatively, dissolved oxygen may also be confounded with sediment organic content, such that amount of organic matter in the sediment could be negatively correlated with dissolved oxygen and positively correlated with *T. plebeius* biomass. Some bivalve larvae select for habitats with high sediment organic content, which may be indicative of food availability (Snelgrove *et al.* 1993). Future research should focus on examining the relative role of dissolved oxygen, organic matter, and flow rate in driving the distribution of *T. plebeius* and *M. arenaria*.

Despite occupying a similar niche in Chesapeake Bay, *T. plebeius* and *M. arenaria* exhibited different seasonal trends in biomass. Biomass of *M. arenaria* declines throughout the summer months, when predation by blue crabs is at its peak (Hines *et al.* 1990); that trend was seen in a seasonal time series for the species in our study, with a pulse of biomass in the summer that was attenuated through the fall. Observed temporal trends also correspond with *M. arenaria* reproductive behavior in Chesapeake Bay, where the fall spawn is more successful than the spring spawn due to decreased predation pressure in the winter months (Blundon & Kennedy 1982a; Baker & Mann 1991). Individuals spawned in the fall are able to settle and grow throughout the winter, when risk of predation is minimal, and this new generation manifests as a springtime spike in biomass. *Tagelus plebeius* spawns in the late spring (Holland & Dean 1977), accounting for the increase in biomass during the summer 2013 sampling period, but not the relatively steady biomass from fall 2011 through fall 2012. *Tagelus plebeius* likely does not exhibit the same seasonal crashes in abundance observed for *M. arenaria* because a robust adult *T. plebeius* population remains in lower Chesapeake Bay. This population allows for higher densities of many difference size classes to exist at any given time, unlike the population of *M. arenaria*, which is characterized by small, young individuals that are almost completely consumed by predators each year, essentially resulting in an "annual crop" rather than a stable population with a sustainable age distribution.

This study was conducted in shallow-water environments, which contain a wide variety of benthic habitats, are generally well-oxygenated, experience fluctuations in temperature and salinity on the scale of hours or days, and are mixed or disturbed by tides and wind events (Breitburg 1990, Booth *et al.* 2000). In deep-water environments of Chesapeake Bay, the distribution of large-bodied, thin-shelled bivalves may not be controlled by the same biotic and abiotic variables as in shallow water. Deep portions of Chesapeake Bay contain sediments that mostly consist of muds and clays (Kerhin *et al.* 1988), experience seasonal hypoxia (Sturdivant *et al.* 2014), and, depending on depth, may not experience the same fluctuations in temperature or salinity as shallow-water environments. The major predators of benthic infaunal bivalves in shallow- and deep-water environments are expected to be similar, with the exception of cownose rays, which mainly inhabit the shallow regions of the Bay (Fisher 2010). The distribution of larger juvenile or adult *M. arenaria* and *T. plebeius* in deep-water habitats is largely unknown; however, the lack of refuge habitat, persistence of predators, and existence of hypoxia at depth indicates that these habitats are unlikely to harbor dense populations of *M. arenaria* and *T. plebeius*.

Future directions

The loss of ecosystem function due to the loss of invertebrate groups has led to unpredictable and serious consequences for 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 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 will likely be associated with a loss in functionality.

Future research should focus on the impact of loss of seagrass on benthic-pelagic coupling in Chesapeake Bay, including both direct links between seagrass 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 seagrass 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 will alter the quantity 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. Further research could be devoted to the contribution of the seagrass-associated bivalve community to sedimentation rates and nutrient cycling in Chesapeake Bay (Caliman *et al.* 2007). In addition, similar experiments could examine the difference (in terms of the role in biogeochemical cycling and providing refuge for infaunal species) between *Z. marina* and similar southern seagrass species such as shoalgrass *Halodule wrightii*, which may replace *Z. marina* in the Chesapeake Bay through northward range expansion. 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 (Kristensen *et al.* 2014; Petersen *et al.* 2015), these steps are necessary to ensure Chesapeake Bay will continue to provide ecosystem goods and services for future generations.

With an absence of evidence for the role of disease or temperature in the decline of *T. plebeius* and *M. arenaria* in lower Chesapeake Bay, and the relationships we detected with habitat and predation, it remains likely that habitat loss and predators are major driving factors keeping these species at low biomass in lower Chesapeake Bay. Extremely low biomass of *M. arenaria*, decimated after tropical storm Agnes in 1972 (Cory & Redding 1976; Haven *et al.* 1976), and a susceptibility of this thin-shelled species to predation by blue crabs fuel a feedback loop that leads to high per-capita rates of predation, which works to keep populations at low levels. Similar dynamics may manifest for *T. plebeius* if populations reach sufficiently low densities. Since *T. plebeius* and *M. arenaria* are a preferred prey item for major predators such as *C. sapidus* and *R. bonasus* (Blundon & Kennedy 1982b; Fisher 2010), it is unlikely that predator switching will provide much relief. However, both species appear able to take advantage of refuge provided by complex habitats. Habitats such as seagrass and oyster shell allow both bivalve species to persist at a low-density refuge, which may be stable. Further work should focus on elucidating the existence and stability of this low-density refuge, and the likelihood that commercial thin-shelled species may continue to persist in Chesapeake Bay.

Conclusion

Loss of structured habitat is occurring world-wide in the form of shrinking seagrass distribution, and this has profound effects on seagrass-associated species (Orth *et al.* 1984, 2006). Loss of structured habitat will lead to loss of functional groups of bivalves in Chesapeake Bay, which may have implications for ecosystem functioning and stability. An understanding of the interaction between the provision of complex substrate such as seagrass and the effects of predators on bivalves may necessitate a closer examination of the effects of seagrass loss on species that are not normally associated with seagrass, but are found in higher abundances in this habitat. One such species is the soft-shell clam, *M. arenaria,* a commercially important species that is currently in decline in Chesapeake Bay (Dungan *et al.* 2002; Homer *et al.* 2011). Studies such as this can elucidate the importance of seagrass for ecosystem functioning and for maintaining bivalve populations, thus helping managers decide the best course of action to prevent bivalve species from disappearing from the Bay entirely.

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TABLES

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 are the maximum observed in one sample. Bivalves were grouped into four functional groups: deep-burrowing suspension-feeding (DBSF), hard-shelled (HS), facultative deposit-feeding (DF), and thin-shelled surface-dwelling (TSSD) bivalves.

Species	*Total collected*	*Maximum density*	*DBSF*	*TSSD*	*DF*	*HS*
Macoma balthica	1,252	2,082			X3	
Tagelus plebeius	394	218	X1			
Macoma mitchelli	375	327			X3	
Aligena elevata	354	345		X		
Amygdalum papyrium	244	527		X		
Mulinia lateralis	101	91				X4
Ensis directus	91	136	X2			
Mya arenaria	81	191	X2			
Mercenaria mercenaria	75	73				X
Parvilucina multilineata	47	218		X		
Gemma gemma	31	45		X		
Petricola pholadiformis	30	173	X2			
Tagelus divisus	26	54	X1			
Geukensia demissa	21	118				X
Lionsia hyalina	9	18		X		
Modiolus modiolus	7	27				X
Noetia ponderosa	3	9				X

1. Fraser 1967; 2. Alexander *et al.* 1993; 3. Blundon & Kennedy 1982a; 4. Blundon & Kennedy 1982b

2. Linear and generalized linear model results for species diversity, species richness, total bivalve density, and functional group densities, functional diversity, a
ɔnal richness. Functional groups include deep-burrowing suspension-feeding (DBSF) bivalves, thin-shelled surface-dwelling (TSSD) bivalves, facultative depos
bivalves, and hard-shelled (HS) bivalves. Functional diversity is the Gini-Simpson index for functional groups. Confidence intervals (95%) for coefficient estim
ed for all significant terms in the model, except for year, season, and river (not shown) and the substrate categorical variable, where only significant comparison
ɜn the two most complex substrates (oyster shell = OS and seagrass = SG) and the other less complex substrates (detrital mud = DT, shell hash = SH, coarse san
ɔwn. Positive coefficient estimates are presented with light gray shading, negative coefficient estimates are presented with dark gray shading, and partially
/e/partially negative coefficients in medium gray shading.

	Species diversity			*Functional groups*				*Functional diversity*	
	Gini-Simpson Diversity	Species Richness	Total Density$_1$	DBSF$_1$	TSSD$_1$	DF$_1$	HS$_1$	Functional diversity index	Functional richness
ate	SG > DT (0.12, 0.40) SG > OS (0.10, 0.38) SG > SH (0.18, 0.40) SG > SA (0.10, 0.46)	SG > DT (0.61, 2.31) SG > OS (0.44, 2.11) SG > SH (0.99, 2.33) SG > SA (0.30, 2.46)	SG > DT (1.36, 1.94) OS > DT (2.38, 3.57) OS > SH (1.10, 1.38) OS > SA (1.39, 1.97) OS > SG (1.50, 2.14)	SG > DT (2.13, 5.27) OS > DT (1.05, 2.86) SG > SA (1.36, 3.81) SG > OS (1.29, 2.93)	OS > SH (1.14, 2.05) SG > SH (1.65, 3.05) SG > OS (1.01, 2.12)	SG < DT (0.33, 0.62) OS > DT (2.05, 3.92) SG < SH (0.16, 0.26) OS > SH (1.08, 1.53) SG < SA (0.24, 0.46) OS > SA (1.62, 2.60) SG < OS (0.12, 0.22)	SG > DT (2.37, 16.16) OS > DT (2.41, 11.96) SG > SH (1.52, 5.01) OS > SH (1.58, 3.62) SG > SA (1.52, 10.38) OS > SA (1.62, 7.36)	SG > DT (0.18, 0.45) SG > SH (0.16, 0.36) SG > SA (0.08, 0.42) SG > OS (0.14, 0.40)	SG > DT (0.58, 1.70) SG > OS (0.70, 1.79) SG > SH (0.80, 1.64)
ate 'mL)		(-6.87E^{-5}, 3.93E^{-4})	(1.00006, 1.0002	(1.0001, 1.0002)	(1.000002, 1.0002)		(1.0001, 1.0004)		(1.49E^{-5}, 3.27E^{-4})
'e % 'ght			[redacted]	(0.98, 1.00)		[redacted]			

	Species diversity			*Functional groups*				*Functional diversity*	
	Gini-Simpson Diversity	Species Richness	Total Density$_1$	DBSF$_1$	TSSD$_1$	DF$_1$	HS$_1$	Functional diversity index	Functional richness
r- °C)			1.003, 1.06)	■	(1.01, 1.11)	(1.06, 1.20)	(1.05, 1.24)		
ty	(-0.03, 0.002)	■	■	(0.98, 1.07)	(1.24, 1.47)	■	■	(-0.03, 0.01)	■
ved n)			(1.002, 1.09)	■	(1.19, 1.35)	(0.99, 1.19)			
pits m^2)	(0.02, 0.11)	(-0.09, 0.41)	■	■		■		(0.01, 0.09)	(-0.02, 0.32)
, nce m^2)		(-0.004, 0.008)	■	■	■	■			
ngth)		(9.67E^{-5}, 0.01)	(1.001, 1.003)	(1.003, 1.007)	(1.001, 1.006)		(1.00004, 1.009)		
nce m^2)			(1.003, 1.009)		■	(1.01, 1.02)		(-0.002, 0.004)	
ngth)					(1.002, 1.006)	(1.001, 1.005)			

k-transformed from a generalized linear model with Poisson distribution and log link.

FIGURES

Figure 1. Mya arenaria landings for the period 1958-1992. Landings are for the Maryland and Virginia portions of Chesapeake Bay combined. Landings after 1992 are not presented, due to the near-collapse of the fishery. Vertical dashed line represents Tropical Storm Agnes (1972). Data source: NMFS Commercial Landings Database.

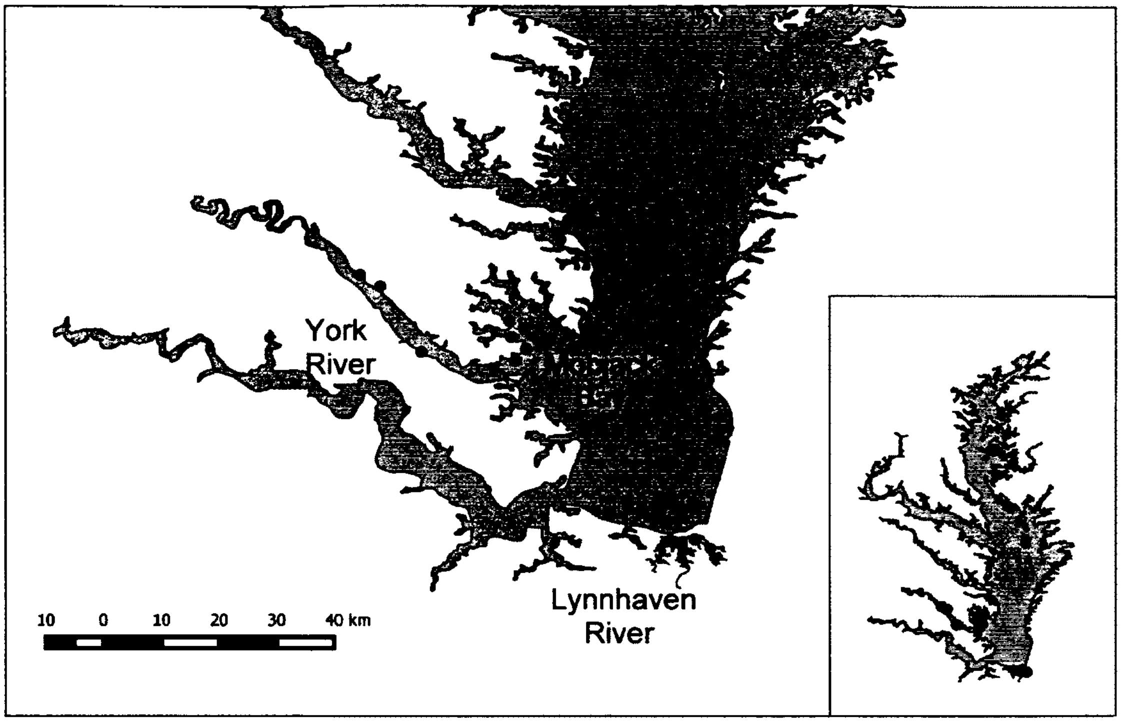

Figure 2. Map of sampling sites in lower Chesapeake Bay, VA, USA. Samples were collected in three subestuaries: Mobjack Bay, the York River, and Lynnhaven. Four sites were sampled in each subestuary.

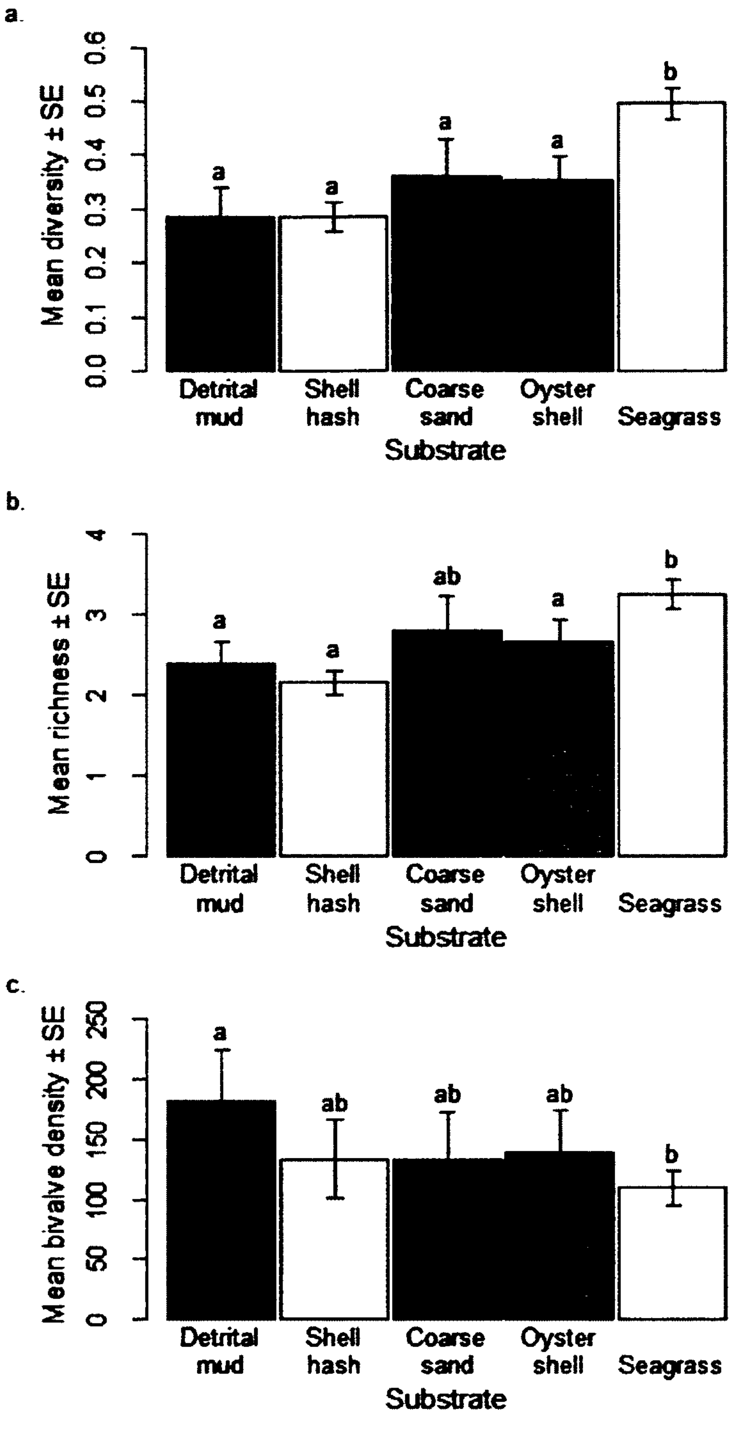

Figure 3. Bivalve species diversity, richness, and total density in different habitats. Means ±1 standard error (SE) for a) Gini-Simpson diversity index, b) species richness, and c) total bivalve density in different habitat types (substrate) in lower Chesapeake Bay. Samples were collected in detrital mud (n = 23), shell hash (n = 76), coarse sand (n = 14), oyster shell (n = 39), and seagrass (n = 64). Letters denote significant differences at $\alpha = 0.05$.

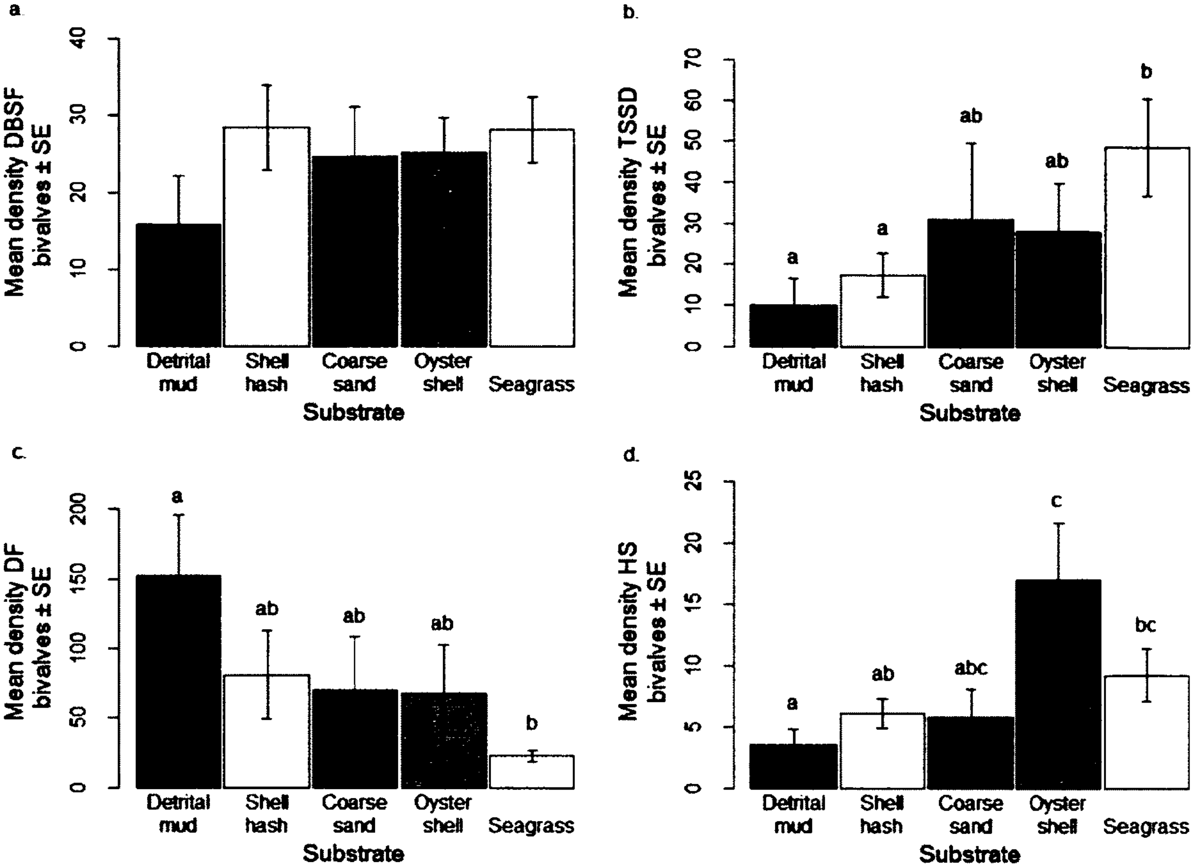

Figure 4. Bivalve functional group densities in different habitats. Means ±1 standard error (SE) for densities of a) deep-burrowing suspension-feeding (DBSF) bivalves, b) thin-shelled surface-dwelling (TSSD) bivalves, c) facultative deposit-feeding (DF) bivalves, and d) hard-shelled (HS) bivalves in different habitat types (substrate) in lower Chesapeake Bay. Samples were collected in detrital mud (n = 23), shell hash (n = 76), coarse sand (n = 14), oyster shell (n = 39), and seagrass (n = 64). Letters denote significant differences at $\alpha = 0.05$.

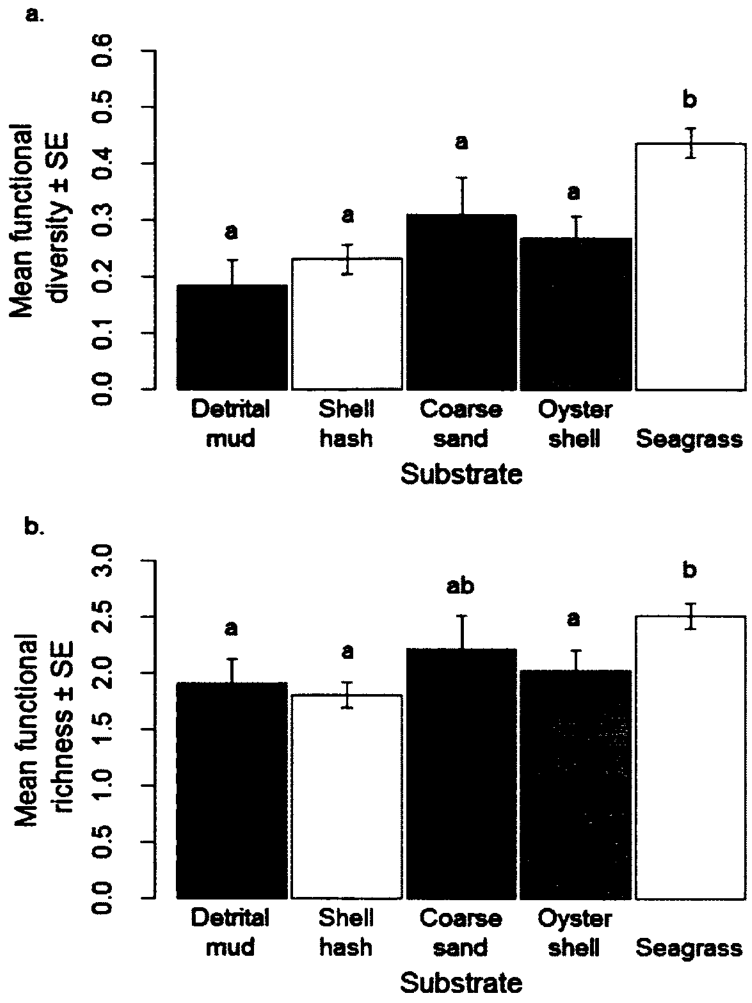

Figure 5. Bivalve functional diversity and richness in different habitats. Means ±1 standard error (SE) for a) Gini-Simpson diversity index applied to functional groups and b) functional species richness in different habitat types (substrate) in lower Chesapeake Bay. Samples were collected in detrital mud (n = 23), shell hash (n = 76), coarse sand (n = 14), oyster shell (n = 39), and seagrass (n = 64). Letters denote significant differences at $\alpha = 0.05$.

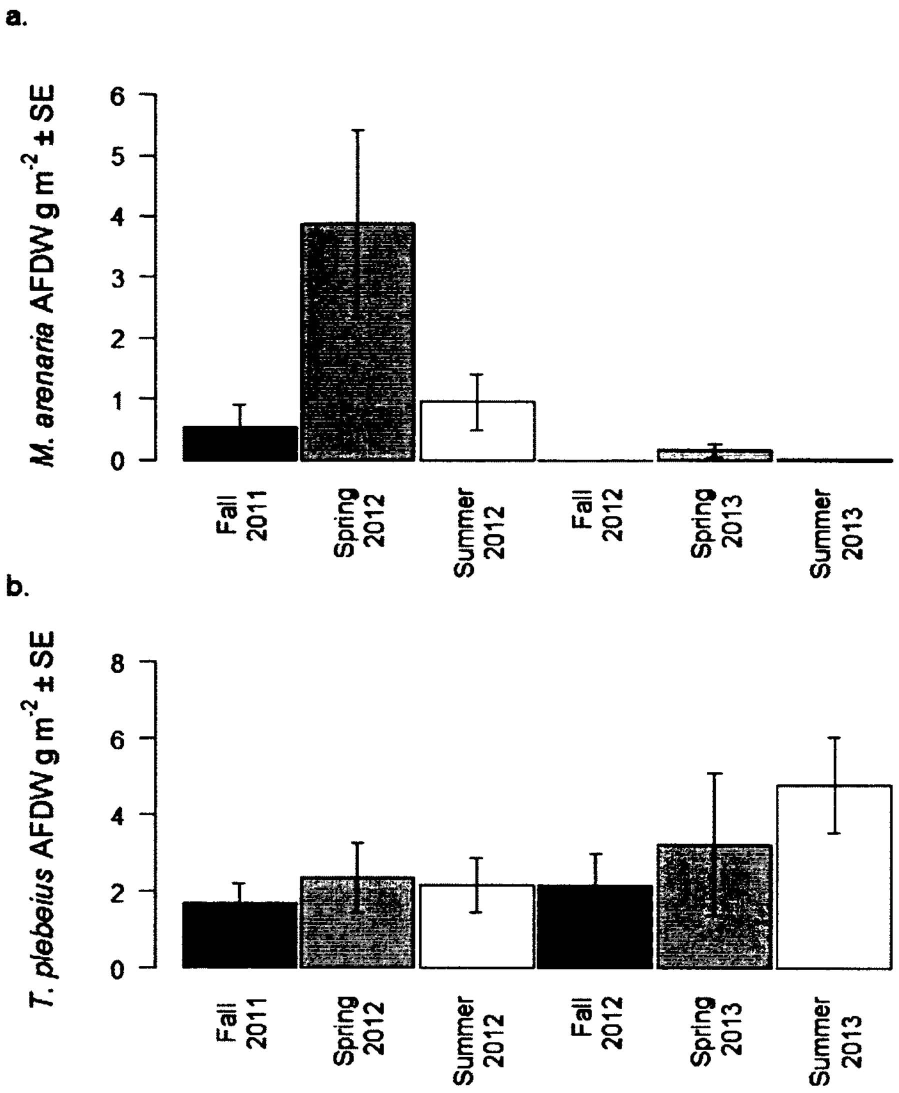

Figure 6. Mean biomass (g m^{-2}) ±1 standard error (SE) for a) *Mya arenaria* and b) *Tagelus plebeius*. Means are shown for each season in chronological order from fall 2011 through summer 2013 (n = 36).

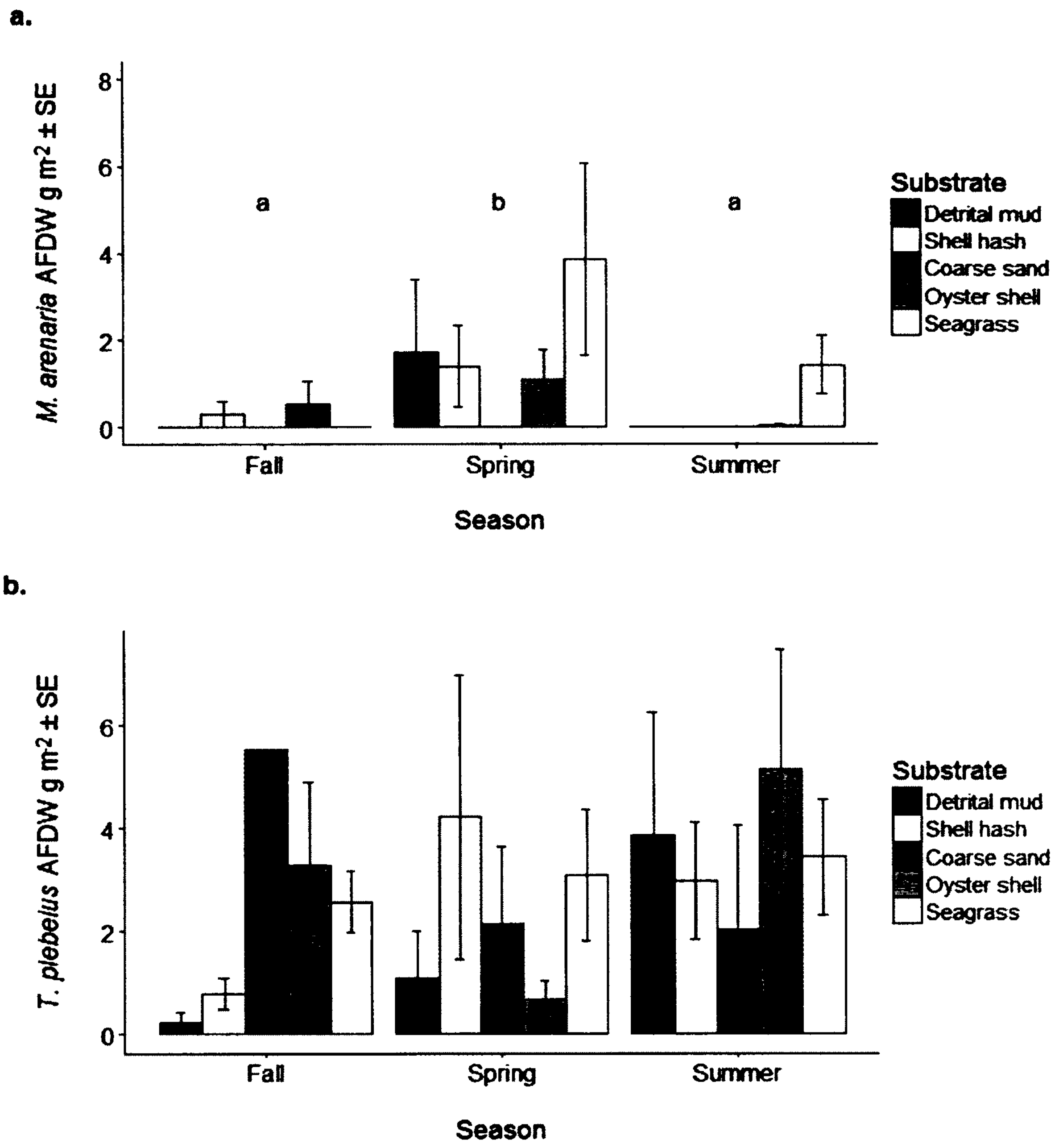

Figure 7. Seasonal trends in biomass for *Mya arenaria* and *Tagelus plebeius*. Mean biomass (g m^{-2}) ±1 standard error (SE) for a) *M. arenaria* and b) *T. plebeius* in different substrates (shown in different color bars) and seasons. Letters denote significant differences at $\alpha = 0.05$. Sample size for detrital mud, shell hash, coarse sand, oyster, and seagrass were: 4, 31, 2, 18, 17 in the fall; 5, 24, 7, 13, 23 in the spring; and 14, 21, 5, 8, and 24 in the summer.

APPENDIX I

Supplementary Table 1. Gini-Simpson diversity index linear model results. Model based on 204 observations. Adjusted $R^2 = 0.151$, F statistic 3.996 on 12 and 191 df, p = 1.60E-05. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	0.605	0.163	3.717	2.65E-04
2012	0.044	0.093	0.477	0.634
2013	-0.064	0.092	-0.703	0.483
Spring	0.062	0.057	1.096	0.274
Summer	-0.012	0.058	-0.214	0.83
River Mobjack	-0.131	0.071	-1.857	0.065
River York	-0.149	0.075	-1.979	**0.049**
Coarse sand	-0.024	0.093	-0.261	0.794
Oyster shell	0.018	0.074	0.246	0.806
Seagrass	0.257	0.071	3.644	**3.46E-04**
Shell hash	-0.037	0.063	-0.586	0.558
No. ray pits	0.022	0.008	2.942	**0.004**
Salinity	-0.014	0.008	-1.682	0.094

Supplementary Table 2. Species richness linear model results. Model based on 192 observations. Adjusted $R^2 = 0.098$, F statistic 3.888 on 11 and 180 df, $p = 0.001602$. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	3.928	0.899	4.369	2.11E-05
River Mobjack	-1.026	0.406	-2.53	**0.012**
River York	-0.822	0.413	-1.987	**0.048**
Coarse sand	0.082	0.541	0.152	0.879
Oyster shell	0.19	0.431	0.441	0.66
Seagrass	1.464	0.431	3.399	**0.001**
Shell hash	-0.193	0.373	-0.518	0.605
Substrate volume	1.62E-04	1.17E-04	1.386	0.167
Crab length	-0.014	0.011	-1.254	0.211
No. ray pits	0.006	0.003	2.004	**0.047**
Salinity	0.054	0.042	1.293	0.198

Supplementary Table 3. Total bivalve density generalized linear model results. Model was fit with family = Poisson, link = log. Model based on 180 observations. McFadden's pseudo $R^2 = 0.434$. Null deviance 4167.0 on 179 df. Residual deviance 2356.6 on 161 df. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	5.772	0.464	12.433	< 2E-16
2012	0.164	0.054	3.024	**0.002**
2013	0.318	0.101	3.141	**0.002**
Spring	0.058	0.13	0.447	0.655
Summer	-0.323	0.089	-3.637	**0.0003**
River Mobjack	0.065	0.091	0.716	0.474
River York	0.567	0.116	4.875	**1.09E-06**
Coarse sand	1.07	0.104	10.31	**< 2E-16**
Oyster shell	0.487	0.092	5.314	**1.07E-07**
Seagrass	0.862	0.087	9.921	**< 2E-16**
Shell hash	1.09E-04	2.40E-05	4.533	**5.81E-06**
Substrate volume	-0.027	0.003	-10.278	**< 2E-16**
Substrate % ash	-0.029	0.003	-8.535	**< 2E-16**
Crab abundance	-0.08	0.01	-7.781	**7.19E-15**
No. ray pits	0.006	0.002	3.908	**9.29E-05**
Fish abundance	0.002	0.001	4.142	**3.44E-05**
Crab length	0.029	0.014	2.161	**0.031**
Temperature	-0.132	0.01	-13.333	**< 2E-16**
Salinity	0.043	0.021	2.052	**0.04**
Dissolved oxygen	5.772	0.464	12.433	**< 2E-16**

Supplementary Table 4. Deep-burrowing and suspension-feeding (DFSF) bivalve abundance generalized linear model results. Model was fit with family = Poisson, link = log. Model based on 192 observations. , McFadden's pseudo $R^2 = 0.165$. Null deviance 942.39 on 191 df. Residual deviance 787.26 on 173 df. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	3.142	0.887	3.541	0.0004
2012	0.664	0.351	1.892	0.058
2013	0.389	0.334	1.167	0.243
Spring	-0.035	0.173	-0.202	0.84
Summer	0.521	0.244	2.132	**0.033**
River Mobjack	-0.79	0.204	-3.878	**0.00011**
River York	-0.306	0.197	-1.558	0.119
Coarse sand	0.389	0.293	1.327	0.185
Oyster shell	0.539	0.255	2.113	**0.035**
Seagrass	1.2	0.23	5.22	**1.79E-07**
Shell hash	0.952	0.226	4.209	**2.56E-05**
Substrate volume	2.00E-04	4.45E-05	4.488	**7.19E-06**
Substrate % ash	-0.012	0.006	-1.961	**0.05**
Crab abundance	-0.017	0.006	-2.901	**0.004**
No. ray pits	-0.053	0.021	-2.542	**0.011**
Crab length	0.005	0.001	4.075	**4.60E-05**
Temperature	-0.094	0.024	-3.936	**8.27E-05**
Salinity	0.023	0.024	0.932	0.351
Dissolved oxygen	-0.095	0.038	-2.519	**0.012**

Supplementary Table 5. Thin-shelled and surface-dwelling bivalve density generalized linear model results. Model was fit with family = Poisson, link = log. Model based on 180 observations. McFadden's pseudo $R^2 = 0.393$. Null deviance 1735.3 on 179 df. Residual deviance 1053.3 on 162 df. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	-10.04	1.226	-8.19	2.61E-16
2012	0.513	0.104	4.933	**8.10E-07**
2013	0.872	0.189	4.609	**4.05E-06**
Spring	1.44	0.302	4.765	**1.88E-06**
Summer	0.936	0.226	4.15	**3.32E-05**
River Mobjack	-0.585	0.26	-2.251	**0.024**
River York	0.131	0.277	0.472	0.637
Coarse sand	0.099	0.264	0.376	0.707
Oyster shell	0.472	0.26	1.813	0.07
Seagrass	-0.33	0.25	-1.323	0.186
Shell hash	1.07E-04	5.14E-05	2.075	**0.038**
Substrate volume	-0.058	0.009	-6.455	**1.09E-10**
Crab abundance	-0.02	0.005	-3.738	**0.000186**
Fish abundance	0.004	0.001	3.538	**4.02E-04**
Fish length	0.004	0.001	2.714	**0.007**
Crab length	0.059	0.024	2.423	**0.015**
Temperature	0.3	0.043	6.911	**4.81E-12**
Salinity	0.237	0.034	7.025	**2.13E-12**
Dissolved oxygen	-10.04	1.226	-8.19	**2.61E-16**

Supplementary Table 6. Deposit-feeding bivalve density generalized linear model results. Model was fit with family = Poisson, link = log. Model based on 180 observations. McFadden's pseudo $R^2 = 0.7268$. Null deviance 5093.3 on 179 df. Residual deviance 1391.3 on 162 df. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	2.456	0.855	2.872	0.004
2012	0.574	0.099	5.793	**6.91E-09**
2013	1.523	0.247	6.17	**6.82E-10**
Spring	-0.396	0.264	-1.501	0.133
Summer	0.066	0.17	0.391	0.695
River Mobjack	1.68	0.159	10.578	**< 2e-16**
River York	0.325	0.169	1.929	**0.054**
Coarse sand	1.04	0.166	6.271	**3.59E-10**
Oyster shell	-0.784	0.158	-4.974	**6.55E-07**
Seagrass	0.789	0.125	6.339	**2.31E-10**
Shell hash	-0.046	0.004	-12.025	**< 2e-16**
Substrate % ash	-0.034	0.006	-6.049	**1.46E-09**
Crab abundance	0.017	0.003	6.522	**6.93E-11**
Fish abundance	0.003	0.001	2.43	**0.015**
Fish length	-0.11	0.018	-6.058	**1.38E-09**
No. ray pits	0.123	0.032	3.879	**1.05E-04**
Temperature	-0.122	0.015	-7.981	**1.45E-15**
Salinity	0.081	0.046	1.787	0.074
Dissolved oxygen	2.456	0.855	2.872	**0.004**

Supplementary Table 7. Hard-shelled bivalve density generalized linear model results. Model was fit with family = Gaussian, link = log. Model based on 192 observations. McFadden's pseudo $R^2 = 0.269$. Null deviance 344.08 on 191 df. Residual deviance 470.58 on 177 df. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	-18.94	915.4	-0.021	0.983
2012	18.2	915.4	0.02	0.984
2013	18.74	915.4	0.02	0.984
Spring	-0.222	0.333	-0.666	0.506
Summer	-1.746	0.378	-4.621	**3.83E-06**
River Mobjack	-0.865	0.386	-2.244	**0.025**
River York	-0.681	0.356	-1.911	0.056
Coarse sand	0.443	0.516	0.859	0.39
Oyster shell	1.681	0.409	4.113	**3.91E-05**
Seagrass	1.823	0.49	3.725	**1.96E-04**
Shell hash	0.807	0.407	1.985	**0.047**
Substrate volume	2.76E-04	7.25E-05	3.81	**1.39E-04**
Crab length	0.004	0.002	1.977	**0.048**
Temperature	0.133	0.042	3.167	**0.002**
Salinity	-0.153	0.043	-3.526	**4.21E-04**

Supplementary Table 8. Functional richness linear model results. Model based on 204 observations. Adjusted $R^2 = 0.144$, F statistic 3.84 on 12 and 191 df, $p = 2.95E\text{-}05$. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	0.147	0.05	2.958	0.004
Coarse sand	0.106	0.079	1.343	0.181
Oyster shell	0.071	0.063	1.118	0.265
Seagrass	0.251	0.057	4.398	**< 0.0001**
Shell hash	0.048	0.057	0.852	0.395
Fish abundance	0.001	0.001	0.642	0.522
No. ray pits	0.017	0.006	2.78	**0.006**

Supplementary Table 9. Functional diversity linear model results. Model based on 180 observations. Adjusted $R^2 = 0.1521$, F statistic 4.21 on 10 and 169 df, $p = 3.15E-05$. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	0.487	0.199	2.453	0.015
2013	-0.064	0.039	-1.617	0.108
River Mobjack	-0.142	0.067	-2.11	**0.036**
River York	-0.142	0.071	-1.999	**0.047**
Coarse sand	0.061	0.084	0.727	0.468
Oyster shell	0.045	0.068	0.666	0.506
Seagrass	0.312	0.069	4.541	**1.06E-05**
Shell hash	0.052	0.06	0.874	0.383
Fish abundance	0.001	0.001	0.815	0.416
No. ray pits	0.017	0.006	2.699	**0.008**
Salinity	-0.012	0.008	-1.424	0.156

Supplementary Table 10. *Tagelus plebeius* presence/absence generalized linear model results. Model based on 216 observations. McFadden's pseudo $R^2 = 0.108$. Null deviance = 297.94 on 215 df, residual deviance 265.86 on 203 df. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	1.439	1.846	0.779	0.436
Year 2012	-0.787	0.519	-1.516	0.129
Year 2013	-0.6	0.633	-0.948	0.343
Season spring	-0.54	0.489	-1.105	0.269
Season summer	0.003	0.493	0.005	0.996
River Mobjack	-0.472	0.52	-0.906	0.365
River York	-0.203	0.397	-0.511	0.609
Coarse sand	0.958	0.874	1.096	0.273
Oyster shell	0.84	0.754	1.114	0.265
Seagrass	2.341	0.639	3.664	**0.0003**
Shell hash	0.651	0.642	1.014	0.311
Substrate % ash	-0.017	0.022	-0.781	0.435
Substrate volume	0.00017	0.00016	1.099	0.272

Supplementary Table 11. *Tagelus plebeius* non-zero biomass AICc results. Model with the highest weight bolded.

Model	*k*	*AICc*	*Delta*	*Weight*
Global	14	474.38	16.37	0.0002
Substrate, rays, environment	12	471.69	13.68	0.0008
Season, substrate (volume and % ash only), rays, environment	10	466.86	8.86	0.009
Environment	**5**	**458.01**	**0.00**	**0.73**
Season, environment	7	460.39	2.38	0.22
Substrate (volume and % ash only), rays, environment	5	464.14	6.14	0.03

Supplementary Table 12. *Tagelus plebeius* non-zero biomass generalized linear model results. Model was fit with family = Gaussian, link = log. Model based on 108 observations. McFadden's pseudo $R^2 = 0.067$. Null deviance = 92.82 on 107 df, residual deviance 86.56 on 104 df. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	2.559	1.488	1.721	0.088
Temperature	-0.037	0.039	-0.957	0.341
Salinity	-0.020	0.035	-0.587	0.559
Dissolved oxygen	-0.244	0.104	-2.351	**0.021**

Supplementary Table 13. *Mya arenaria* presence/absence generalized linear model results. Model based on 204 observations. McFadden's pseudo $R^2 = 0.454$. Null deviance = 135.25 on 203 df, residual deviance 73.84 on 189 df. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	16.18	7.075	2.287	0.022
Year 2012	1.137	2.554	0.445	0.656
Year 2013	-2.388	2.32	-1.03	0.303
Season spring	2.347	1.569	1.496	0.135
River Mobjack	-4.067	2.105	-1.932	0.053
River York	-0.219	1.775	-0.123	0.902
Coarse sand	-13.23	1533	-0.009	0.993
Oyster shell	3.889	2.15	1.809	0.07
Seagrass	5.67	2.081	2.725	**0.006**
Shell hash	1.696	1.835	0.924	0.355
Substrate volume	-0.0004	0.001	-0.695	0.487
Substrate % ash	-0.079	0.052	-1.526	0.127
Temperature	-0.157	0.17	-0.925	0.355
Salinity	-0.234	0.198	-1.183	0.237
Dissolved oxygen	-0.904	0.284	-3.185	**0.001**

Supplementary Table 14. Positive *Mya arenaria* biomass AICc results. Model with the highest weight bolded.

Model	*k*	*AICc*	*Delta*	*Weight*
Global	13	108.75	22.82	< 0.0001
Year, river, substrate (volume and % ash only), crabs	**10**	**85.93**	**0.00**	**0.83**
River, substrate, crabs	11	111.04	25.11	< 0.0001
Year, substrate, crabs	11	105.23	19.31	0.0001
Substrate (volume and % ash only), crabs	6	89.09	3.17	0.17
Substrate (including categories), crabs	9	98.82	12.89	0.001

Supplementary Table 15. Positive *Mya arenaria* generalized linear model results. Model was fit with family = Gaussian, link = log. Model based on 21 observations. McFadden's pseudo $R^2 = 0.791$. Null deviance = 26.28 on 20 df, residual deviance 5.49 on 12 df. Significant variables at $\alpha = 0.05$ are bolded.

	Estimate	*Std. Error*	*t value*	*p*
Intercept	-8.255	5.033	-1.64	0.127
Year 2012	2.875	1.174	2.449	**0.031**
Year 2013	1.626	2.28	0.713	0.489
River Mobjack	2.468	1.375	1.795	0.098
River York	1.895	1.046	1.811	0.095
Substrate volume	0.002	0.001	2.868	**0.014**
Substrate % ash	0.026	0.034	0.753	0.466
Crab abundance	0.043	0.022	2.00	0.069
Average crab size	-0.005	0.01	-0.49	0.633

CHAPTER 3

Habitat complexity mediates benthic predator-prey interactions in Chesapeake Bay

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ABSTRACT

Density-dependent predation may determine whether prey persists or faces local extinction. In Chesapeake Bay, the soft-shell clam *Mya arenaria* (thin-shelled, deep-burrowing infaunal; *Mya* hereafter) exhibits large population declines when predators are active and persists at very low densities. In contrast, the hard clam *Mercenaria mercenaria* (armored, shallow-burrowing infaunal; *Mercenaria* hereafter) has a stable population and age distribution. We examined the potential for habitat and predators to drive densities and distributions of *Mya* in a field caging experiment, where juvenile clams were placed in mud, sand, or seagrass with different predator exclusion treatments for 5 d. We also examined the impacts of habitat complexity on blue crab predator-prey interactions for both bivalves in laboratory mesocosm experiments, which examined proportional survival of *Mya* and *Mercenaria* (at two densities) and blue crab handling time, search time, and encounter rate in sand, shell hash, oyster shell, or seagrass. Bivalves experienced significantly greater mortality in sand than in the structurally complex habitats. In the field, clams exposed to predators suffered 76.6% greater mortality as compared to caged individuals. Predator exclusion treatments confirmed that blue crabs were likely responsible for most of the mortality of juvenile *Mya*. In laboratory mesocosm experiments, *Mya* had lower survival in sand than in shell hash or oyster shell habitats, though survival in seagrass was not significantly different from survival in sand. There was a tendency for crabs to miss one or more prey in seagrass, shell, and oyster shell habitats, suggesting that seagrass may still serve as a refuge for low densities of *Mya*. Predators had shorter search times and lower encounter rates with prey at low densities, likely due to the added cost of inefficient foraging; however, this effect was more pronounced for *Mya* than for *Mercenaria*. *Mercenaria* had higher survival than *Mya* in mesocosm experiments, likely because predators feeding on *Mercenaria* spent less time foraging than those feeding on *Mya*. *Mya* may retain a low-density refuge from predation even with the loss of structurally complex habitats, though a loss of habitat refuge may result in clam densities that are not sustainable. A better understanding of density-dependent predator-prey interactions is necessary to prevent loss of food web integrity and to conserve marine resources.

INTRODUCTION

Predators exhibit top-down control on communities, influencing the abundance, size structure, and distribution of prey by restricting their survival or activity in time and space (Garrity and Levings 1981, Micheli 1997, Beal 2006). Predators also influence community function by preying upon dominant species (Randall 1961, Dayton 1971, Lubchenco and Gaines 1981). To understand the structure and function of a community, it is important to consider the impact of the natural guild of predators. The influence of a predator guild on a prey population is largely the result of the behavior of individual predators within the guild (Micheli 1997).

Optimal foraging theory characterizes predator foraging behavior as a function of the costs and benefits associated with foraging. The evolutionary basis for optimal foraging theory is that predators make choices to maximize net energy gain, and thus increase fitness (Pyke 1984). As prey density decreases, an optimal forager will leave the prey patch, since the costs of foraging outweigh the benefits of finding prey (Abrams 1982). This is the theoretical basis for the characterization of density-dependent predator-prey interactions. Prey populations experience the effects of predation differently depending on how abundant the prey species is and, for actively foraging predators, how quickly the predator can find and consume prey (Hassell 1978). The degree to which a predator can reduce prey abundance is a function of the probability of encountering a prey item, and the probability that the prey item will be eaten, given that it has been encountered. Both factors depend on the characteristics of the prey, the predator, and other environmental factors (Lubchenco and Gaines 1981).

Bivalve mollusks exhibit a number of morphological and behavioral characteristics to defend against predators. Armor or aggregation decreases rates of predation, allowing predators and prey to coexist in the same space. For example, the hard clam *Mercenaria mercenaria* exhibits armor that protects it from predation by blue crabs *Callinectes sapidus*; clams larger than 40 mm cannot be crushed and therefore coexist with crabs (Blundon and Kennedy 1982b). Other bivalves must avoid predators to survive; the shell of a soft-shell clam *Mya arenaria* is thin and has a permanent gape, indicating that for this species, armor is not an important mode of protecting against attack by predators (Vermeij 1987). To avoid predation, *Mya arenaria* achieves a refuge by burrowing 25-30 cm in the sediment, out of range of foraging predators, which rarely consume clams buried deeper than 10 cm (Blundon and Kennedy 1982a).

Habitat also plays an important role in predator defense strategies of marine bivalves. Predators in habitats that are not complex have a greater effect on prey than those in complex habitats (Sih et al. 1985, Stoner 2009). Vegetated or shell habitat provides a refuge from predation for many prey (Stoner 2009, Long and Whitefleet-Smith 2013), and increased sediment grain size allows infaunal species to avoid predators more effectively than fine sediments (Blundon and Kennedy 1982a, Quammen 1984, Seitz et al. 2001). Complex habitats make foraging inefficient, and as the cost to forage becomes too high, predators may opt to conserve energy or forage elsewhere (Abrams 1982, Sponaugle and Lawton 1990).

The functional response is a way to quantify predator foraging efficiency (Hassell 1978). A predator's functional response is the relationship between the number of prey consumed per predator and prey density (Solomon 1949). Predators that search for prey exhibit a density-dependent functional response because the encounter rate depends on prey density. In a type II density-dependent response, handling rate and attack rate remain constant as prey density increases (Hassell 1978). Prey consumed per predator increases with increasing prey density, but the rate of increase declines to an upper asymptote. The asymptote is reached when the predator becomes satiated and spends less time foraging, or when the predator is limited by the amount of time it takes to consume prey (Hassell 1978). A type III sigmoidal density-dependent response occurs when a predator becomes more active as prey density rises, which means attack rate is a function of prey density (Hassell 1978). Type II and type III functional responses are very different biologically, since type III functional responses create a refuge for prey at low densities, which may result in prey persistence over time, even if a population is driven to low abundance (Hassell and May 1973, Hassell 1978, Eggleston et al. 1992).

The main parameters in a functional response model are encounter rate and handling time (Hassell 1978), both of which change as a function of prey density, prey behavior, and habitat type. For the purposes of this study, the encounter rate was defined as the number of encounters with prey divided by the amount of time a predator spends foraging, or actively looking for prey; and the handling time was defined as the amount of time a predator spends manipulating or eating a prey item. For predators of armored bivalves, the consumption rate is determined more by handling time than encounter rate; in this case, a type II functional response is more likely (Seitz et al. 2001). For burrowing, thin-shelled bivalves, encounter rate is more important than handling time for their predators (Micheli 1997), which means that a density-dependent sigmoidal (type III) response is likely (Seitz et al. 2001). The biological mechanism behind a type III response is that when a predator is foraging optimally, low encounter rates often lead to low activity levels or emigration from the area (Lipcius and Hines 1986). The functional response of a predator-prey interaction can also be habitat specific. Reduced sediment penetrability (Seitz et al. 2001) or increased vegetative cover (Lipcius et al. 1998) may lead to decreased encounter rate, and this may change the functional response by creating or strengthening a low-density refuge from predation.

In Chesapeake Bay, two commercially valuable clam species, the soft-shell clam *Mya arenaria* (hereafter, *Mya*) and the hard clam *Mercenaria mercenaria* (hereafter, *Mercenaria*) have very different population dynamics. *Mya* exists in the Bay at low abundance except immediately after spring recruitment, and juveniles are nearly completely consumed by predators each year (Chapter 2; Figure 8). *Mercenaria* is fairly abundant throughout the year, and all size classes persist in the Bay (Figure 8). The different dynamics of these species may be due to predator-prey dynamics, since the two species exhibit different predator avoidance strategies. Specifically, the persistence of *Mya* at low abundance may be due to a low-density refuge, especially in complex habitats that prevent efficient foraging by the species' main predators, the blue crab *Callinectes sapidus* (Hines et al. 1990, Lipcius et al. 2007) and the cownose ray *Rhinoptera bonasus* (Fisher 2010). This study aims to examine the nature of blue crab-bivalve predator-prey interactions for these two infaunal bivalves, including the role of structural refuge (in the form of complex habitat) on these interactions. In the field, we experimentally examined predation on *Mya* using different cage types (full cage, stockade, and uncaged) to address predation by the main predators, blue crabs and cownose rays, and different substrate types (mud, sand, and seagrass) to examine the potential for structural refuge from predation for *Mya*. In the lab, we determined the functional response of blue crabs feeding on either *Mya* or *Mercenaria* in habitats of varying complexity (sand, shell hash, oyster shell halves, and seagrass). We measured specific parameters of predator-prey interactions, including handling time, encounter rate, and search time (time the predator spent foraging) for the different bivalve species, habitat types, and bivalve densities.

In field caging experiments, we hypothesized the following: 1) blue crabs and cownose rays would both be sources of mortality for *Mya* (evidenced as a significant difference in *Mya* survival among all caging treatments); and 2) the presence of seagrass would increase clam survival rates as compared to sand and mud (for stockade and uncaged plots). In laboratory mesocosm experiments, we hypothesized the following: 1) predators on *Mya* would exhibit a type III functional response and predators on *Mercenaria* would exhibit a type II functional response (evidenced as a significant species-density interaction); 2) complex habitats would increase the extent of the low-density refuge for species using density as a refuge, which would manifest as increased proportional survival in complex habitats as compared to sand, but only for *Mya* (evidenced as a significant species-habitat interaction); 3) *Mercenaria*'s armor would lead to increased handling time (evidenced as a significant main effect of species on handling time); 4) low densities, complex habitat, and deep-burrowing prey would result in decreased blue crab search time, due to the added cost of inefficient foraging (evidenced as a 3-way interaction between species, density, and habitat), and 5) there would be a decreased encounter rate at low densities of *Mya* (evidenced as a significant species-density interaction).

MATERIALS AND METHODS

Field caging experiment

A caging study was conducted in near-shore habitats containing patchy seagrass, sand, and mud in May 2014 near the mouth of the York River, VA (Figure 9). Ten replicate 0.25 m^2 plots were randomly assigned one of three caging treatments: full cage, stockade, or uncaged. Full cages were constructed of 13-mm galvanized wire mesh with PVC frames (0.6 m height, 0.5 m width, 0.5 m length), sunk into the sediment approximately 10 cm, and secured with PVC legs that sunk into the ground an additional 30-40 cm. Stockades were constructed by placing 8 10-ft PVC poles around the plot at 25-cm intervals. Stockades kept cownose rays out of the plots, while still allowing for crab and fish predation. Uncaged plots were marked with two PVC poles on the diagonals. There were n = 10 replicates of each cage type in each habitat.

Juvenile *Mya* were collected from the York River and held in flow-through tanks until experimentation. Only *Mya* that actively burrowed in sand over a 24-hour period were used. Clams were marked with permanent marker and planted towards the center of the plot at densities of 12 clams per plot (48 m^{-2}), similar to the density used in previous caging studies (Skilleter 1994). A cage was placed over all planted clams to allow them to acclimate overnight and achieve a stable burrowing depth (Lipcius and Hines 1986), and acclimation cages were removed from stockade and uncaged treatments. After 5 d, the contents of all plots were collected to a depth of 40 cm using a suction sampler (Eggleston et al. 1992). Remaining bivalves were counted and shell fragments were noted as evidence of crab predation. Hinges of crushed clam shells were counted, and recovery rates of crushed clams are expressed as the percent of missing clams recovered as crushed shell and are adjusted according to the average number of clams retrieved in caged plots. Partial cages were not used to control for caging artifacts due to the short nature of this study and the tendency for partial cages to attract blue crabs. Only one density was used in this study due to the presence of wild *Mya* in the area, and the consequent logistical difficulties associated with creating reliable densities.

Proportional survival data were box-cox transformed ($\lambda = 0.34$) to achieve normality and homogeneous variance, and analyzed using two-way ANOVA, with cage type (3 levels: full cage, stockade, and uncaged) and habitat (3 levels: sand, mud, and seagrass) as fixed factors, with $\alpha = 0.05$ for main effects and $\alpha = 0.20$ for interaction terms (Underwood 1997). Post-hoc pairwise comparisons were done using Tukey honest significant difference (HSD) tests. From a pilot caging experiment in 2012, we used a simulation of resampled data to determine that our sample size of $n = 10$ resulted in the following estimates of statistical power: 1.00 for the main effect of cage type, 0.42 for the main effect of habitat, and 0.87 for the interaction effect. All analyses were completed using R statistical software (R Core Team 2015).

Laboratory mesocosm experiment

Soft-shell clams (*Mya*, thin-shelled deep infaunal) and hard clams (*Mercenaria*, armored shallow infaunal) were exposed to blue crab *C. sapidus* predation in a mesocosm experiment conducted in the Seawater Research Laboratory at the Virginia Institute of Marine Science. Mesocosm tanks of 0.87 m diameter and 0.59 m height were partitioned with corrugated plastic to form a rectangular experimental arena (40 cm x 70 cm). Tank temperature was held constant at 26-27 °C and the water was aerated by an aquarium heater and air stone, respectively, placed outside the experimental arena. Sand was added to the tank to 25 cm depth, and an additional 25 cm of the tank was filled with filtered water from the York River. Trials were randomly assigned one of four substrate treatments: sand, sand/shell hash, sand/oyster shell, or sand/seagrass. For trials receiving shell or oyster shell, a constant volume of 0.5-L crushed shell hash or oyster shell halves was added to the center of the mesocosm tank. Eelgrass (*Zostera marina*) and widgeongrass (*Ruppia maritima*) shoots and rhizomes were collected from the York River and used to construct seagrass mats for use in trials receiving seagrass. Seagrass mats were constructed with 0.5 liter of seagrass tied onto plastic 1-cm Vexar mesh meant to simulate a rhizome mat. Holes measuring approximately 25 cm^2 were cut at regular intervals to allow crabs to forage for clams buried under the simulated seagrass mat. The mesh and attached seagrass roots were placed in the center of the tank and completely covered with sand. The ability of crabs to forage in trials with the simulated seagrass mat was verified by observing crab encounters with clams throughout the experiment.

Juvenile *Mya* were collected from the York River and held in flow-through tanks until experimentation. Hard clams *Mercenaria* were obtained from Cherrystone Aqua-Farms in Virginia. Only hard clams with shell lengths < 40 mm were used in the study because blue crabs are able to consume clams of this size (Arnold 1984, pers. obs.). Bivalves were placed in the sediment siphon up, away from the edge of the tank to avoid edge effects, and allowed 24 h to achieve a stable burial depth (Lipcius and Hines 1986). Each species was planted at two densities as determined from the literature, one low and one medium density, which is sufficient to determine whether the functional response is type II or III (Lipcius and Hines 1986, Taylor and Eggleston 2000). Low densities for both species were 4 clams per tank, and medium densities were 11 clams per tank for *Mercenaria* and 16 clams per tank for *Mya* (Sponaugle and Lawton 1990, Taylor and Eggleston 2000).

Callinectes sapidus were collected from the York River via crab pots baited with frozen Atlantic menhaden (*Brevoortia tyrannus*). All crabs were acclimated to the lab for 1 week or longer and fed fish or clam meat three times per week. It was not possible to use a different crab for each trial due to space requirements, nor was it possible to use each crab the same number of times due to losses throughout the experiment. Crabs were used between one and three times, and crabs were randomly assigned to trials so there was no bias inherent in the re-use of crabs.

At the start of the experiment, one adult male blue crab with a carapace width $\geq$ 100 mm was added to each tank receiving a predator treatment. Bivalves were exposed to blue crab predation for 48 h, as is common for similar mesocosm studies (Eggleston et al. 1992). Remaining bivalves were excavated and counted upon termination of the experiment. There were six replicates of each substrate/density combination, as well as an equal number of mesocosms set up without predators, which served as controls (though clams rarely died in predator-free controls and they are not analyzed or discussed further).

Proportional survival data were box-cox transformed ($\lambda = 0.91$) to achieve normality and homogeneous variance, and analyzed using three-way ANOVA, with density (2 levels: low and medium), species (2 levels: *Mya* and *Mercenaria*) and habitat (4 levels: sand, shell hash, oyster shell, and seagrass) as fixed factors, with $\alpha = 0.05$ for main effects and $\alpha = 0.20$ for interaction terms (Underwood 1997). Effect size and standard error estimates from a similar experiment completed by Lipcius and Hines (1986) were used to calculate power to see a significant main effect of density, which was 0.95 for $n = 6$. Post-hoc pairwise comparisons were done using Tukey HSD tests. Analysis of the number of mesocosm trials with all of the clams eaten, a portion of the clams eaten, and none of the clams eaten was completed using a chi-square test with Monte Carlo simulation of p values due to the presence of zeroes in the contingency table.

For half of the trials ($n = 3$) predator behavior was recorded using an infrared-sensitive camera system. A red spotlight was used to improve night-time video quality without disrupting crab behavior (Cronin and Forward 1988). Videos were used to calculate search time, encounter rate, and handling time. Search time (h) was defined as the total time spent exhibiting foraging behavior, such as probing the sediment with legs or claws or lifting items to mouthparts. Encounter rate (hr^{-1}) was defined as the number of encounters (picking up bivalve) divided by the search time. Handling time (h) was defined as the total time spent manipulating or eating a bivalve, divided by the number of encounters. Handling time, search time, and encounter rate were fourth-root transformed and compared for the two bivalve species in different habitat treatments and at different densities using three-way ANOVAs of the same form as those used for analysis of proportional survival. Post-hoc pairwise comparisons were done using Tukey HSD tests.

RESULTS

Field caging experiment

Over the 5-day caging experiment, mean water temperature at the nearby YKTV2 weather buoy was 18.76 °C (± 1.63 SD). Cownose rays generally enter the Bay in large numbers when water temperatures reach 17 °C in the spring (Fisher 2010). Rays were first caught in pound nets on May 9th (5 d prior to the start of the experiment on May 14th; pers. comm. R.A. Fisher, VIMS) and were observed in the vicinity of the cages during the study. All replicates ($n = 10$) for the stockade and uncaged plots survived the experiment and were subsequently sampled. At least one cage was lost from each habitat, leaving $n = 9$ replicates in mud, $n = 7$ replicates in sand, and $n = 8$ replicates in seagrass.

As compared to the full cage, there was a decrease in proportional survival of 75.7% in stockades ($p < 0.001$) and 77.4% in uncaged plots ($p < 0.001$; Figure 10), but the effect of one main effect depended on the conditions of the other. Stockade and uncaged had similar survival ($p = 1.00$; Figure 10). Mud had significantly lower survival than sand ($p = 0.002$) or seagrass ($p = 0.001$; Table 3). Seagrass and sand had similar survival ($p = 1.00$; Table 3). Due to a significant habitat x cage interaction, main effects need to be interpreted with caution. The significant habitat x cage treatment interaction was driven by the full cage treatment, which had different patterns of survival than the other caging treatments (Supplementary Table 16). Survival of clams in stockades placed in mud was lower than might be expected with just main effects of substrate and cage type (Supplementary Table 16).

On average, 49.5% of missing clams were recovered as crushed shells within the plots. Mean recovery of crushed shells varied little among caging types and habitats. The highest occurred in stockade plots in sand, with 61% (± 31% SD) of missing clams recovered as crushed shells, and lowest occurred in uncaged plots in mud, with 28% (± 31% SD) of missing clams recovered as crushed shells.

Laboratory mesocosm experiment

In mesocosm experiments, mean proportional survival ranged from 0.27 (*Mya* in seagrass at medium densities) to 1.00 (*Mercenaria* in seagrass at medium densities). Crabs ate at least one *Mercenaria* in 18 out of 48 trials, and ate all offered *Mercenaria* in only one trial (low density in shell). Predation of *Mya* was more common, with at least one *Mya* eaten in 38 out of 48 trials. In the sand at low densities, crabs either ate all of the available *Mya* (occurred 3 times), or none of them (occurred 3 times; Figure 11a). In the more complex habitats (shell hash, oyster shell, and seagrass), crabs offered low densities of clams usually ate none of them (occurred 13 out of 18 trials); only occasionally would a crab eat a portion (occurred 3 times) or all (occurred 2 times) of the clams (Figure 11b-d). There was no significant difference in the frequency of occurrence of these events (all clams eaten, a portion of the clams eaten, and no clams eaten) among habitat types (p = 0.24).

Mya had significantly lower survival than *Mercenaria* (p = 0.01; Table 4), but the effect of one main effect depended on the conditions of the others. Bivalves had lower proportional survival in trials with medium bivalve densities than in trials with low bivalve densities (p = 0.03; Table 4). There were no significant differences in habitat type (p = 0.30; Table 4). *Mya* in medium densities had lower survival than the other species x density combinations, driving a significant species x density interaction (Supplementary Table 17). In sand and seagrass, *Mya* had lower survival than the other species x habitat combinations, driving a significant species x habitat interaction (Figure 12a-d; Supplementary Table 18).

Handling time was significantly lower in low-density trials than in medium-density trials (Figure 13a,b; p = 0.05; Table 5), but the effect of one main effect depended on the conditions of the others. The two treatments with the longest mean handling times were *Mercenaria* at medium density in shell (1.31 h) and *Mercenaria* at medium density in sand (0.76 h). All other treatments had mean handling times of 0.30 h or less. The overall mean handling times for *Mercenaria* and *Mya* were 0.18 h and 0.03 h, respectively. In shell hash, *Mercenaria* had longer handling times than the rest of the species x habitat combinations, driving a significant species x habitat interaction (Supplementary Table 19).

Search time was shorter in low-density trials than in medium-density trials (Figure 13c,d; p = 0.003; Table 6), but the effect of one main effect depended on the conditions of the others. The two treatments with the longest mean search times were *Mya* at medium density in seagrass (5.67 h) and *Mya* at medium density in oyster shell (5.56 h). The overall mean search times for *Mercenaria* at low and medium densities were 1.22 h and 1.91 h, respectively. The overall mean search times for *Mya* at low and medium densities were 0.89 h and 4.16 h, respectively. *Mya* at medium densities had longer search times than the other species x density combinations, driving a significant species x density interaction (Supplementary Table 20). However, relatively long search times for medium densities of *Mya* only occurred in certain habitats (sand, oyster shell, and seagrass), resulting in a three-way interaction (Supplementary Table 21).

Encounter rate was significantly less in low-density trials than in medium-density trials (Figure 13e,f; $p = 0.02$; Table 7). The two treatments with the highest mean encounter rates were *Mya* at medium density in sand (4.08 h^{-1}) and *Mya* at medium density in seagrass (3.23 h^{-1}). The overall mean encounter rates for *Mercenaria* at low and medium densities were 0.79 h^{-1} and 1.80 h^{-1}, respectively. The overall mean encounter rates for *Mya* at low and medium densities were 0.81 h^{-1} and 2.85 h^{-1}, respectively.

DISCUSSION

Blue crabs were the main predators of *Mya* in all habitats, with no significant difference between stockades and uncaged plots and high incidence of crushed shells, which served as evidence of crab predation rather than fish predation. This was in line with our hypothesis that crab predation would be important. Despite evidence in the literature that schooling rays can result in mass mortality of bivalves (Peterson et al. 2001), and evidence from gut content analysis that cownose rays consume *Mya* (Fisher 2010), we did not observe evidence that cownose rays increased predation in uncaged plots relative to stockade plots. These results were contrary to our hypothesis and indicate that over the time and spatial scale of this study, rays were not a major source of mortality for *Mya*.

Predation-related mortality was high for juvenile *Mya* that were not protected by a cage. Over a period of five days, exposure to predators decreased survival of juvenile *Mya* by 76.6% as compared to caged individuals. Clam survival was habitat dependent, and both sand and seagrass provided more of a refuge from predation than mud. *Mya* has previously been shown to achieve a low-density refuge in sand (Lipcius and Hines 1986, Seitz et al. 2001); however, our results went against our hypothesis that the added complexity afforded by seagrass habitats provides extra refuge for juvenile *Mya*.

In the laboratory study, there was an effect of habitat on predator-related mortality only for *Mya*, which had lower survival in sand and seagrass than in shell hash or oyster shell habitats. However, in the case of a prey species that achieves a low-density refuge from predation, proportional survival may not be the best measure of success. Shell, oyster, and seagrass habitats had higher occurrence of trials with at least one clam left, which may be biologically significant. Habitat that allows survival of one or a few clams may maintain the low-density refuge for *Mya*.

Predators on *Mercenaria* (armored infaunal) and *Mya* (thin-shelled infaunal) had significantly different functional responses. Predators on *Mya* had a type III sigmoidal functional response, with a negative relationship between density and proportional survival. Predators on *Mercenaria* had a type II hyperbolic functional response, exhibiting either a positive relationship between density and proportional mortality or no density dependence, depending on the habitat. This difference is relevant to population dynamics and persistence of these two bivalve species because a type II functional response is unstable and can lead to local extinction of prey if they are driven to low densities, but a type III functional response may lead to prey persistence at low density

(Murdoch and Oaten 1975, Hassell 1978). The type II functional response of predators feeding on *Mercenaria* means this bivalve species must remain at relatively high densities to achieve population stability. Conversely, the type III functional response of predators feeding on *Mya* allows the species to persist, even at very low density.

The differences in functional response of predators feeding on *Mya* and *Mercenaria* were likely due to differences in predator behavior. Predators had shorter search time and encounter rate in low densities, in agreement with our hypotheses. At low densities, encounter rate did not differ between the two bivalve species, indicating blue crabs had less trouble finding deep-burrowing clams than we hypothesized. There was no evidence that blue crabs spent less time foraging in complex habitats or when exposed to deep-burrowing prey; on the contrary, blue crabs spent more time searching for *Mya* at medium densities than they did searching for *Mercenaria* at medium densities, indicating crabs may have a preference for *Mya* as prey. This tendency of blue crabs to pass up on *Mercenaria* as prey may explain why handling times for *Mercenaria* were not significantly greater than handling times for *Mya*; while many crabs spent the extra time opening up the heavily armored clams, many predators also gave up without investing much time into the encounter.

Seagrass did not provide a refuge from predation for *Mya* in the field or in the laboratory experiment. However, seagrass in both studies was patchy; mesocosms were small, and caging sites were chosen so that the three habitat types (mud, sand, and seagrass) were in close proximity. Prey patch size and distance between patches (patch lag) can affect predator foraging behavior (Hines et al. 2009). Fragmented seagrass may not be able to provide much protection from generalist predators such as blue crabs, especially if they feed efficiently at patch edges (Laurance and Yensen 1991). Despite little evidence for seagrass as a refuge from predation from this study, *Mya* are more likely to be found in seagrass than all other shallow-water habitat types in lower Chesapeake Bay (Chapter 2), indicating that dense, contiguous seagrass stands may still provide a refuge from predation for *Mya*. Future research examining the effect of seagrass density or patch size on the survival of juvenile *Mya* is warranted.

Rays were not a major source of mortality for *Mya* placed in small (0.25 m^2) plots in the current study; however, ray predation on infauna remains an important phenomenon that is episodic and patchy in nature. Results from experimental manipulations of small patches of prey do not always agree with experiments conducted with larger patches (Thrush et al. 1997, Whitlatch et al. 1997, Long and Hines 2012). Schooling rays respond to relatively large prey patches (75-100 m; Hines et al. 1997), and thus may or may not have been attracted to areas where the small, high-density patches of juvenile *Mya* were placed. However, rays were observed in the area throughout the study, and many wild Mya were found in samples collected in seagrass (pers. obs.), indicating that at least in seagrass, the experimental plots were part of a larger prey patch that would be expected to induce foraging by schooling rays. Future research should focus on examining the spatial scales at which ray and blue crab predation are important for the survival of juvenile *Mya*.

Declines in complex habitat will likely lead to declines in thin-shelled species such as *Mya*. Oyster shell and shell hash provided juvenile *Mya* some protection from predation in mesocosm trials; however, in lower Chesapeake Bay thick layers of shell are uncommon. Loss of many bivalves in the Bay, including oysters (Rothschild et al. 1994, Beck et al. 2011) and large-bodied clams (Dungan et al. 2002, Homer et al. 2011, Chapter 2), will make hard-bottom shell-hash habitat even more rare in the future. Seagrass is also declining in polyhaline regions of Chesapeake Bay (Orth and Moore 1983), resulting in a decrease of many potential sources of highly complex benthic habitat in the Bay and a subsequent decrease in refuge for thin-shelled clams. *Mya* may retain a low-density refuge from predation even with the loss of structurally complex habitats, though a loss of habitat-mediated refuge may result in clam densities that are not sustainable.

Loss of complex habitat in Chesapeake Bay may have little impact on armored species such as *Mercenaria.* We did not see an effect of habitat in the current study, yet in previous research, *Mercenaria* had higher survival in crushed oyster shell habitats than in sand or mud (Arnold 1984). This inconsistency is likely due to the use of larger clams in the current study (~30 mm shell height: SH) as compared to the previous study, which used clams 5-10 mm SH (Arnold 1984). Ontogenetic shifts in functional response may drive spatial distributions of hard-shelled bivalves in Chesapeake Bay, which are most dense in oyster shell habitats (Chapter 2*).* However, the effect of habitat on survival of recruits does not appear to impact population dynamics of *Mercenaria*, which were found in multiple size classes throughout the year in lower Chesapeake Bay. Future research should examine whether complex habitat reduces blue crab encounter rates with small (< 10 mm) *Mercenaria* to determine the relationship between this species and complex habitat over its entire ontogeny.

Relevance for conservation

Understanding the mechanism for bivalve refuges from predation is important in a changing world. Loss of structured habitat such as seagrass, mangroves, coral reefs, and oysters is occurring world-wide (Duarte et al. 2008). There is a current research need for models that can be used to forecast the impacts of global change, such as habitat loss, on predator-prey interactions (Hunsicker et al. 2011). We demonstrated that efforts to understand the effect of habitat loss on predator-prey interactions should consider both prey density and the mechanisms prey use to defend themselves against predators.

Nonlinear predator-prey dynamics can result in catastrophic changes and regime shifts (Hughes et al. 2005, Sinclair and Byrom 2006). An examination of the functional response is key in predicting the result of predator-prey interactions over time, and determining if a population crash can be expected in a food web, potentially leading to a regime shift. For instance, functional responses will be a major factor in determining if a species driven to low abundance is likely to become locally extinct, or if it is likely to persist (Hassell and May 1973). Documenting the functional response of bivalve species with a variety of different physical characteristics can help ecosystem managers decide on which species to focus conservation efforts, since species with a type II functional response are at higher risk of local extinction (Gascoigne and Lipcius 2004, Kramer and Drake 2010), and populations exhibiting a type III functional response are generally more stable over time (Lipcius and Hines 1986, Bellmore et al. 2015, Uszko et al. 2015).

A better understanding of density-dependent predator-prey interactions can be used to inform a variety of ecosystem management decisions. For example, functional responses can be used to determine a threshold density for reintroduction of endangered or depleted species (Sinclair et al. 1998), stock enhancement, (Stoner 2009, Long and Whitefleet-Smith 2013), and pest control (Boukal et al. 2007, Madadi et al. 2011). Effective bivalve seeding efforts that take into account predation may help restore marine bivalves, many of which have experienced severe declines in the recent past (Whetstone and Eversole 1981, Rothschild et al. 1994, Beal and Kraus 2002, Beck et al. 2011). A better understanding of density-dependent predator-prey interactions will assist in the effort to maintain the integrity of marine trophic interactions and the viability of marine resources.

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TABLES

Table 3. ANOVA summary table for field caging study proportional survival data. Three types of caging treatments (full cage, stockade, and uncaged) were placed in three substrate types (mud, sand, and seagrass); all were included in the ANOVA model as fixed factors. Data were box-cox transformed ($\lambda = 0.34$) prior to analysis. Significant p values (at $\alpha = 0.05$ for main effects and $\alpha = 0.20$ for interaction terms) are bolded.

	Df	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
Substrate	2	5.89	2.94	8.66	**0.0004**
Cage	2	22.9	11.45	33.69	**< 0.0001**
Substrate x Cage	4	6.12	1.53	4.5	**0.0025**
Residuals	81	27.52	0.34		

Table 4. ANOVA summary table for mesocosm study proportional survival data. Two species (*Mya arenaria* and *Mercenaria mercenaria*) were offered to blue crabs *Callinectes sapidus* at two densities (low and medium) in tanks with four different habitats (sand, sand with shell hash, sand with oyster shell halves, and sand with live seagrass); all were included in the ANOVA model as fixed factors. Data were box-cox transformed ($\lambda = 0.91$) prior to analysis. Significant p values (at $\alpha = 0.05$ for main effects and $\alpha = 0.20$ for interaction terms) are bolded.

	Df	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
Species	1	2.03	2.03	14.87	**0.0002**
Density	1	0.54	0.54	3.97	**0.05**
Habitat	3	0.75	0.25	1.83	0.15
Species x Density	1	1.03	1.03	7.51	**0.01**
Species x Habitat	3	0.96	0.32	2.35	**0.08**
Density x Habitat	3	0.28	0.09	0.69	0.56
Species x Density x Habitat	3	0.25	0.08	0.62	0.60
Residuals	80	10.93	0.14		

Table 5. ANOVA summary table for handling time of blue crabs *Callinectes sapidus* feeding on juvenile clams in mesocosm study. Two species (*Mya arenaria* and *Mercenaria mercenaria*) were offered to blue crabs at two densities (low and medium) in tanks with four different habitats (sand, sand with shell hash, sand with oyster shell halves, and sand with live seagrass); all were included in the ANOVA model as fixed factors. Data were fourth-root transformed prior to analysis. Significant p values (at $\alpha = 0.05$ for main effects and $\alpha = 0.20$ for interaction terms) are bolded.

	Df	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
Species	1	0.25	0.25	2.87	0.10
Density	1	0.38	0.38	4.28	**0.05**
Habitat	3	0.33	0.11	1.23	0.32
Species x Density	1	0.002	0.002	0.03	0.88
Species x Habitat	3	0.53	0.18	2.01	**0.13**
Density x Habitat	3	0.24	0.08	0.91	0.45
Species x Density x Habitat	3	0.07	0.02	0.25	0.86
Residuals	32	2.84	0.09		

Table 6. ANOVA summary table for search time of blue crabs *Callinectes sapidus* feeding on juvenile clams in mesocosm study. Two species (*Mya arenaria* and *Mercenaria mercenaria*) were offered to blue crabs at two densities (low and medium) in tanks with four different habitats (sand, sand with shell hash, sand with oyster shell halves, and sand with live seagrass); all were included in the ANOVA model as fixed factors. Data were fourth-root transformed prior to analysis. Significant p values (at α = 0.05 for main effects and α = 0.20 for interaction terms) are bolded.

	Df	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
Species	1	0.06	0.06	0.69	0.41
Density	1	0.93	0.93	10.1	**0.003**
Habitat	3	0.08	0.03	0.31	0.08
Species x Density	1	1.05	1.05	11.38	**0.002**
Species x Habitat	3	0.31	0.1	1.13	0.35
Density x Habitat	3	0.41	0.14	1.47	0.24
Species x Density x Habitat	3	0.58	0.19	2.08	**0.12**
Residuals	32	2.95	0.09		

Table 7. ANOVA summary table for encounter rate of blue crabs *Callinectes sapidus* feeding on juvenile clams in mesocosm study. Two species (*Mya arenaria* and *Mercenaria mercenaria*) were offered to blue crabs at two densities (low and medium) in tanks with four different habitats (sand, sand with shell hash, sand with oyster shell halves, and sand with live seagrass); all were included in the ANOVA model as fixed factors. Data were fourth-root transformed prior to analysis. Significant p values (at $\alpha = 0.05$ for main effects and $\alpha = 0.20$ for interaction terms) are bolded.

	Df	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
Species	1	0.03	0.03	0.07	0.79
Density	1	2.33	2.33	6.46	**0.02**
Habitat	3	1.28	0.43	1.19	0.33
Species x Density	1	0.34	0.34	0.95	0.34
Species x Habitat	3	0.70	0.23	0.65	0.59
Density x Habitat	3	1.38	0.46	1.27	0.30
Species x Density x Habitat	3	0.58	0.19	0.54	0.66
Residuals	32	11.53	0.36		

FIGURES

Figure 8. Size frequency histograms of *Mercenaria mercenaria* (left) and *Mya arenaria* (right) in lower Chesapeake Bay. Samples were collected in spring (a-b), summer (c-d), and fall (e-f) for two years starting in fall 2011. Size classes (bins) are expressed as biomass (g AFDW m^{-2}) for *Mercenaria* and shell length (mm) for *Mya*. Data from Glaspie and Seitz (*in prep*).

Figure 9. Map of caging sites near the mouth of the York River, VA. Thick black lines represent areas where cages were placed, all of which had interspersed seagrass, sand, and mud.

Figure 10. Survival of juvenile *Mya arenaria* exposed to a natural suite of predators near the mouth of the York River, VA. Shown are mean proportional survival (± 1 SE) after 5 d in the field. Bivalves were placed in full cages (full), stockades, or uncaged plots. Plots were in different habitats (substrate, denoted by different color bars). There were n = 10 replicates for each cage type-substrate combination.

Figure 11. Foraging success for crabs feeding on clams in different habitats. Proportion of the laboratory mesocosm trials in which all (black), some (partial, gray), or none (white) of the *Mya arenaria* clams were eaten by crabs. Proportions are shown for low and medium densities of prey in a) sand, b) shell, c) oyster, and d) seagrass.

Figure 12. Density-dependent predation in different habitats. Mean juvenile *Mya arenaria* and *Mercenaria mercenaria* proportional survival (± 1 SE) in mesocosms when exposed to blue crab predation in a) sand, b) shell hash, c) oyster shell, and d) seagrass. Solid black lines are mean proportional survival for *Mya* at two initial densities of 4 and 16 per tank, and dashed black lines are mean proportional survival for *Mercenaria* at two initial densities of 4 and 11 per tank.

Figure 13. Behavior of blue crab *Callinectes sapidus* feeding on juvenile *Mya arenaria* and *Mercenaria mercenaria*. Shown are means (± 1 SE) of a) handling time for crabs feeding on *Mya*, b) handling time for crabs feeding on *Mercenaria*, c) search time for crabs feeding on *Mya*, d) search time for crabs feeding on *Mercenaria*, e) encounter rate for crabs feeding on *Mya*, and f) encounter rate for crabs feeding on *Mercenaria*. Lines of different colors and patterns represent different habitat types, and means were calculated from n = 3 trials.

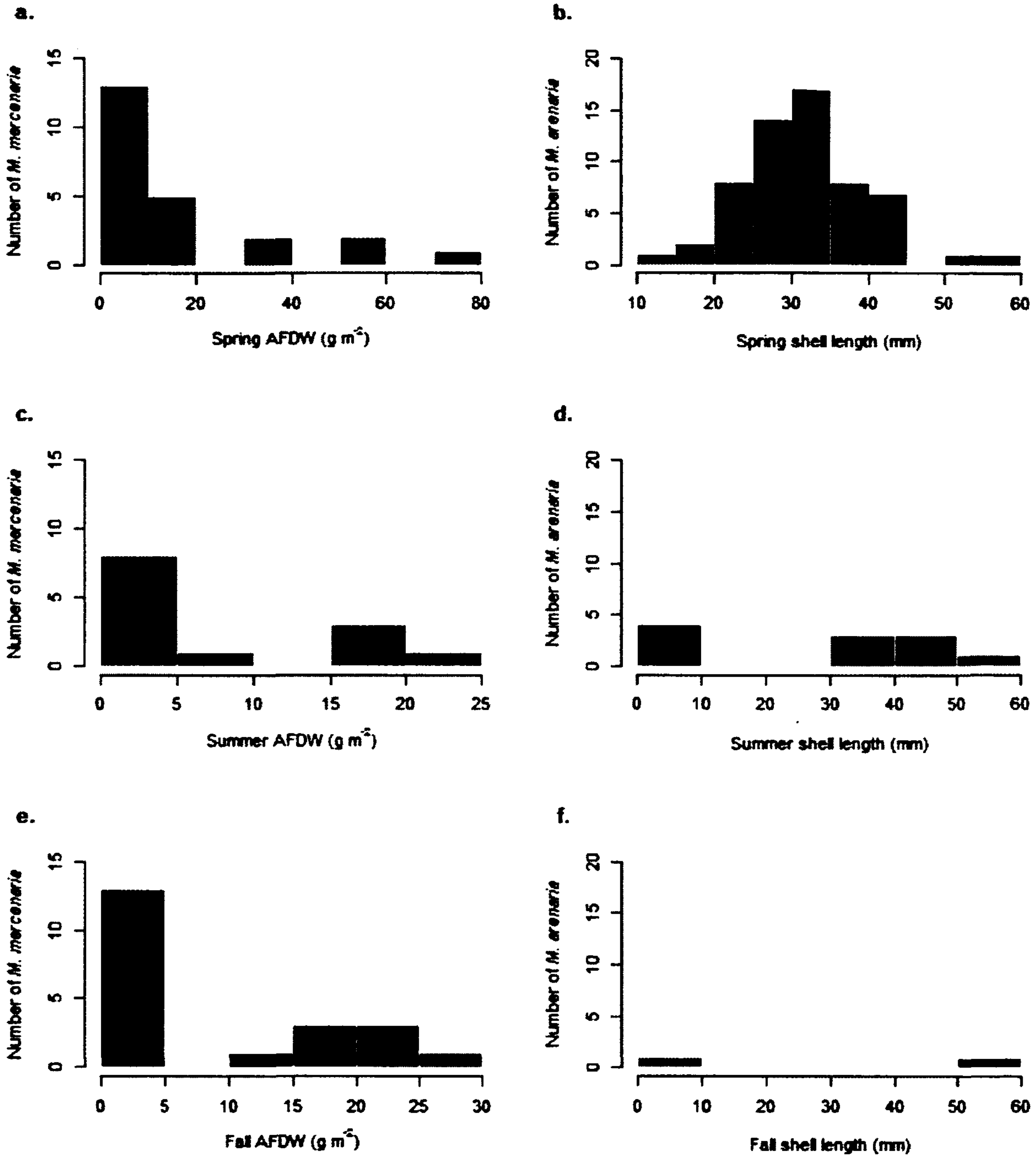

Figure 8. Size frequency histograms of *Mercenaria mercenaria* (left) and *Mya arenaria* (right) in lower Chesapeake Bay.

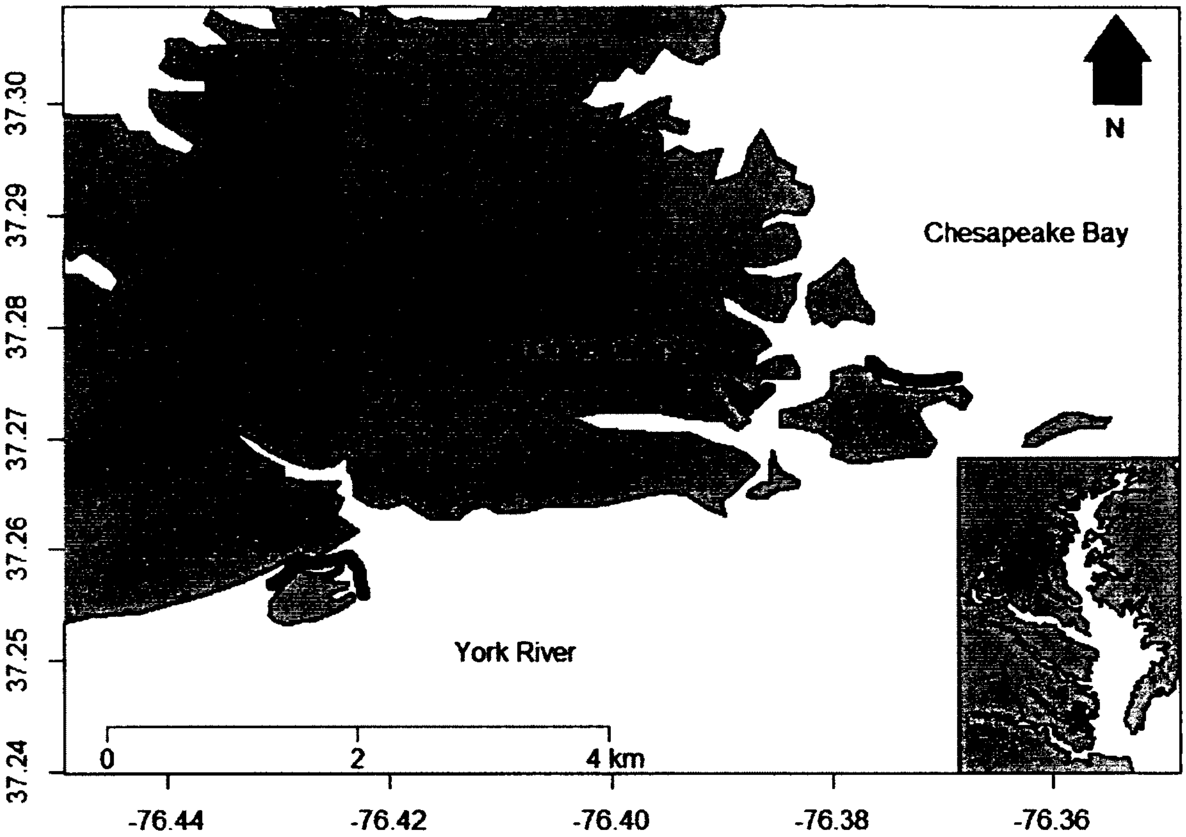

Figure 9. Map of caging sites near the mouth of the York River, VA.

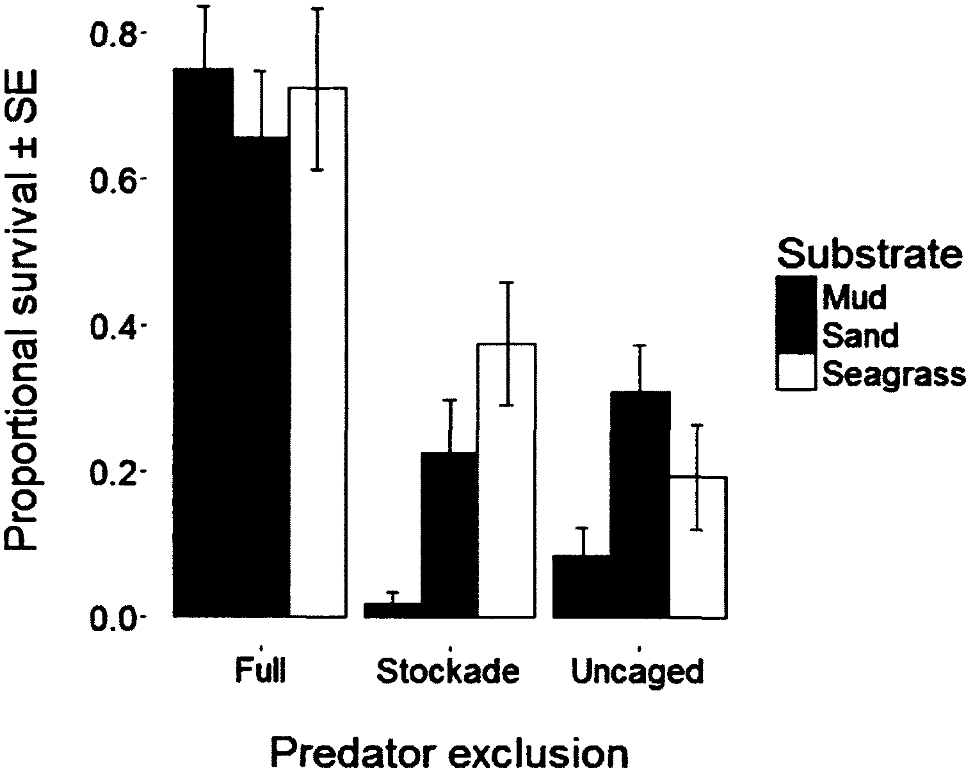

Figure 10. Survival of juvenile *Mya arenaria* exposed to a natural suite of predators near the mouth of the York River, VA.

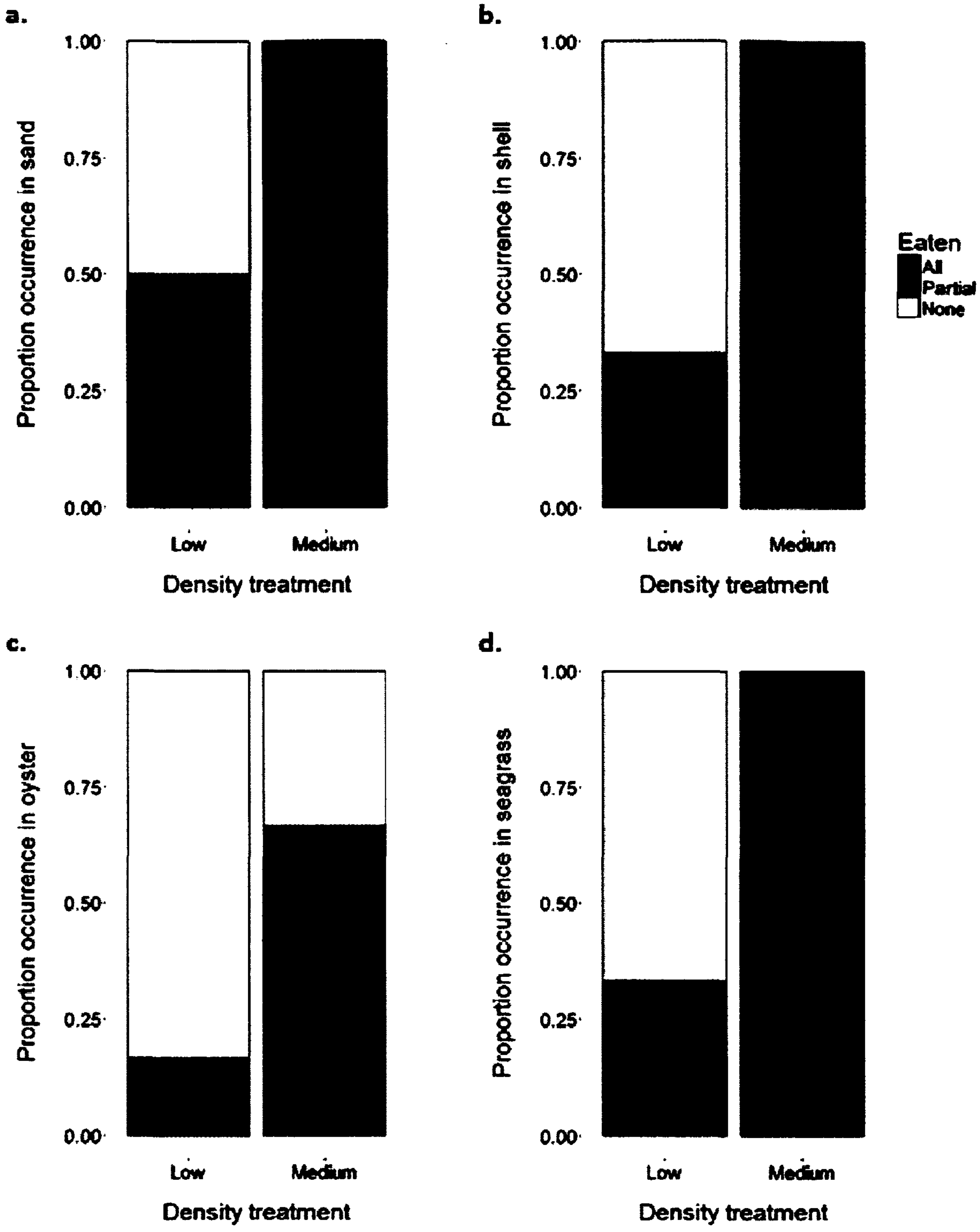

Figure 11. Foraging success for crabs feeding on clams in different habitats.

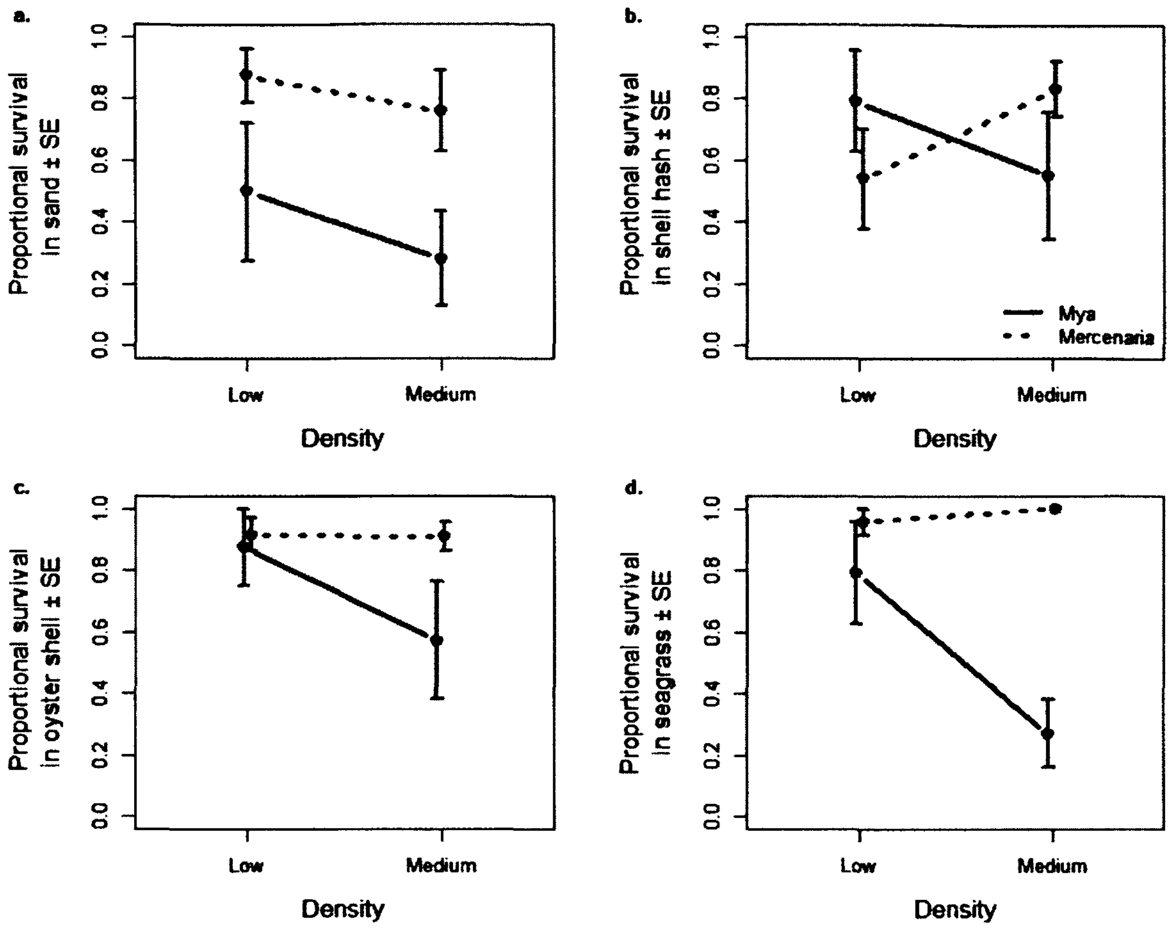

Figure 12. Density-dependent predation in different habitats.

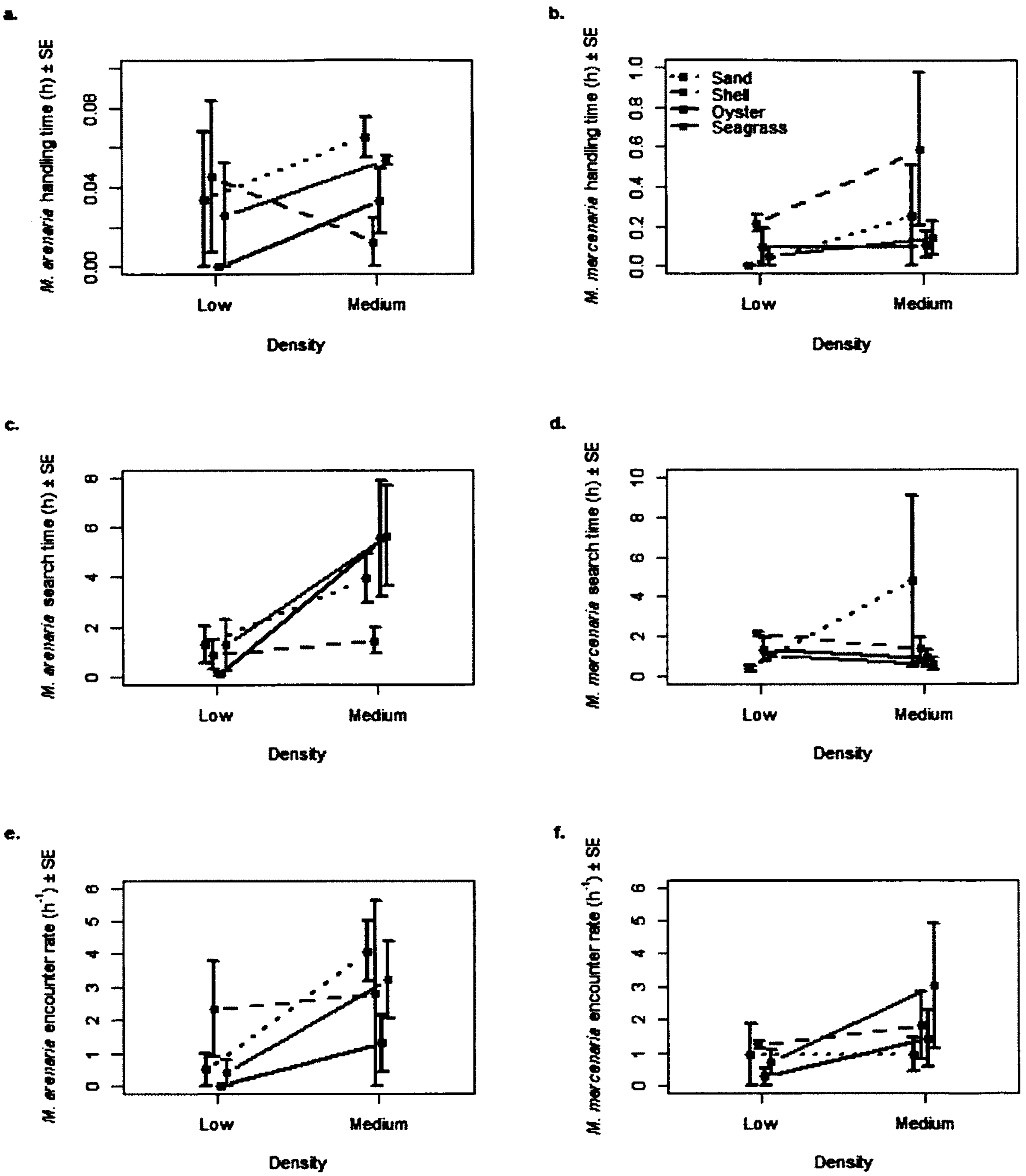

Figure 13. Behavior of blue crab Callinectes sapidus feeding on juvenile *Mya arenaria* and *Mercenaria mercenaria*.

APPENDIX II

Supplementary Table 16. Summary of Tukey HSD results for the caging study interaction term between substrate and cage type. For each pairwise comparison, 95% confidence intervals (CI) and Bonferroni-adjusted p values are presented. Data were box-cox transformed ($\lambda = 0.34$) prior to analysis and are not back-transformed. Only interactions with significant p values at $\alpha = 0.20$ are shown.

Comparison	*Difference*	*Lower CI*	*Upper CI*	*Adjusted p value*
Mud x Stockade-Mud x Full	-1.9	-2.5	-1.29	< 1.0E-7
Sand x Stockade-Mud x Full	-1.16	-1.76	-0.55	8.00E-07
Seagrass x Stockade-Mud x Full	-0.93	-1.54	-0.33	0.00013
Mud x Uncaged-Mud x Full	-1.64	-2.25	-1.03	< 1.0E-7
Sand x Uncaged-Mud x Full	-1.15	-1.76	-0.55	9.00E-07
Seagrass x Uncaged-Mud x Full	-1.3	-1.91	-0.69	< 1.0E-7
Mud x Stockade-Sand x Full	-1.84	-2.49	-1.18	< 1.0E-7
Sand x Stockade-Sand x Full	-1.1	-1.75	-0.44	2.00E-05
Seagrass x Stockade-Sand x Full	-0.87	-1.53	-0.22	0.00154
Mud x Uncaged-Sand x Full	-1.58	-2.23	-0.93	< 1.0E-7
Sand x Uncaged-Sand x Full	-1.09	-1.75	-0.44	2.10E-05
Seagrass x Uncaged-Sand x Full	-1.24	-1.89	-0.59	9.00E-07
Mud x Stockade-Seagrass x Full	-1.99	-2.62	-1.35	< 1.0E-7
Sand x Stockade-Seagrass x Full	-1.25	-1.88	-0.61	4.00E-07
Seagrass x Stockade-Seagrass x Full	-1.02	-1.66	-0.39	5.10E-05
Mud x Uncaged-Seagrass x Full	-1.73	-2.36	-1.09	< 1.0E-7
Sand x Uncaged-Seagrass x Full	-1.24	-1.88	-0.61	4.00E-07
Seagrass x Uncaged-Seagrass x Full	-1.39	-2.02	-0.75	< 1.0E-7
Sand x Stockade-Mud x Stockade	0.74	0.14	1.34	0.005
Seagrass x Stockade-Mud x Stockade	0.96	0.37	1.56	4.60E-05
Sand x Uncaged-Mud x Stockade	0.74	0.15	1.34	0.004
Seagrass x Uncaged-Mud x Stockade	0.6	0	1.19	0.05
Mud x Uncaged-Seagrass x Stockade	-0.71	-1.3	-0.11	0.01

Supplementary Table 17. Summary of Tukey HSD results for the mesocosm study proportional mortality interaction term between species and density. For each pairwise comparison, 95% confidence intervals (CI) and Bonferroni-adjusted p values are presented. Data were box-cox transformed ($\lambda = 0.91$) prior to analysis and are not back-transformed. Only interactions with significant p values at $\alpha = 0.20$ are shown.

Comparison	*Difference*	*Lower CI*	*Upper CI*	*Adjusted p value*
Mya x medium-Mya x low	0.36	0.08	0.64	0.007
Mya x medium-Mercenaria x low	0.44	0.16	0.72	0.0005
Mya x medium-Mercenaria x medium	0.5	0.22	0.78	0.0001

Supplementary Table 18. Summary of Tukey HSD results for the mesocosm study bivalve proportional mortality interaction term between species and habitat. For each pairwise comparison, 95% confidence intervals (CI) and Bonferroni-adjusted p values are presented. Data were box-cox transformed ($\lambda = 0.91$) prior to analysis and are not back-transformed. Only interactions with significant p values at $\alpha = 0.20$ are shown.

Comparison	*Difference*	*Lower CI*	*Upper CI*	*Adjusted p value*
Mya x sand-Mercenaria x oyster	0.56	0.09	1.03	0.01
Mya x seagrass-Mercenaria x oyster	0.42	-0.05	0.89	0.12
Mercenaria x sand-Mya x sand	-0.46	-0.93	0.01	0.06
Mercenaria x seagrass-Mya x sand	-0.65	-1.12	-0.18	0.001
Mercenaria x seagrass-Mya x seagrass	-0.5	-0.97	-0.03	0.03

Supplementary Table 19. Summary of Tukey HSD results for the mesocosm study *Callinectes sapidus* handling time interaction term between species and habitat. For each pairwise comparison, 95% confidence intervals (CI) and Bonferroni-adjusted p values are presented. Data were fourth-root transformed prior to analysis and are not back-transformed. Only interactions with significant p values at $\alpha = 0.20$ are shown.

Comparison	*Difference*	*Lower CI*	*Upper CI*	*Adjusted p value*
shell x Mercenaria-oyster x Mya	0.54	-0.02	1.1	0.06
shell x Mercenaria-shell x Mya	0.47	-0.09	1.02	0.15
shell x Mercenaria-sand x Mercenaria	0.46	-0.1	1.02	0.17

Supplementary Table 20. Summary of Tukey HSD results for the mesocosm study *Callinectes sapidus* search time interaction term between species and density. For each pairwise comparison, 95% confidence intervals (CI) and Bonferroni-adjusted p values are presented. Data were fourth-root transformed prior to analysis and are not back-transformed. Only interactions with significant p values at α = 0.20 are shown.

Comparison	*Difference*	*Lower CI*	*Upper CI*	*Adjusted p value*
Mya x med-Mya x low	0.57	0.24	0.91	0.0003
Mya x med-Mercenaria x low	0.35	0.02	0.69	0.04
Mercenaria x med-Mya x med	-0.37	-0.70	-0.03	0.03

Supplementary Table 21. Summary of Tukey HSD results for the mesocosm study *Callinectes sapidus* search time interaction term between species, density, and habitat. For each pairwise comparison, 95% confidence intervals (CI) and Bonferroni-adjusted p values are presented. Data were fourth-root transformed prior to analysis and are not back-transformed. Only interactions with significant p values at α = 0.20 are shown.

Comparison	*Difference*	*Lower CI*	*Upper CI*	*Adjusted p value*
shell x Mercenaria x low-oyster x Mya x low	0.77	-0.15	1.69	0.18
oyster x Mya x med-oyster x Mya x low	1.04	0.12	1.96	0.02
sand x Mya x med-oyster x Mya x low	0.96	0.04	1.88	0.03
seagrass x Mya x med-oyster x Mya x low	1.06	0.14	1.98	0.01

CHAPTER 4

The perfect storm: Extreme weather and predators drive phase shift in dominant bivalve

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Cite as: Glaspie, C. N., Seitz, R. D., and Lipcius, R. N. *In prep.* The perfect storm: Extreme weather and predators drive phase shift in dominant Chesapeake Bay bivalve.

SUMMARY

Extreme weather events are expected to increase in frequency, duration, and severity due to anthropogenic climate change, and they have been implicated in ecosystem phase shifts in terrestrial and marine systems. As these events become more severe, it is necessary to understand their effects on ecosystem changes. Tropical storm Agnes in 1972 was a 100-year storm that reduced salinity and increased sedimentation throughout Chesapeake Bay, and was suspected of altering long-term ecosystem dynamics. Here we show that Agnes resulted in a phase shift for the soft-shell clam *Mya arenaria*, which was once a biomass dominant in Chesapeake Bay. Tropical storm Agnes caused extremely low salinity throughout the Bay and a massive die-off of bivalves, including *M. arenaria*. This storm altered predator-prey dynamics between *M. arenaria* and the blue crab *Callinectes sapidus*, shifting from a system controlled from the bottom-up by prey resources to a system controlled from the top-down by predator pressure on bivalves. Predation by *C. sapidus* is sufficient to sustain the low-density stable state where *M. arenaria* densities hover 40 years later. Two species may exhibit nonlinear dynamics that result in phase shifts, and extreme weather events may serve as a natural pulse stressor, triggering the phase shift. Considering the frequency of stochastic storm events and the preponderance of multispecies interactions exhibiting nonlinear dynamics, phase shifts are likely much more common than ecological literature suggests. Identification of species that are most at risk to shifts in state will help preserve communities that are resilient or resistant to extreme climate events.

TEXT

Extreme weather events are costly, and are likely to become even costlier with predicted increases in the intensity and frequency of extreme events due to anthropogenic climate change [1,2]. In the US alone, there were 59 climate disasters exceeding $1 billion USD between 2010 and 2015 [3]. When examining the cost of extreme weather, ecological impacts are rarely considered, even though the impacts of such events on the ecosystem may be enormous [4,5]. Traditionally, the impacts of these ecosystem changes have been hard to quantify, though when they are quantified it becomes clear how valuable ecosystem integrity is for humanity [6].

Understanding the impacts of extreme climate events on ecosystems is essential to make predictions for the future and to prevent unwanted ecological surprises [7]. Biotic interactions such as predator-prey dynamics contain nonlinearities that result in largely unpredictable ecosystem properties [8]. Shifts in predator-prey interactions may occur due to differences between predators and prey in terms of tolerance to stressors [9]. When strong or frequent extreme weather events occur, they may cause mass mortality of one or a few species with low tolerance [10–12]. Such declines in abundance of one or a few species may lead to an alternative stable state [13,14]. Multiple stable states occur when the relative abundances of species within a community are altered due to a perturbation, but persist after the perturbation is finished [8].

Tropical storm Agnes, which reached the Chesapeake Bay watershed the 21st-23rd of June 1972, has long been suspected of resulting in long-term changes for the Bay [15]. Tropical storm Agnes was a 100-year storm that caused sustained, extremely low salinities (Figure 14) and increased sedimentation throughout Chesapeake Bay [16–18]. This storm has been blamed for the loss of seagrass in certain areas of Chesapeake Bay [15], high mortality rates and recruitment failure in oysters *Crassostrea virginica* [19], and declines in abundance of the soft-shell clam *Mya arenaria*. These clams suffered a mass mortality event after the storm due to salinities falling below the species' tolerance limit of 2.5 throughout much of the Bay for at least two weeks after the storm [20,21].

Mya arenaria was abundant enough to support a commercial fishery in Chesapeake Bay prior to 1972 [22], but declined abruptly after Tropical Strom Agnes and now exists in Chesapeake Bay at low abundance (Chapter 2). Attempts to expand a commercial fishery in Virginia waters in the late 1960s (i.e. Haven 1970) were never realized. The commercial fishery for this species in the Maryland portion of the Bay has been rendered non-profitable by recent low abundance of *M. arenaria* [23], resulting in the nearly complete collapse of a fishery valued at an average of over $4 million per year between 1972 and 1994 [24].

The failure of *M. arenaria* to recover from storm-related declines has been attributed to predation, habitat loss, disease, rising temperatures, and overfishing. The upper and lower Chesapeake Bay have different habitats, disease dynamics, climates, and fisheries; therefore, these factors are unable to explain the persistence of *M. arenaria* at low density in both regions [23,25]. In particular, disease has been blamed for recent declines in *M. arenaria* [23]; however, disease is most effective at regulating populations when densities are high, which is not the case for *M. arenaria* [26]. Given this evidence regarding potential drivers for the decline in *M. arenaria*, this study examines the effects of predation on population dynamics of *M. arenaria*. Specifically, we focus on one of the main predators in Chesapeake Bay, blue crabs *Callinectes sapidus* (Chapter 3), which consume juvenile and adult *M. arenaria* [27,28].

We show that tropical storm Agnes in 1972 resulted in a phase shift for *M. arenaria*, which was maintained at low abundance likely due to predation by the blue crab *C. sapidus*. Changepoint analysis identified an abrupt shift in clam abundance in 1972, the year of Tropical Storm Agnes (Figure 15). Before the storm, crab abundance was positively correlated with clam abundance with a lag of 1 y ($r = 0.67$, $p = 0.01$), indicating that each year, clams were feeding juvenile crabs that recruited to the fishery at one year of age. After the storm, clam abundance was negatively correlated with crab abundance with a lag of 2 y ($r = -0.58$, $p = 0.01$), indicating that each year, crabs were consuming juvenile clams that would have recruited to the fishery two years later. This is evidence of a phase shift from a system controlled from the bottom-up by prey resources, to a system controlled from the top-down by predator pressure on prey.

Predator-prey models confirmed the presence of a coexistence low-density steady state at 1.4 clams m^{-2}, providing the theoretical proof-of-concept that *M. arenaria* can exist in a low-density stable state in the face of blue crab predation. Trajectories approached a steady state near the specified carrying capacity (200 clams m^{-2}), or they approached a steady state at low density (Figure 16a). There was also a third, unstable steady state at 20.9 clams m^{-2} from which trajectories diverged Figure 16b).

In the field, juvenile *M. arenaria* exposed to predators suffered an increase in mortality of 76.6% as compared to caged individuals (Chapter 3). Predator exclusion treatments confirmed that blue crabs were likely responsible for most of the mortality of juvenile *M. arenaria* (Chapter 3). Mortality rates predicted by the model were very similar to mortality rates observed in the field if crab densities were 4.8 m^{-2}, which is a typical density for juvenile crabs in the summer months (Wood in prep).

Predator-prey models with these two species alone are capable of reproducing observations of clam densities and mortality rates, consistent with the idea that blue crabs are the main driver of *M. arenaria* population dynamics. The low-density steady state predicted by the predator prey model is similar to observed densities of *M. arenaria* in the Chesapeake Bay; adult *M. arenaria* persist in the upper and lower Chesapeake Bay at average densities of 0.35 m^{-2} and 3.41 m^{-2}, respectively, despite high recruitment (Seitz et al. in prep). It is likely that high recruitment is due to a few remaining high-density populations of adults that persist in structured habitat such as dense seagrass (Seitz et al. in prep), which act as sources of juveniles to other habitats that support the low densities predicted by the model and observed by Seitz et al. (in prep).

The observations, theory, and mechanistic basis suggest that *M. arenaria* was subjected to a storm-driven phase shift to low abundance, which has been maintained by blue crab predation. As extreme weather events become more common with climate change, it is important to examine the potential for such perturbations to produce phase shifts that may permanently change basin-scale trophic dynamics. Evidence for storm-driven phase shifts in coral reefs [14], kelp ecosystems [13], and soft-sediment communities (current study) suggest that management of these ecosystems should include an examination of nonlinear interactions and the potential for phase shifts. Identification of species that are most at risk to shifts in state will help preserve communities that are resilient or resistant to extreme weather events, minimizing ecological and economic losses.

METHODS

Changepoint analysis of time series was conducted in R statistical software (v. 3.0.2) using the changepoint package [29] on *Mya arenaria* landings (NMFS Commercial Landings Database) and adult female *Callinectes sapidus* abundance (VIMS trawl survey) in Chesapeake Bay from 1955-1994, with an AIC penalty and using the segment neighbor algorithm [30,31]. This time period was chosen for analysis because it begins when *M. arenaria* landings data first became available and ends before the slow decline in landings post-1994, when the fishery began to collapse.

Predator-prey ordinary differential equation (ODE) models were modified to include a type III functional response and a constant density of predators:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - f(N)P$$

$$\frac{dP}{dt} = P$$

where N is the density of prey, P is the density of predators, r is the intrinsic per capita growth rate, K is the carrying capacity, and $f(N)$ takes the form of a type III functional response:

$$\text{Type III: } f(N) = \frac{N^2bT}{1+cN+bT_hN^2}$$

where T is the time available for foraging, T_h is the handling time, and b and c are components of the attack rate in a type III response [32,33].

Models were parameterized using data from the literature as follows: P = 0.06 m^{-2} (Maryland DNR Fisheries Service Statistics), r = 1.75 yr^{-1} [34], K = 200 m^{-2} [35], T = 1 yr, T_h

= 0.001483 yr [36], b = 26.29743 yr^{-1} [36], and c = 0.143 [36]. Models were analyzed for steady states. To examine mortality rates, we solved the equation for number consumed:

$$N_E = N - f(N)\,P$$

where N_E = the number of clams eaten calculated for a period of 5 days at an initial density of N = 48 m^{-2} to match the field predation experiments (Chapter 3). We then calculated mortality as:

$$M = \frac{N - N_E}{N} * 100\,\%$$

where M = percent mortality. Density of predators P was allowed to vary to achieve M = 76.6%, and the resultant predator density that achieved observed mortality rates of juvenile *M. arenaria* was compared to published juvenile blue crab densities for Chesapeake Bay.

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AUTHOR CONTRIBUTIONS

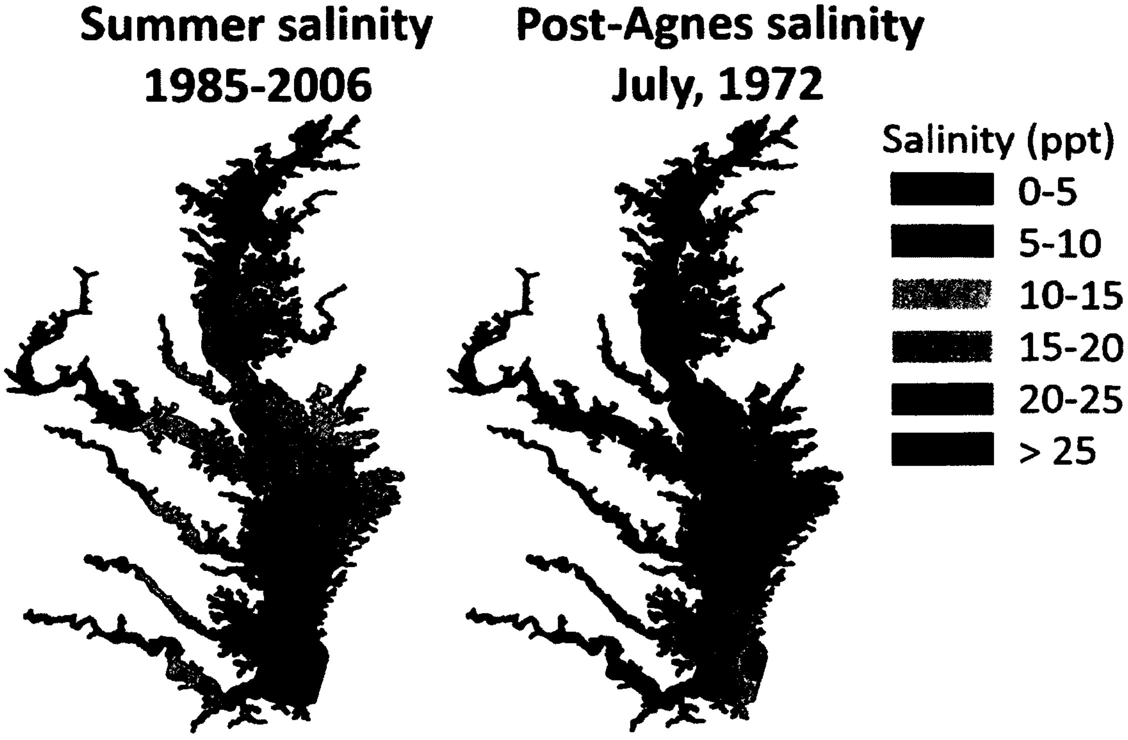
CNG performed the analysis and wrote the manuscript. CNG, RDS, and RNL contributed substantially to study conception and design, interpretation of the data, and manuscript revisions.

FIGURES

Figure 14. Salinity profiles for average summer (left) and post-Agnes (right) conditions. Post-Agnes salinities were measured over the period June 29 – July 3, 1972 [16]. Average salinity profile obtained from Chesapeake Bay Program [36].

Figure 15. Time series for *Mya arenaria* landings (red) and adult female blue crab abundance (blue). Blue crab abundances are log transformed means per tow. Vertical dashed line represents Tropical Storm Agnes (1972), and the location of the changepoint from time series analysis. Data sources: *Mya arenaria* landings (NMFS Commercial Landings Database), adult female *Callinectes sapidus* abundance (VIMS trawl survey).

Figure 16. Slope field diagrams for predator-prey models. Diagrams show trajectories (in different colors) representing different initial densities of *Mya arenaria* for a) the full vector field (with trajectories converging at carrying capacity and a near-zero steady state) and b) a zoomed-in view of the low-density stable steady state at 1.4 clams m^{-2} and an unstable steady state at 20.9 clams m^{-2}. Short red lines represent slopes of trajectories at regularly spaced points.



Summer salinity 1985-2006

Post-Agnes salinity July, 1972

Figure 14. Salinity profiles for average summer (left) and post-Agnes (right) conditions.

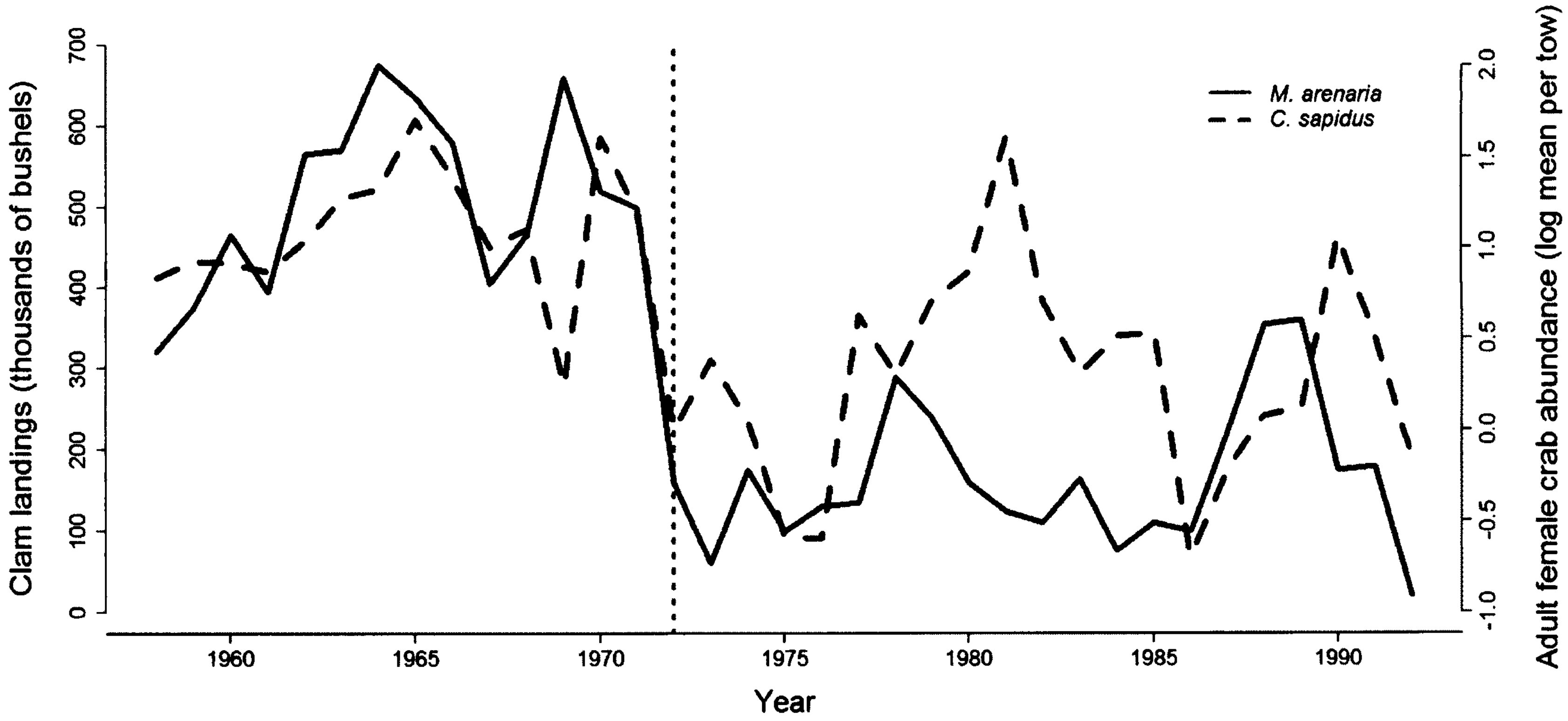


Figure 15. Time series for *Mya arenaria* landings (red) and adult female blue crab abundance (blue).

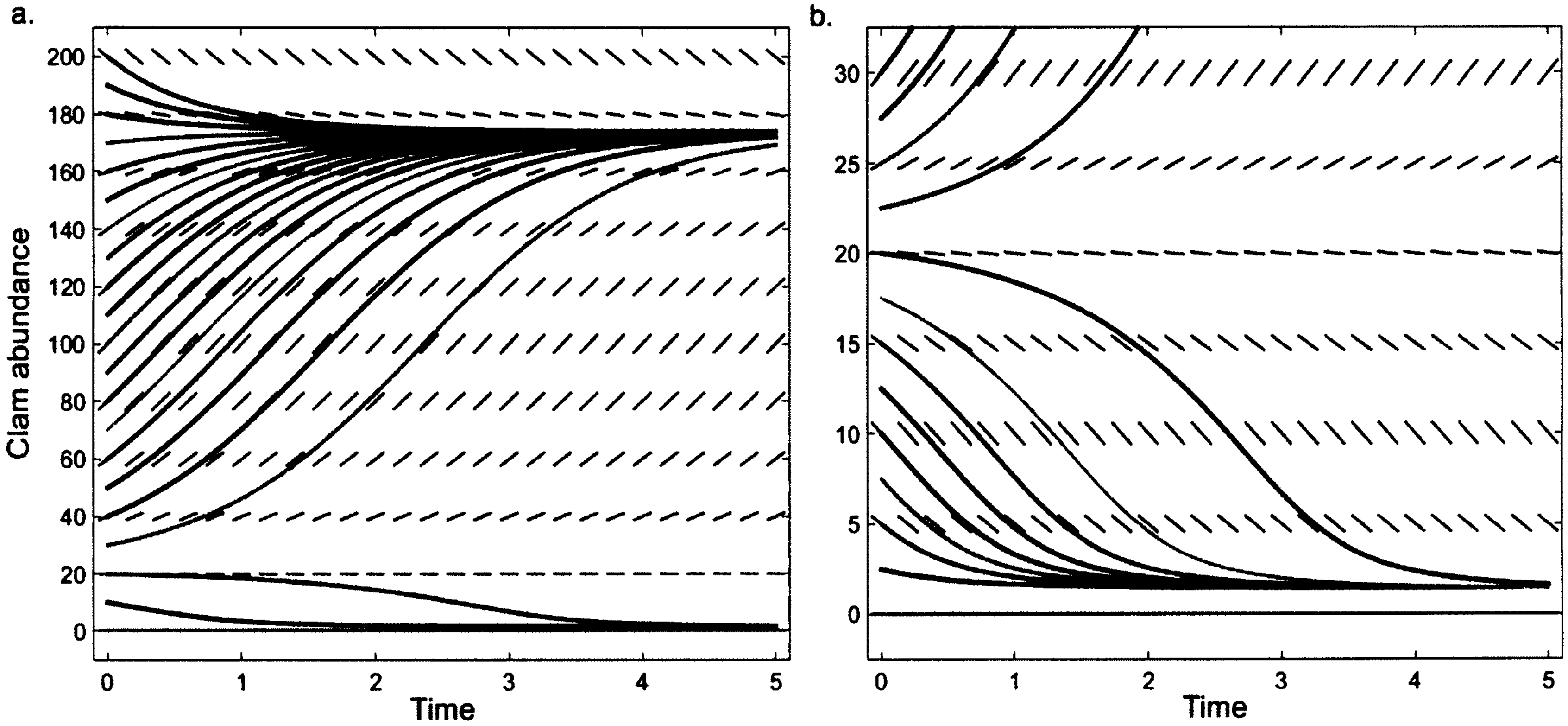


Figure 16. Slope field diagrams for predator-prey models.

CHAPTER 5

Acidification alters predator-prey interactions of blue crab *Callinectes sapidus* and soft-shell clam *Mya arenaria*

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ABSTRACT

Acidification due to anthropogenic CO_2 pollution will exacerbate episodic or persistent acidification that already occurs in coastal environments worldwide. Acidification impacts physiology, morphology, and behavior of coastal and estuarine species, resulting in altered metabolism, shell thinning, and impaired cognition. While these factors often decrease the fitness of individual species, the degree to which predator-prey interactions will be impacted is largely unknown. In this mesocosm study, we examined the effect of CO_2 acidification on crab-bivalve predator-prey interactions, in particular clam growth, clam behavior, clam mortality due to predation, and crab behavior. *Mya arenaria* were grown in CO_2-acidified water (pH 7.2) or ambient conditions (pH 7.8) for 30 d to examine growth and mortality. To determine that effect of acidification on clam responsiveness to mechanical disturbance, a probe was slowly moved towards clams until they ceased pumping, and the distance between the probe and the clam's siphon was noted. Clams were exposed to predation by blue crabs *Callinectes sapidus,* which were held under acidified or ambient conditions for 48 h. Infrared videography was used to measure blue crab handling time, search time, and encounter rate for each trial. Acidified clams had lower shell weights than ambient clams, indicating that shell dissolution occurred. Acidification reduced the responsiveness of *M. arenaria* to a mechanical disturbance that simulated an approaching predator. There was no significant difference in clams consumed between acidified or ambient treatments. However, crab behavior was altered: as compared to ambient trials, crabs in acidified trials had higher encounter rate, lower search time, and increased occurrence of crabs eating only a portion of the prey available. Acidification-induced changes in food-web structure, driven by altered predator preference, may sever the connection between the benthos and upper trophic levels, which could have drastic consequences for ecosystem function and commercial fisheries.

INTRODUCTION

Anthropogenic CO_2 emissions are expected to decrease open ocean pH by 0.3 to 0.4 units by the end of the century in a process known as ocean acidification (Orr et al. 2005, Solomon et al. 2007). In coastal ecosystems, ocean acidification is exacerbated by other anthropogenic and natural processes that lower pH, including runoff from land (especially acid sulfate soil runoff; Dove and Sammut 2013), upwelling (Feely et al. 2008), respiration (Feely et al. 2010), and eutrophication (Wallace et al. 2014). As a result, coastal organisms encounter frequent and often extreme fluctuations in pH, and are expected to be more tolerant of acidification than open-ocean species (Widdicombe & Spicer 2008).

The expectation that coastal species will be more tolerant of acidification than open-ocean species has been challenged, and recent research suggests that acidification impacts physiology, morphology, and behavior of coastal and estuarine species (Briffa et al. 2012, Donohue et al. 2012, Dodd et al. 2015). Major physiological changes in coastal species will include hypercapnia, which has been observed in crustaceans (Spicer et al. 2007, Donohue et al. 2012) and fish (Esbaugh et al. 2012) and may negatively impact metabolic efficiency (Michaelidis et al. 2007, Pane & Barry 2007). Acidification is expected to have negative effects on the morphology of many calcified organisms by inhibiting their ability to precipitate $CaCO_3$ to build their shells (Gazeau et al. 2007). For this reason, bivalve mollusks are expected to be some of the most sensitive organisms to changes in ocean pH, including common coastal bivalves such as oysters and mussels (Gazeau et al. 2007, Hendriks et al. 2010, Amaral et al. 2012a). Acidification alters the behavior of coastal organisms, influencing many processes including settlement behavior (Clements et al. 2016), shelter selection (de la Haye et al. 2011), homing (Devine et al. 2012), and predator-prey interactions (Bibby et al. 2007, Dodd et al. 2015).

The effect of acidification on predator-prey dynamics has been identified as an area of needed research (Parker et al. 2013). The majority of acidification studies on bivalves, and nearly all such studies related to predator-prey dynamics, focus on armored, reef-building species such as oysters or mussels (Parker et al. 2013, Kroeker et al. 2014). The parameters that have traditionally been used to study the effects of acidification on armored bivalves are calcification rate or shell strength, metrics that may not be important for thin-shelled or deep-burrowing bivalves that dominate in many estuaries (Boesch 1977, Hagy 2002, Seitz et al. 2008, Beukema et al. 2010). For these reasons, the impact of acidification on predator-prey interactions involving thin-shelled bivalves is largely unknown.

Two research approaches are necessary to relate the effects of acidification to a community scale: 1) it is necessary to examine the impacts of acidification on a wide range of predator-prey interactions involving species with different life history characteristics; and 2) research should examine acidification-related changes in the parameters of predator-prey interactions. One such parameter is predator handling time (the time a predator spends manipulating or eating a prey item), which is expected to decrease with shell thinning and result in greater mortality for bivalve prey under acidified versus ambient conditions. Another parameter is search time (the amount of time a predator spends foraging, or actively looking for prey), which declines under acidification compared to ambient conditions (Dodd et al. 2015, Glaspie & Seitz in press). A third parameter, encounter rate (the number of prey encounters over the search time), may change due to altered predator or prey behavior in acidified conditions (Cripps et al. 2011, de la Haye et al. 2011, 2012, Devine et al. 2012).

The goal of this study was to examine the effect of acidification on predator-prey interactions involving a thin-shelled, commercial bivalve (the soft-shell clam *Mya arenaria*) and a commercially important crustacean predator (the blue crab *Callinectes sapidus*). This study was conducted in Chesapeake Bay, the largest estuary in the U.S. In Chesapeake Bay, the blue crab is a dominant species that can control prey resources (Eggleston et al. 1992). The blue crab is a generalist predator that grows up to 280 mm carapace width, is found along the Atlantic and Gulf coasts of North America (Williams 1990), and is the main predator of bivalves in Chesapeake Bay (Hines et al. 1990). The soft-shell clam *M. arenaria* is distributed on the east coast of North America from Virginia to Canada in estuarine waters (Baker & Mann 1991), and has been introduced to the west coast of North America from California to Alaska (Strasser 1999). Soft-shell clams comprise a substantial portion of the U.S. commercial mollusk landings, which were worth more than $2.8 billion in 2014 (NMFS 2015). They serve as biomass dominants in their native and introduced ranges (Strasser 1999), and are a preferred prey item for many commercially important species such as blue crabs (Hines et al. 1990, Eggleston et al. 1992). *Mya arenaria* is a deep-burrowing (greater than 30 cm), thin-shelled bivalve that avoids predators by achieving a spatial refuge (Hines & Comtois 1985, Abraham & Dillon 1986).

The objectives of the current study were to: 1) examine the effects of CO_2 acidification on *M. arenaria* mortality and growth; 2) examine the effects of CO_2

acidification on the responsiveness of *M. arenaria* to (mechanical disturbance); 3) quantify the change in predation-related mortality of *M. arenaria* due to CO_2-acidification of the clams and their predators, *C. sapidus*; and 4) quantify the change in handling time, encounter rate, and search time of *C. sapidus* on bivalve prey due to exposure of both predators and prey to CO_2-acidified water. We hypothesized that in comparison to bivalves and crabs exposed to ambient pH conditions: 1) acidified clams would have decreased growth (biomass and shell mass) and increased mortality due to growth in acidified water; 2) acidified clams would exhibit decreased responsiveness to a simulated predator; 3) acidified clams would have higher predation-related mortality when exposed to acidified *C. sapidus*; and 4) blue crabs preying on clams in CO_2-acidified water would have significantly lower handling time and search time, and significantly higher encounter rates.

MATERIALS AND METHODS

Clam growth and mortality

This study was conducted in the Seawater Research Laboratory at the Virginia Institute of Marine Science in Gloucester Point, VA, from June through August 2015. Four tanks (76 x 33 cm) were filled with 8 cm sand and seawater from the York River, VA. Juvenile *M. arenaria* clams collected from the York River were added to each tank, such that tanks contained 74-84 clams of average size 28.48 mm (SD 4.41 mm). Two tanks were maintained at ambient pH with air bubbled through air stones, and two tanks were acidified with CO_2 mixed with air and maintained by an automated controller

(Omega mini panel-mount pH controller, PHCN-201), pH electrode (Omega PHE-1411), and solenoid valve (Grainger Redhat solenoid valve 4EKU5). The pH was gradually lowered from 7.8 to 7.2 over six days and then maintained at 7.2 for three weeks for a total exposure period of four weeks. A pH of 7.2, or a total reduction of 0.6 pH units, is within the moderate range of pH reductions in similar experiments involving bivalves or crustaceans (Donohue et al. 2012, Fernández-Reiriz et al. 2012, Clements et al. 2016).

Bivalves were fed marine microalgae concentrate (Shellfish Diet 1800) twice per day, and water was changed three times per week using filtered water from the York River with ambient temperature and salinity. Temperature, salinity, dissolved oxygen, and pH were measured three times per week using a YSI (Model 85, Yellow Springs Instruments) and a pH probe (Omega PHE-1411). Alkalinity was measured once per week using an Aquarium Pharmaceuticals carbonate hardness test kit. Dead clams in experimental tanks were removed daily and any deaths were noted.

After a total of four weeks in acidified or ambient seawater, 10 clams were randomly chosen from both the acidified and ambient treatments. Clams were measured for shell length (mm), dried in a drying oven for 24 hours, and ashed in a muffle furnace at 550 °C for five hours. Ash-free dry weight (AFDW; dry weight minus ash weight, in g) was calculated as a measure of biomass, and ash weight (g) was calculated as a measure of shell mass. Both biomass and shell mass were standardized by dividing by shell length (g mm^{-1}).

Clam behavior

After four weeks of growth in acidified or ambient conditions, eight clams from each treatment were randomly selected and placed in a tank (76 x 33 cm) filled with 8 cm sand and filtered York River water. Clams were placed one per tank, 4 cm from the tank wall, siphon up, and pushed into the sand so they were completely covered. Clams were allowed time to resume pumping, usually about 15 minutes, before the start of the experiment. At the start of the experiment, to simulate an approaching predator, a metal probe was inserted 2 cm into the sand at the opposite end of the tank from the clam. The probe was slowly moved towards the clam at a rate of 1-2 cm s^{-1} until the clam ceased pumping (a behavior used to avoid predation), at which point the distance between the probe and the siphon (cm) was noted. This process was repeated three times for each clam, and the average distance of pumping cessation was calculated for each individual.

Predator-prey interactions

Callinectes sapidus were collected from the York River via crab pots baited with frozen Atlantic menhaden (*Brevoortia tyrannus*). All crabs were acclimated to the lab for one week or longer and fed fish or clam meat three times a week. Crabs were held individually or in pairs in tanks (76 x 33 cm) where they were exposed to either CO_2-acidified (pH 7.2) or ambient (pH 7.8) water and starved for 48 h prior to the start of the experiment. This time of exposure is long enough to produce a physiological response in other decapod crustaceans (Pane & Barry 2007).

Clams were exposed to blue crab predation in tanks (76 x 33 cm) filled with 8 cm sand and 25 cm water from the York River with ambient temperature and salinity (~ 22.85 and 25.4 °C, respectively). Mesocosm chambers were set up in the same manner as growth tanks, so that tanks were either acidified with bubbled CO_2 or maintained at ambient pH conditions with bubbled air. Treatments and tank positions were randomized. To prevent shock, no animals switched acidification treatments; all animals placed in acidified mesocosm tanks had been previously exposed to acidified water, and all animals placed in ambient mesocosm tanks had been previously exposed to ambient water. Four *M. arenaria* were placed in the sediment with their siphons up, away from the edge of the tank to avoid edge effects and were allowed 24 h to achieve a stable burial depth (Lipcius & Hines 1986). Upon the start of the experiment, a crab was added to the mesocosm and allowed to feed for 48 h. After 48 h, predators were removed and surviving clams were counted. A different crab was used in each trial. There were seven replicates for each treatment (acidic and ambient) with crabs, and three replicate trials for each treatment without predators, which served as controls. No clams died in any predator-free controls, so clam mortality in treatment tanks was assumed to be from crab predation, and the predator-free controls will not be discussed further.

An IR-sensitive video system was used to estimate search time, encounter rate, and handling time. Search time (h) was defined as the total time spent exhibiting foraging behavior, such as probing the sediment with legs or claws or lifting items to mouthparts. Encounter rate (hr^{-1}) was defined as the number of encounters (picking up bivalve) divided by the search time. Handling time (h) was defined as the total time spent manipulating or eating a bivalve, divided by the number of encounters. We also noted the amount of time crabs spent burrowed (h), and time spent exhibiting movements not related to foraging (agitated pacing behaviors or escape attempts).

Statistical design

Mortality was examined using a linear model containing week, treatment, temperature, salinity, dissolved oxygen, pH, and alkalinity. Between-treatment differences in clam biomass and shell mass in week four were examined using bootstrap hypothesis testing with 10,000 simulations. Clam behavior (distance from a disturbance upon cessation of pumping activity), proportion of clams eaten in mesocosm experiments, handling time, encounter rate, and search time were also examined as a two-sample comparisons (acidic versus ambient) using bootstrap hypothesis testing. Confidence intervals (95%) were developed for several variables, including percent of time crabs spent inactive and percent of time crabs spent exhibiting movement not related to foraging. Analysis of the number of mesocosm trials with all of the clams eaten, a portion of the clams eaten, and none of the clams eaten was completed using a chi-square test with Monte Carlo simulation of p values due to the presence of zeros in the contingency table. All analyses were completed using R statistical software (R Core Team 2015).

RESULTS

Clam growth and mortality

Average pH over the course of the study was lower and less variable in the acidified treatment (mean = 7.2, SD = 0.1) than in the ambient treatment (mean = 7.8, SD = 0.2; Figure 17a). The maximum pH observed throughout the course of the experiment was 8.1 in the ambient treatment, and the minimum observed was 6.9 in the acidified treatment. Temperature was fairly consistent among tanks, spiking in the first 10 d due to a heat wave and decreasing to an average of 26.1 °C (SD = 1.0) after the start of week two (Figure 17b). Salinity gradually increased throughout the study, from a minimum salinity of 21.84 to a maximum salinity of 23.65 (Figure 17c). Dissolved oxygen was variable among tanks and unrelated to pH treatments, with a mean concentration of 5.2 mg L^{-1} (SD = 0.6; Figure 17d). Alkalinity was higher in acidified tanks (mean = 10.0 dKH, SD = 0.1) than in ambient tanks (mean = 8.4 dKH, SD = 0.2; Figure 17e).

There was minimal mortality throughout the experiment. The greatest losses occurred 9-14 d after the start of the study, with five clams lost from the acidified treatment and four clams lost from the ambient treatment. Some additional losses (10 clams) occurred in one tank (Ambient 1) during weeks 2-3, after some warm temperatures were observed several days before. Clam mortality did not differ by week or between treatments, and was unrelated to changes in temperature, salinity, dissolved oxygen, pH, and alkalinity ($F_{7,44} = 0.79$, $p = 0.60$, $R^2 = 0.11$). At the end of the experiment, there was no difference in biomass of clams grown in acidified or ambient conditions (p = 0.14). However, there was a difference in shell mass between clams grown in acidified and ambient treatments (p = 0.03; Figure 18).

Clam behavior

Upon exposure to a mechanical disturbance used to simulate a predator (a probe moving through the sand at a steady rate towards a buried clam), clams that had spent four weeks in CO_2-acidified water allowed the probe to get closer before reacting than clams that were grown in ambient conditions (p = 0.01; Figure 19). Clams grown in ambient conditions reacted (be ceasing pumping behavior) when the predator-simulating probe was 29.6 cm away on average (95% CI [17.9, 41.4]), whereas acidified clams did not react until the probe was 11.1 cm away on average (95% CI [6.3, 15.9]).

Predator-prey interactions

There was no difference in average number of clams eaten per tank between acidified and ambient treatments (p = 0.53). The average number of clams eaten per trial in the acidified treatment was 2.9 (SE = 0.5), whereas the average number of clams eaten per trial in the ambient treatment was also 2.9 (SE = 0.7). In the ambient treatment, crabs either ate all of the available clams (occurred 5 times), or none of them (occurred 2 times; Figure 20). In the acidified treatment, crabs either ate all of the acidified clams (occurred 3 times), or a portion of the clams available (occurred 4 times); however, there was never a trial where an acidified crab failed to find and consume at least one acidified clam (Figure 20). There was a significant difference in the frequency of occurrence of these events (all clams eaten, a portion of the clams eaten, and no clams eaten) between the two treatments ($p = 0.04$).

Handling time for crabs preying on clams grown in the ambient treatment was not different from handling time for crabs and clams in the acidified treatment ($p = 0.33$; Figure 21a). Handling time for crabs consuming acidified clams was 0.043 h on average (95% CI [0.019, 0.067]), whereas handling time for crabs consuming ambient clams was 0.053 h on average (95% CI [0.014, 0.091]). The encounter rate for trials with acidified clams was greater than the encounter rate for trials with ambient clams ($p = 0.04$; Figure 21b). The encounter rate for trials with ambient clams was 2.1 clams h^{-1} (95% CI [0.5, 3.8]), whereas the encounter rate for trials with acidified clams was 6.1 clams h^{-1} (95% CI [2.6, 9.5]). The search time for crabs in trials with acidified clams was less than the search time for crabs in trials with ambient clams ($p = 0.05$; Figure 21c). The search time for trials with ambient clams was 1.242 h on average (95% CI [0.558, 1.927]), whereas the search time for trials with acidified clams was 0.534 h on average (95% CI [0.110, 0.959]). The minimum search time in any trial was 0.155 h in an acidified trial, and the maximum search time was 1.984 h in an ambient trial. Acidified crabs spent an average 55% of the time burrowed or resting still (95% CI [25%, 84%]), and ambient crabs spent an average 71% of the time burrowed or resting still (95% CI [50%, 91%]; Figure 22). Acidified crabs spent an average 43% of the time exhibiting agitated, non-foraging related movement patterns or escape behavior (95% CI [13%, 73%]), and ambient crabs spent an average 23% of the time exhibiting non-foraging related movement patterns (95% CI [2%, 44%]; Figure 22).

DISCUSSION

After the grow-out period, there were no differences in clam mortality or biomass between acidified clams and clams grown under ambient conditions, which was contrary to our hypothesis. This is meaningful because there is a need for acidification studies that address the effect of multiple stressors on an organism's survivability (Fabry et al. 2008). Due to the nature of this experiment, which used water directly from the York River and was completed in a laboratory that was not temperature controlled, the clams experienced a heat wave (near the beginning of the experiment), a dry spell (near the beginning of the experiment), a natural drop in pH (for both acidified and ambient treatments, around day 22), and natural fluctuation in dissolved oxygen throughout the experiment. These results indicate that even with exposure to natural stressors found in estuaries, and without the threat of predators, *Mya arenaria* is tolerant to pH 7.2 over the short term.

Clams that spent four weeks in acidified water had lower shell mass than clams grown under ambient conditions, which supported our hypothesis. Shell thinning or weakening has been observed for other shelled mollusks, including bivalves (Amaral et al. 2012b) and gastropods (Bibby et al. 2007). This decrease in shell mass of acidified clams in relation to ambient conditions did not affect the predator's handling time, which was similar for both acidified and ambient clams. However, shell growth and integrity are still important for *M. arenaria*, which must grow quickly to achieve a burial depth refuge from predation (Zaklan & Ydenberg 1997), and must be strong enough to withstand pressure from sediments (Savazzi & Sälgeback 2004, Dorgan 2015). There are likely energetic costs associated with maintaining growth and shell integrity that could not be sustained in acidified conditions.

Clam behavior was altered by growth in acidified conditions. Compared to ambient clams, acidified clams allowed an approaching predator-simulation probe to get 18.57 cm closer before ceasing pumping. Cessation of pumping is a behavior which aids the clam in avoiding detection by predators (Weissburg & Zimmer-Faust 1993, Nakaoka 2000, Hay 2009, Smee & Weissburg 2015). In encounters with blue crabs, this decreased predator avoidance behavior was the likely mechanism behind the encounter rates that were nearly three times higher in acidified trials as compared to ambient trials.

Predator behavior also differed in acidic treatments as compared to ambient treatments, even though this shift in behavior did not manifest in altered consumption rates. Changes in predator behavior included the following: 1) in ambient trials, two crabs failed to eat any *M. arenaria* over the 48-hr trial, an event which was never observed in acidified trials; 2) on four occasions, acidified crabs ate only a portion of the available clams, an event that was never observed with ambient crabs and ambient clams; and 3) acidified crabs spent less time foraging than ambient crabs. This decrease in search time likely compensated for increased encounter rates, leading to no net increase in predator-related mortality for acidified clams as compared to ambient clams.

The results of the current study agree with previous research on crustacean-bivalve predator-prey interactions, suggesting that a decrease in foraging may be a common response of crab predators to acidification. In a similar study, mud crabs *Panopeus herbstii* spent less time before giving up an unsuccessful predation attempt when they were acidified, as compared to controls (Dodd et al. 2015). In a previous experiment examining interactions between Sydney rock oysters *Saccostrea glomerata* that were exposed to acid sulfate soil effluent and mud crabs *Scylla serrata* that were not exposed to acidification, crabs still foraged less when offered acidified oysters as compared to the control (Glaspie & Seitz in press).

Briffa et al. (2012) suggest acidification by CO_2 can influence the behavior of predators in three ways. The first is by making predatory behaviors such as foraging more costly by altering metabolic processes in the predator. Marine crustaceans experience physiological consequences of acidification, including decreased extracellular pH (Donohue et al. 2012), which may influence metabolism and energy budget. However, it is unlikely that crabs did not forage due to increased cost of activity, because in both the current study and Dodd et al. (2015), a decrease in foraging did not coincide with a decrease in other activities such as cleaning, aggressive behaviors, walking, or swimming.

The second way acidification might influence behavior of predators is through the disruption of information-gathering and decision-making processes (Briffa et al. 2012). Low pH reduces the ability of some organisms, such as hermit crabs and reef fish, to sense their environment and make decisions that maximize their fitness (Cripps et al. 2011, de la Haye et al. 2011, 2012, Devine et al. 2012). It is unlikely that the observed changes in crab behavior (i.e. a decrease in foraging behavior and an increased incidence of consuming only a portion of the prey in acidified versus ambient trials) is a result of impaired information-gathering or decision-making processes because this shift in behavior has been observed for both acidified and non-acidified crabs (Glaspie & Seitz in press).

The third proposed way acidification influences predator behavior is through predator avoidance of polluted areas (Briffa et al. 2012). Little is known regarding the avoidance behavior of marine crustaceans exposed to acidification. However, crabs are commonly found in acidified portions of estuaries experiencing acid-sulfate soil acidification (Russell & Helmke 2002, Amaral et al. 2011). In the current study, this mechanism is an unlikely cause of the observed alterations in blue crab behavior because acidified blue crabs did not spend a significantly greater amount of time pacing or attempting to escape than ambient crabs.

We propose a fourth scenario by which predator behavior may be influenced by CO_2 acidification: predators avoid prey that is lower quality due to acidification, due to changes in optimal foraging behavior. In this scenario, the reason for a decrease in crab foraging activity when crabs are presented with acidified prey is a lower nutritional value of acidified clams. Extreme stress, such as changes in temperature, salinity, or acidification, may lead to changes in prey tissue condition (Mitra & Flynn 2005). In particular, acidification that leads to bivalve shell dissolution, as observed in the current study, may necessitate allocation of more resources to shell growth and less to tissue maintenance (Lannig et al. 2010, Hiebenthal et al. 2012, 2013). The stress that *M. arenaria* experience under acidified conditions may reduce tissue quality to the point that blue crabs *C. sapidus* are not willing to exert the energy it would take to consume acidified clams (Glaspie & Seitz in press). In this case, predator information-gathering processes are unaffected; crabs could have assessed prey quality from the first prey item they consumed, since all acidified crabs consumed at least one acidified clam.

Future research should focus on the impact of acidification on prey quality and the implications for predator fitness. Current research on the impacts of acidification on prey quality is confined to zooplankton-phytoplankton predator-prey systems in marine (Rossoll et al. 2012) and aquatic (Locke & Sprules 2000) environments. Zooplankton predators fed low-quality, acidified prey had lower fecundity than zooplankton fed non-acidified prey (Locke & Sprules 2000, Rossoll et al. 2012). Fully-crossed acidification feeding trials and multiple-choice feeding experiments are a necessary next step in elucidating the mechanisms behind decreased foraging rates observed for crabs offered acidified prey.

A decrease in blue crab foraging on clams experiencing estuarine and atmospheric acidification will result in unpredictable changes in coastal marine food webs. Acidification-induced changes in food web structure, driven by altered predator preference, may sever the connection between the benthos and upper trophic levels. In estuaries, which are some of the most productive areas in the world, truncation of the food web could have drastic consequences for ecosystem function and commercial fisheries. Elucidating the mechanisms behind changes in trophic interactions due to acidification is the first step in making viable predictions and conservation actions that may preserve these ocean resources for future generations.

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FIGURES

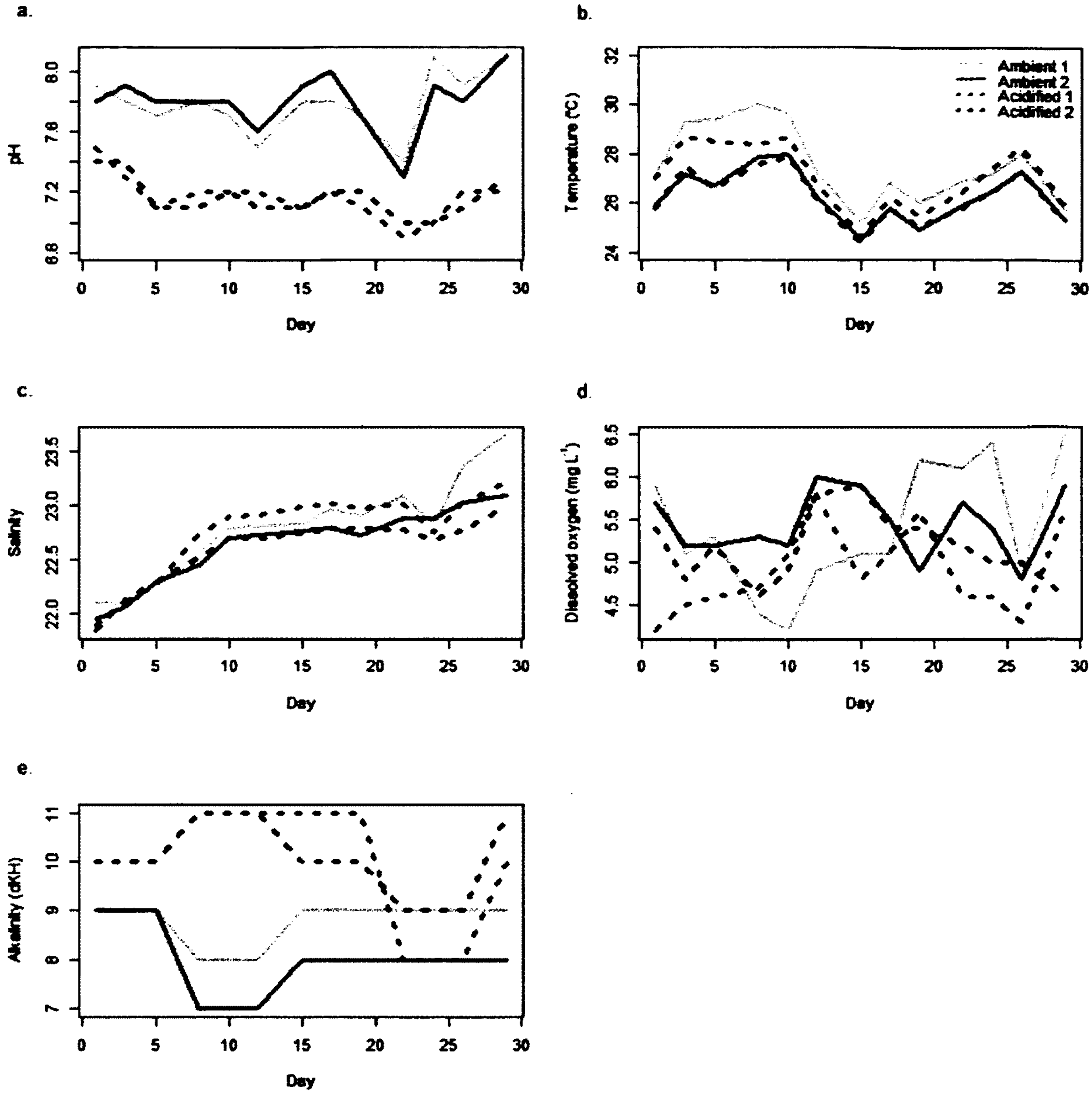

Figure 17. Environmental variables over the course of the 4-week grow-out period for *Mya arenaria*. Measurements were taken 3 times per week for a) pH, b) temperature, c) salinity, and d) dissolved oxygen; measurements were taken twice per week for e) alkalinity. Color and line type indicate different tanks and treatments (Ambient 1, Ambient 2, Acidified 1, Acidified 2).

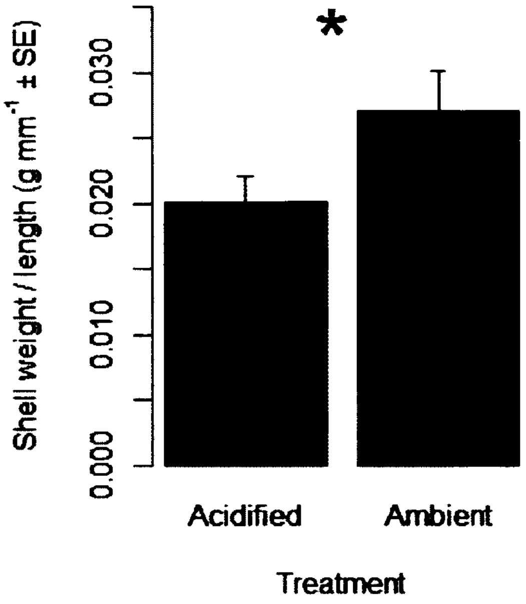

Figure 18. Shell weight (ash weight) for clams grown in acidified or ambient conditions. Weights (g) were standardized by shell length and are shown as means (± 1 SE). Asterisk denotes significant difference at $\alpha = 0.05$; $n = 10$.

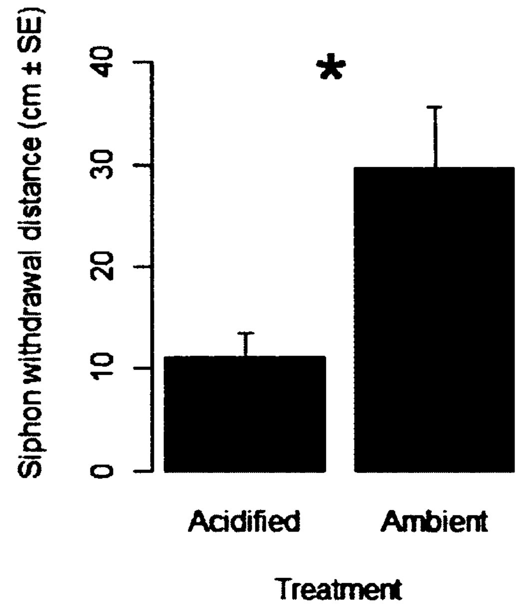

Figure 19. Distance between predator-simulation probe and siphon upon cessation of feeding. Shown are mean distance (in cm, ± 1 SE) for clams in acidified or ambient conditions. Asterisk denotes significant difference at $\alpha = 0.05$; $n = 8$.

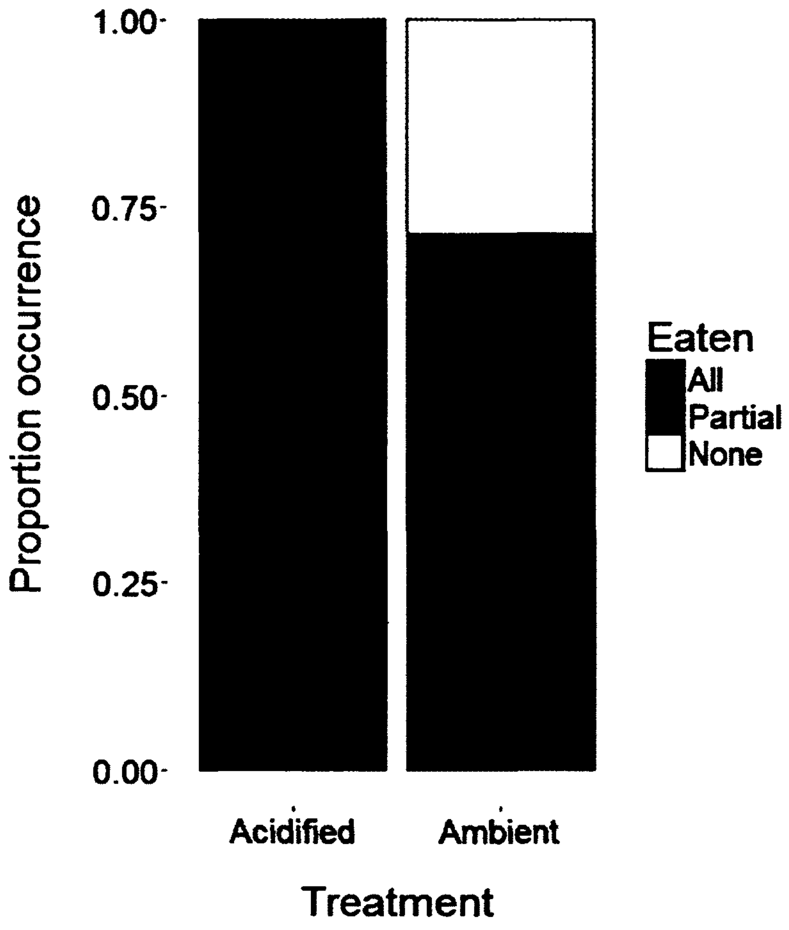

Figure 20. Foraging success for acidified and ambient crabs feeding on clams. Proportion of the trials in which all (black), some (partial, gray), or none (white) of the clams (*Mya arenaria*, 4 total in each trial) were eaten for crabs (*Callinectes sapidus*) and clams in acidified or ambient water.

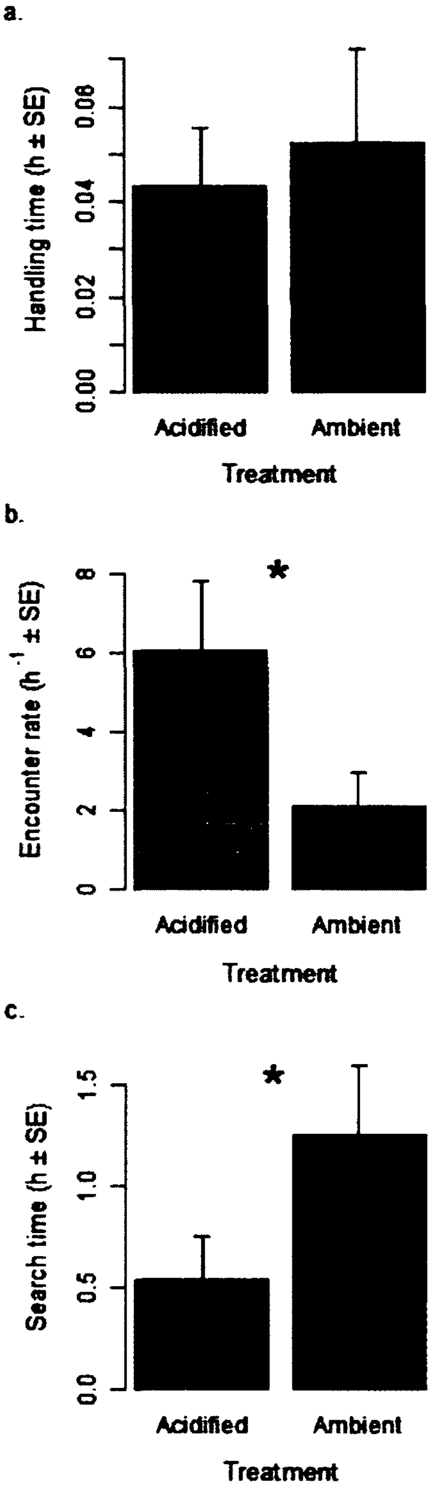

Figure 21. Crab behavior for acidified and ambient crabs feeding on clams. Means (± 1 SE) for blue crab *Callinectes sapidus* a) handling time, b) encounter rate, and c) search time when exposed to acidified or ambient water and prey *Mya arenaria*. Asterisk denotes significant difference at $\alpha = 0.05$; $n = 4$.

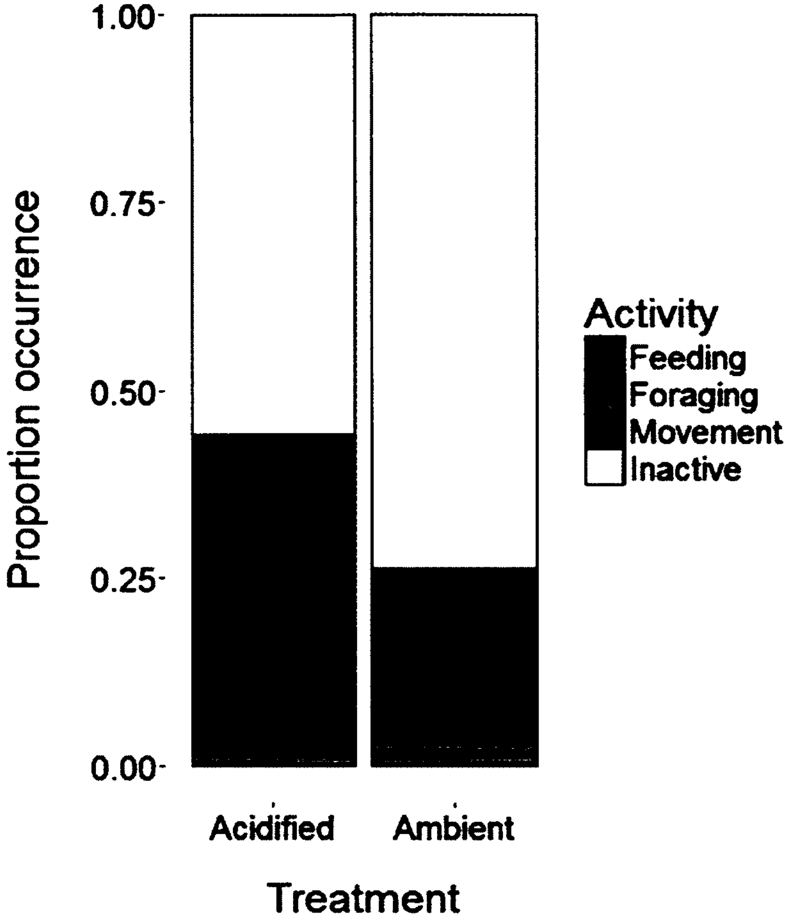

Figure 22. Relative amount of time crabs spent exhibiting various behaviors. Proportion of the time crabs spent feeding (black), foraging (light gray), exhibiting non-foraging movement (dark gray), and inactive (white) in acidified or ambient water, n = 4.

CHAPTER 6

Density-dependent predation and climate change in marine environments

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ABSTRACT

Density-dependent predation is a stabilizing force in ecosystem dynamics, yet anthropogenic stressors may alter components of density-dependent processes, either strengthening or weakening predators' impacts in natural systems. Herein, we synthesize current evidence for alterations in density-dependent predation due to climate change, extreme weather events, habitat loss, hypoxia, and acidification in marine ecosystems. Climate warming and extreme weather events mainly impacted the number of predators in an area (numerical response), while habitat loss, hypoxia, and acidification impacted an individual predator's interactions with different densities of prey (the functional response). Extreme weather events may be especially devastating for prey that do not hide from predators because they are more susceptible to local extinction at low densities. Habitat loss and hypoxia will impact cryptic species, which benefit from the added refuge provided by structured habitat and are more available to predators during times of hypoxia. Climate warming and acidification may impact many different types of species by changing metabolism (in the case of warming) and behavior (in the case of acidification) of predators and prey. Adaptive management strategies for ecosystems impacted by global change should consider the role of density-dependent predation in maintaining stability.

INTRODUCTION

Predators play a key role in ecosystem stability and function by consuming dominant competitors (Dayton 1971; Lubchenco and Gaines 1981; Boudreau and Worm 2012). Ecosystems that have lost their major predators may become drastically altered in a phenomenon called a trophic cascade, which is defined as occurring when "the impact of a predator on its prey's ecology trickles one more feeding level to affect the density and/or behavior of the prey's prey" (Silliman and Angelini 2012). A classic example is kelp forests in southwest Alaska, which were transformed to overgrazed barrens when otters were lost from the ecosystem; otters were no long able to control populations of urchins, which in turn overwhelmed kelp forests with their unchecked grazing (Estes *et al.* 2009).

Predators can also destabilize ecosystems or collapse food webs if they become too abundant, or if their prey do not have natural defenses against predation. This may occur when predators invade a new area. This is the case on the Antarctic shelf, where the king crab *Neolithodes yaldwyni* has expanded its range due to warming temperatures (Smith *et al.* 2012). On the Antarctic continental shelf, king crabs prey upon a diverse array of organisms that have not coexisted with crushing predators for 14 million years (Smith *et al.* 2012). Crabs have impacted the Antarctic marine ecosystem by disturbing or mixing sediment, reducing diversity of bottom-dwelling organisms, and reducing abundance of echinoderms such as sea stars in the areas they are invading, as compared to areas free of king crabs (Smith *et al.* 2012).

Generally, predators and their prey have evolved over time to coexist. Prey have anti-predator behaviors or morphological adaptations to avoid being eaten (Bibby *et al.* 2007; Whitlow 2010). Similarly, predators have adaptations or behaviors that help them to forage optimally and take advantage of prey when they are available (Meire and Ervynck 1986; Rindone and Eggleston 2011).

One of the ways the balance between predator and prey adaptations manifests in nature is through density-dependent predation. Predators can exhibit a numerical response to prey densities by increasing reproduction rates due to an overabundance of prey (demographic response) or by gathering in areas with relatively high densities of prey (aggregative response; Holling 1959). An individual predator may also adjust its predation rate to prey density through a 'functional response' (changes in consumption rate of a predator in response to prey density). Consumption rate can increase linearly with prey density (type I functional response); increase to an asymptote due to limits associated with prey handling, ingestion, and metabolism (type II functional response); or remain low while prey are at low density, providing a low-density refuge from predation (type III functional response; Holling 1959).

Certain characteristics of a predator-prey system can help predict which functional response will be observed. Type I responses are often found in organisms that do not actively search for prey, such as filter feeders, and type I responses are not reviewed here. Both type II and type III functional responses are common among vertebrate and invertebrate predators (Hassell *et al.* 1977). Type II functional responses are common for predators preying upon armored or defended organisms (Figure 23b). Predators that feed upon cryptic or otherwise hard-to-find prey will likely exhibit a type

III functional response (Figure 23c). Prey that avoid predators can achieve a low-density refuge; thus, the functional response can explain the distribution of prey items, and can be used to predict the persistence of prey species at low densities (Figure 24; Eggleston et al. 1992).

Density-dependent mechanisms tend to stabilize population dynamics (Royama 1992; Turchin 2003), while stressors, particularly stochastic perturbations in environmental conditions, destabilize populations (Byrnes *et al.* 2011). Sudden mortality as a result of environmental degradation can result in drastic fluctuations in populations of organisms, and populations that exhibit dramatic fluctuations are more prone to extinction (Heino 1998). Models of predator-prey dynamics predict that density-dependent predation decreases the amplitude and frequency of prey fluctuations due to climate change, stabilizing population dynamics of the prey (Wilmers *et al.* 2007). In addition, density-dependent processes, including a predator's functional response, maintain population viability when a population is reduced to low levels (Cushing 1975).

Despite the capacity to stabilize populations experiencing negative consequences of global change, density-dependent predation processes stand to be substantially altered by global change. Anthropogenic CO_2 emissions have increased, resulting in global changes in climate, increases in extreme weather events such as severe storms or droughts, and ocean acidification (Doney *et al.* 2012). Human population growth and conversion of coastal land for agriculture, industrial, and urban usage has led to nutrient pollution in coastal environments (Rabalais *et al.* 2009), increasing ecosystem metabolism and contributing to hypoxia and acidification in estuaries and near-shore systems (Feely *et al.* 2010, Duarte *et al.* 2013). Humans also alter the availability of foundation habitat species such as seagrass, mangroves, corals, and oysters, which are being lost from coastal waters (Duarte *et al.* 2008). This review examines the current evidence for alterations in density-dependent predation due to climate change, extreme weather events, habitat loss, hypoxia, and acidification in marine ecosystems.

CLIMATE WARMING

If warm years are expected to be good for prey populations, predators serve a major role by keeping the prey population in check. Density-dependent predation stabilizes population size such that extremely good or poor recruitment events result in a similar number of individuals added to the adult population. For example, in the Bristol Channel, the dominant species of burrowing shrimp *Crangon crangon* exhibits a fairly constant adult population size each year, despite spikes or dips in recruitment (Henderson *et al.* 2006). Since this species serves as an important predator and an important prey resource, keeping shrimp abundance constant stabilizes the ecosystem and prevents drastic fluctuations in trophic levels that depend on the shrimp (Henderson *et al.* 2006).

However, if there are many warm years in a row, prey may overwhelm their predators and bring about very extreme population fluctuations (Wilmers *et al.* 2007). Warm periods have been implicated in population explosions of the crown-of-thorns starfish *Acanthaster planci*, which consume coral (Uthicke *et al.* 2015). When predators of planktonic crown-of-thorns cannot consume enough individuals to prevent spikes in the number of new recruits (Dulvy *et al.* 2004), there may be a climate-mediated break-down of density-dependent predation. While the exact mechanisms for explosion in crown-of-thorns have not yet been identified, the implications for ecosystem health are clear: an overabundance of crown-of-thorns has devastated corals in Fiji (Dulvy *et al.* 2004) and the Great Barrier Reef (Uthicke *et al.* 2015). Any predator-prey system with a high-density refuge from predation (i.e. systems with a type II or III functional response) is at risk of warming-induced outbreaks of prey.

High-density refuges from predation may be altered under increased temperature. Under a warming scenario, predators increase predation rates disproportionately on higher prey densities (Ewald *et al.* 2013), which may shrink or remove the possibility of a coexistence refuge for predators and prey. Organisms without a low-density refuge may not be able to persist under a scenario of increased predation rates; thus, predator-prey interactions that assume a type II functional response are most at risk in a scenario of warming-induced increases in predator metabolism (Table 8).

EXTREME WEATHER EVENTS

Thermal stress or extreme weather events will have negative effects on prey resources that may ripple through the food web. Storms that drove dominant species to low abundance led to a phase shifts or trophic restructuring in estuarine soft-sediment environments (Chapter 4), kelp forests (Byrnes *et al.* 2011), and coral reefs (Mumby *et al.* 2007). Density-dependent processes such as Allee effects can result in local extinction once a population is driven to low density by environmental stressors such as habitat loss, drought, or over exploitation (Brook *et al.* 2008). An Allee effect is a positive relationship between a population's fitness and population density, which results in extremely low population growth at low population densities (e.g., reductions in fertilization success; Gascoigne & Lipcius 2004). Allee effects can occur when populations are driven to extremely low levels, as can occur with a type II functional response (Table 8; Gascoigne & Lipcius 2004).

Stressors that impact the availability of food resources or the abundance of predators can result in concentration of organisms in areas that are favorable for growth and survival. If the stressor creates spatial heterogeneity in a food resource, predators may gather at any remaining areas with relatively high densities of prey and form a consumer front, which in turn can devastate any remaining food resources (Silliman *et al.* 2013). A consumer front was defined by Silliman *et al.* (2013) as a "super concentration in abundance of mobile grazers or predators that locally overwhelms the carrying and/or renewal capacity of prey, resulting in sharp gradients in resource abundance and the collective movement of consumers from prey-depleted areas to adjacent prey-abundant habitats." If the resource in this scenario is a foundation species, such as coral, seagrass, or kelp, this can have drastic consequences for the ecosystem (Silliman *et al.* 2013). For example, the marsh periwinkle snail *Littoraria irrorata* aggregates at the edge of the nearest healthy marsh grass *Spartina alteriflora* when drought kills off patches of the marsh (Silliman 2005). High densities of snails overwhelm their food resource and can result in complete removal of marsh (Silliman 2005). Such an increase in consumer density would likely overwhelm prey that achieves a high-density coexistence refuge (type II). However, species that maintain a low-density refuge from predation by avoiding predators in space or time (type III) may be able to persist, because consumer fronts tend to form in areas where there is a steep gradient in prey density, and not in areas where prey are rare (Lauzon-Guay *et al.* 2008; Table 8).

HABITAT LOSS

Structured habitat such as seagrass, salt marsh, mangrove, coral, or oyster reef provide a refuge from predation for a number of benthic species (Gilinsky 1984; Sih *et al.* 1985). For example, complex habitats increased survival and diversity of epifaunal (surface-dwelling) invertebrates exposed to fish predation in macroalgae (Moran *et al.* 2010) and seagrass (Stoner 1982) as compared to less complex habitats. Seagrass, shell, and gravel habitats increased survival of infaunal (burrowing) invertebrates exposed to fish and crab predation as compared to sand (Arnold 1984; Irlandi 1994).

Loss of structured habitat increases vulnerability to predators by increasing attack rate (Brook *et al.* 2008; Stoner 2009). Complex habitats deter predators by increasing the time and effort a predator must spend foraging (Abrams 1982; Sponaugle and Lawton 1990). Inefficient foraging lowers encounter rates with prey, which in turn leads to low activity levels or emigration from the area (Lipcius & Hines 1986, Stoner 2009, Chapter 3). This means complex habitats that prevent efficient predator foraging provide a refuge for prey (Orth *et al.* 1984; Summerson and Peterson 1984). Loss of these habitats will result in more efficient predators and prey populations that are more vulnerable to predation (Panel 1).

The impacts of habitat loss will be most severe for rare prey with little spatial or temporal refuge from predation, and for prey with generalist predators that do not rely on the preferred prey habitat (Gascoigne and Lipcius 2004; Ryall and Fahrig 2006). Rare species may be most at risk because complex habitat provides refuge from local extinction for organisms that persist at low-density (Seitz *et al.* 2001). Generalist predators will have the largest impact on rare prey because their population size does not depend on the availability of a specific prey item or habitat type. For example, in Chesapeake Bay, the relatively rare burrowing clam *Mya arenaria* is preyed upon by a dominant generalist predator, the blue crab *Callinectes sapidus* (Chapter 3). *Mya arenaria* persists in patches of seagrass, despite heavy predation by blue crabs (Chapter 2, Chapter 3). Chesapeake Bay is experiencing seagrass declines in polyhaline regions (Orth *et al.* 2010); therefore, the refuge from predation-driven local extinction provided for this species may be lost (Chapter 2, Chapter 3, Seitz *et al. in prep*).

HYPOXIA

Hypoxia, defined as a low oxygen environment (Diaz and Rosenberg 1995), occurs in marine environments as episodic or persistent zones that form towards the bottom of the water column. Organisms with low mobility may become trapped in hypoxic zones, which leads to death or sublethal effects on behavior and metabolism. Therefore, hypoxia impacts predator-prey interactions through a combination of impacts on both predator and prey.

Hypoxia restricts prey in space, drawing pelagic species towards the water surface (Domenici *et al.* 2007) and benthic, infaunal species towards the sediment surface (Long *et al.* 2008). This makes prey more available to predators, which increases encounter rates. Hypoxia may change prey behavior in a variety of other ways, resulting in prey that are relatively easy to capture as compared to prey unaffected by hypoxia. Hypoxia may alter the decision-making process in fish prey, negatively impacting escape behavior (Domenici *et al.* 2007). Hypoxia also leads to changes in fish schooling behavior, increasing the volume of the school (Domenici *et al.* 2002), which may result in slow school movement through the water column and increase the risk of predation for fish under low oxygen conditions, as compared to fish in water where oxygen is not limiting (Domenici *et al.* 2007). Hypoxia is expected to impact species that avoid predators by decreasing or eliminating spatial refuges that would otherwise be present under normoxic (normal oxygen) conditions.

Hypoxia also impacts predators; many predators decrease feeding rates in hypoxic conditions as compared to normal conditions, including fish (Chabot and Dutil 1999) and crabs (Seitz *et al.* 2003). Thus, though prey are more available under hypoxic conditions as compared to when oxygen is available, predators may not be able to take advantage of prey if they are also exposed to hypoxia. However, in many systems hypoxia is episodic, allowing predators to move in and take advantage of exposed prey after hypoxic conditions relax. For example, benthic predators in Chesapeake Bay feed efficiently on infaunal prey during the hypoxic season, likely because non-stressed predators from outside the hypoxic zone move in after hypoxic conditions end and consume prey that linger near the sediment surface (Long and Seitz 2008).

ACIDIFICATION

The impact of acidification on predator-prey interactions has largely focused on the degree to which acidification reduces prey defenses. Acidification is expected to hamper the ability of calcifying organisms to build their shells (Gazeau *et al.* 2007).

Since shells are often used for defense against predation, a reduction in shell building will decrease a predator's handling time, or the amount of time required for a predator to consume its prey, and may increase prey mortality. For example, drilling gastropods required less time to consume acidified Sydney rock oysters *Saccostrea glomerata*, which had weaker shells than the control, allowing for a higher predation rate (Amaral *et al.* 2012). Decreased calcification will likely have a greater effect on prey that rely on armor for protection from predation as compared to prey that do not (Table 8). In some cases, decreased handling time does not equate to increased predation rates due to behavioral modification of the prey, such as increased avoidance behavior (Bibby *et al.* 2007), or an effect of acidification on the predator such as weakened claw strength (Landes & Zimmer 2012; Panel 1).

Acidification may impact predator-prey interactions by altering prey behavior. Prey decision-making may be compromised; for example, marine gastropods that leap away from predators to avoid being eaten were observed to jump towards the predator or delay time to jumping when exposed to acidification, increasing their risk of being eaten (Watson *et al.* 2014). Under acidic conditions, reef fish lose the ability to distinguish between predators and non-predators when exposed to predation (Dixson *et al.* 2010), and burrowing clams allow predators to get closer before ceasing feeding activity and trying to conceal their presence (Chapter 5; Panel 1). Each of these examples would result in an increased encounter rate and higher predation rates, putting prey species that avoid their predators most at risk under acidification (Table 8).

Acidification impacts predator behavior as well, decreasing search time and encounter rates. Acidified predators do not spend as much time foraging as those that are not acidified (Glaspie and Seitz *in press*; de la Haye *et al.* 2012, Chapter 5; Panel 1), which may strengthen the high-density coexistence refuge in a type II functional response (Table 8). In addition, acidification reduces the capability of predators to sense their prey (de la Haye *et al.* 2012; Dixson *et al.* 2015), potentially leading to decreased encounter rates and strengthening the low-density refuge in a type III functional response (Table 8). These changes in predator behavior may ameliorate impacts of acidification on prey in some cases (Panel 1). Moreover, decreased predator effectiveness may threaten the health of predators and negatively impact the flow of energy to higher trophic levels.

MANAGEMENT IMPLICATIONS

Density-dependent processes are often not considered in conservation management, and this results in an underestimation of the vulnerability of species to extinction (Brook *et al.* 2008). Density-dependent mortality is a necessary component of an adaptive management strategy that can cope with climate change (Hulme 2005; Stenseth *et al.* 2010). Nonlinear predator-prey dynamics can result in catastrophic changes and phase shifts (Hughes *et al.* 2005, Sinclair & Byrom 2006, Chapter 4). Management plans that take into account the relative densities of key species in the ecosystem and adapt accordingly will have the best chance of preventing or reversing these unexpected regime shifts and promoting ecosystem stability in natural environments that are increasingly stressed by human activities.

Future research should focus on documenting the functional response of predators in key trophic interactions or predator-prey interactions involving threatened or commercially important species. Documenting the functional response of bivalve species with a variety of different physical characteristics can help managers focus limited resources on species that are at the highest risk of decline. For example, Allee effects are a major concern in the management of endangered or heavily exploited species, because species that exhibit Allee effects are at higher risk of local extinction (Gascoigne and Lipcius 2004; Kramer and Drake 2010). Thus, an understanding of the impacts of global change on density-dependent predation may necessitate a management strategy that focuses on prey species that generally exhibit a type II functional response in interactions with predators, especially in areas where extreme weather events are likely to cause mass mortality events. Likewise, a management strategy to prevent declines in a prey species that exhibit a type III functional response in predator-prey interactions may involve restoration of structured habitat. This approach will allow managers to work with ecological principles to give threatened or exploited species the best chance of overcoming stressors related to global change.

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TABLES

Table 8. Aspects of density-dependent predation impacted by global change. Global change impacts on numerical response (NR) or functional response (FR) are identified. We predict the relative risk of each aspect of global change summarized here for organisms with a type II hyperbolic functional response or a type III sigmoidal functional response.

Aspect of global change	Process affected	FR or NR?	Component of response affected	Most at risk	References
Climate warming	Metabolic increase (prey)	NR	Demographic	Type II/III	Dulvy *et al.* 2004; Uthicke *et al.* 2015
Climate warming	Metabolic increase (predator)	FR	Foraging time	Type II	Ewald *et al.* 2013
Extreme weather	Allee effect	NR	Demographic	Type II	Brook *et al.* 2008; Byrnes *et al.* 2011
Extreme weather	Consumer front	NR	Aggregative	Type II	Silliman *et al.* 2013
Habitat loss	Provision of refuge	FR	Encounter rate	Type III	Brook *et al.* 2008, Stoner 2009, Chapter 3
Hypoxia	Prey behavior	FR	Encounter rate	Type III	Domenici *et al.* 2002, Long and Seitz 2008
Acidification	Calcification	FR	Handling time	Type II	Amaral *et al.* 2012
Acidification	Prey behavior	FR	Encounter rate	Type III	Dixson *et al.* 2010, Watson *et al.* 2014, Chapter 5
Acidification	Predator behavior	FR	Foraging time/ encounter rate	Type II/III	de la Haye *et al.* 2012, Dixson *et al.* 2015, Glaspie and Seitz *in press*, Chapter 5

FIGURES

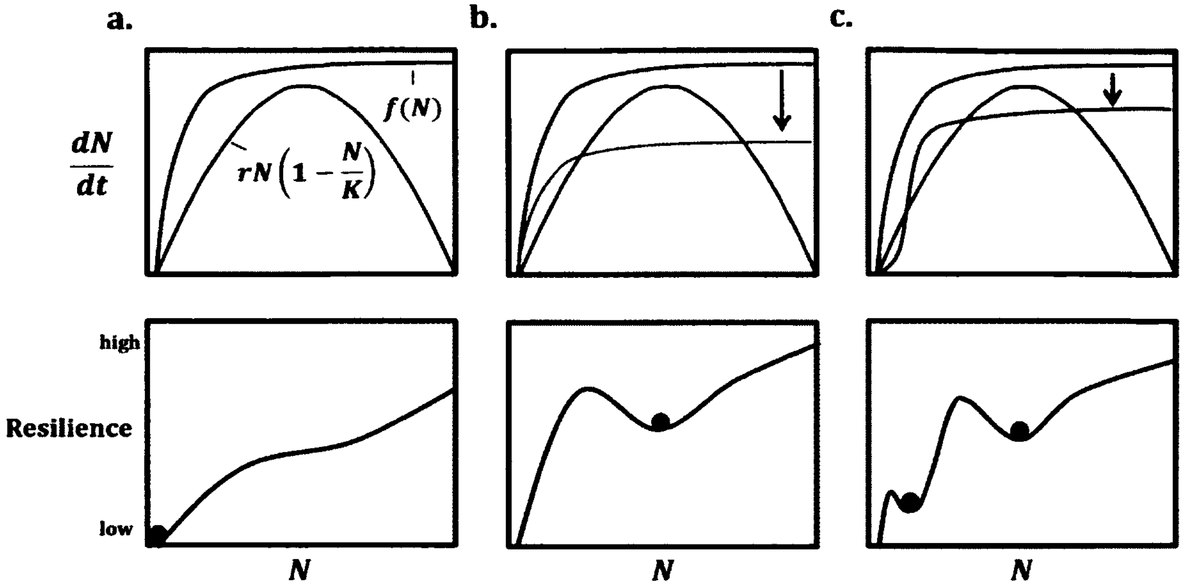


Figure 23. Growth curves and stable states manifesting in density-dependent predation. Without prey defense (a), the top panel shows prey growth rate (blue curve) is less than the removal of prey by predators (black line, denoting a type II density-dependent functional response) for all prey densities (*N*). The bottom panel indicates this predator-prey system does not maintain resilience and populations crash (blue circle denotes a single stable state at zero). When prey have armor (b), the amount of prey a predator may consume in a given amount of time is limited, decreasing the asymptote of the functional response curve (orange), and moderate densities of prey are stable due to increased predator handling time and decreased predation rates. The bottom panel indicates a medium-density stable state for prey (blue circle). When prey avoid their predators (c), low densities of prey are stable due to decreased encounter rates at low prey densities, driving a type III sigmoidal functional response (green line). The bottom panel indicates a low-density stable state (red circle) and a medium-density stable state (blue circle) for prey.

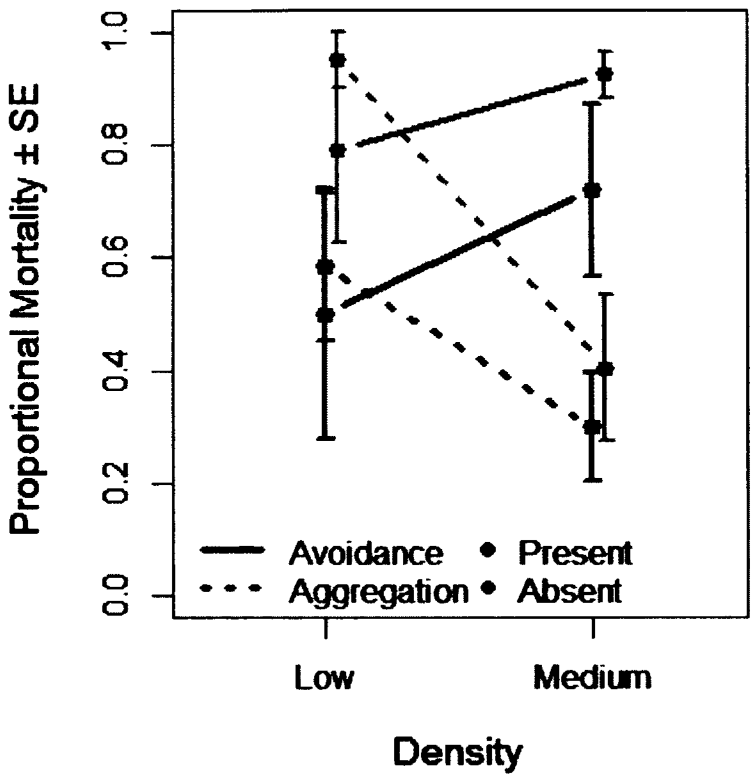


Figure 24. Functional response for armor versus avoidance species. Shown are mean proportional mortality (± 1 SE) for a species that avoids predators (avoidance, exhibited by the soft-shell clam *Mya arenaria*) and a species that lives in aggregations (a form of armor adopted by the ribbed mussel, *Geukensia demissa*) when exposed to blue crab predation. Solid lines are mortality for *M. arenaria* at two initial densities of 4 (low) and 16 (medium) per tank, with defense present (black) or absent (gray). Dashed lines are mortality for *G. demissa* at two initial densities of 12 (low) and 40 (medium) per tank, with defense present (black) or absent (gray). Proportional mortality is higher for low densities than for medium densities of prey that use armor or aggregation to avoid being eaten (type II functional response). Proportional mortality is higher for medium densities than for low densities of prey that avoid their predators in a type III functional response. Removing the prey's defense strategy of avoidance or aggregation increased proportional mortality for both prey types. Full methods can be found in Appendix III.

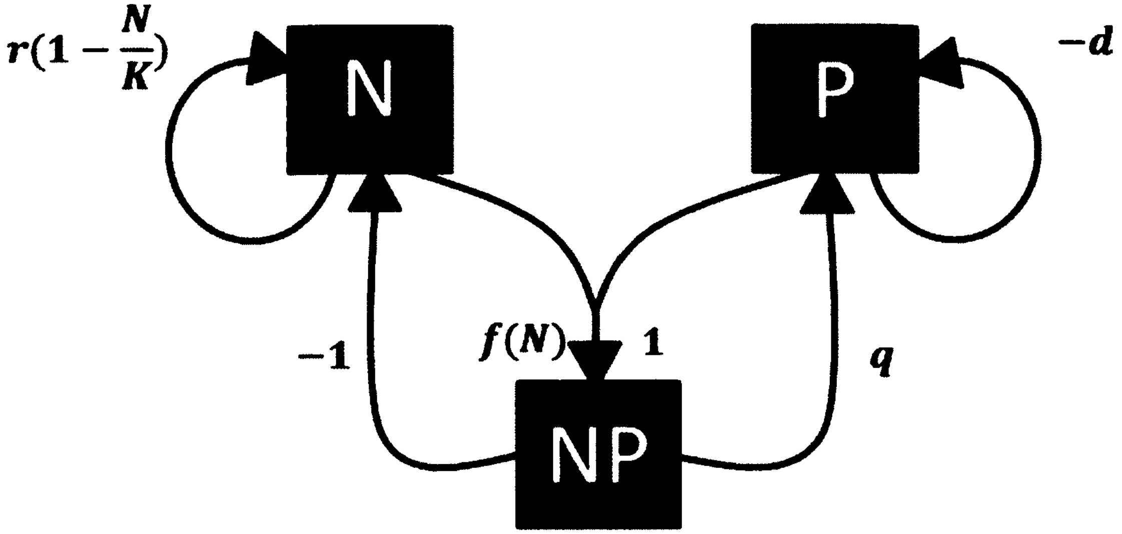


Figure 25. Diagram of the predator-prey system. N refers to prey abundance, P refers to predator abundance, and NP refers to a predator-prey encounter, which in this model, always leads to prey death. Arrows represent feedbacks between the predators, the prey, and their interaction, with the following parameters: r is the intrinsic per capita growth rate, K is the carrying capacity, q is the efficiency with which predators convert prey into new predators, and d is the death rate. The functional response $f(N)$ assumes a type III sigmoidal response:

$$f(N) = \frac{N^2bT}{1 + cN + bT_hN^2}$$

where T is the time available for foraging, a is the attack rate, T_h is the handling time, and b and c are components of the attack rate in a type III response (Long *et al.* 2012).

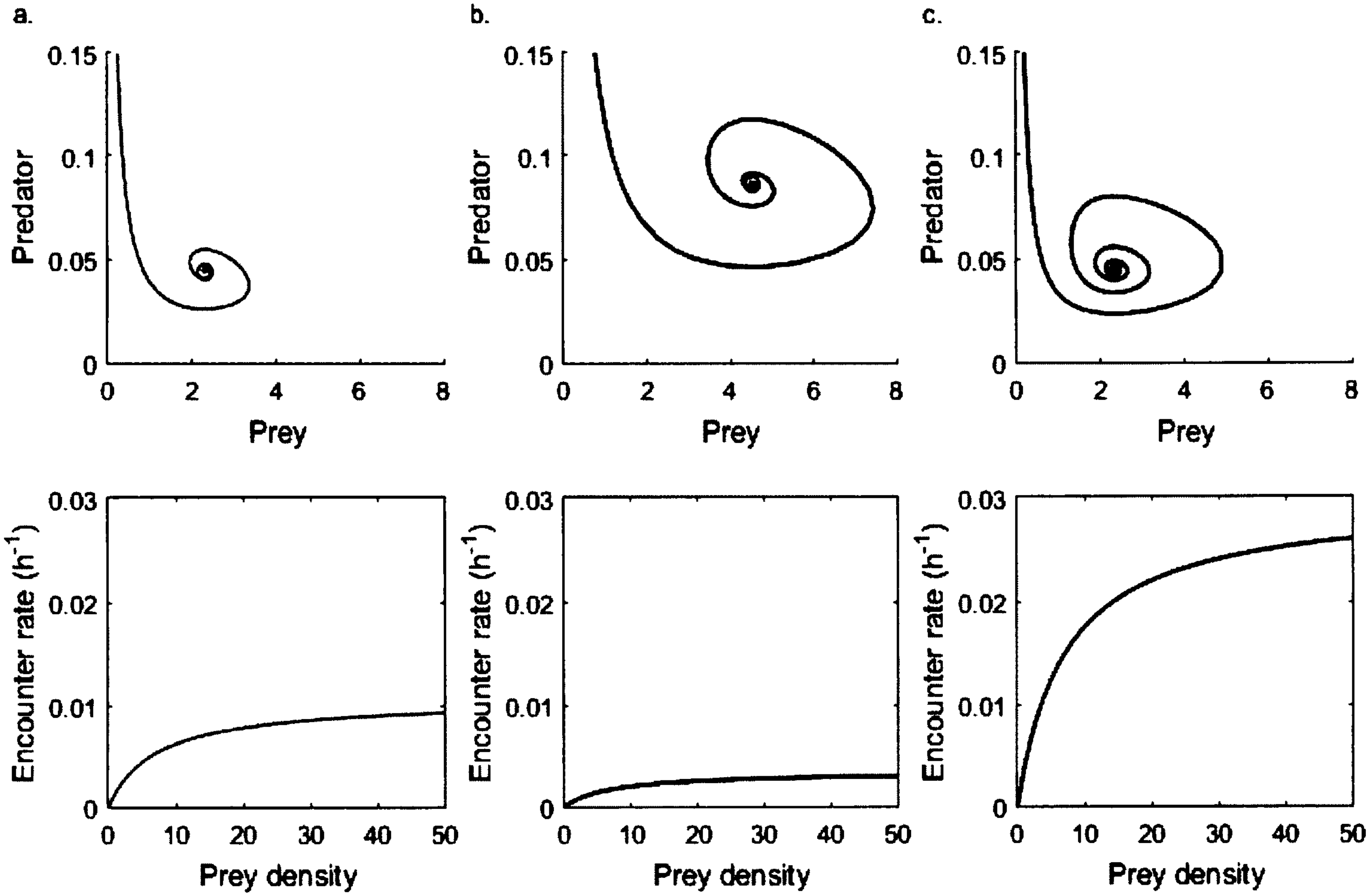


Figure 26. Theoretical predator and prey oscillations (type III functional response) with structured habitat and acidification. Top row. Predator and prey trajectories converge to a low-density stable state. Models parameterized based on a *Mya arenaria – Callinectes sapidus* predator-prey system for: a) the base scenario in sand; b) in complex oyster shell habitat; and c) under a scenario of acidification. Bottom row: encounter rate function used for each scenario. Parameter values listed in Supplementary Table 22.

PANELS

Panel 1. Simulations of predator-prey dynamics under scenarios of habitat loss and acidification.

Predation may exacerbate the effects of some anthropogenic stressors and ameliorate the impacts of other stressors on prey (Landes & Zimmer 2012, Chapter 3, Chapter 5). Studies involving habitat loss and acidification have focused heavily on density-dependent predation, especially specific parameters of the functional response such as handling time (the time a predator spends manipulating or eating a prey item), search time (the amount of time a predator spends foraging, or actively looking for prey), and encounter rate (the number of prey encounters over the search time; Rindone & Eggleston 2011, Dodd *et al.* 2015). These parameters can change as a function of prey density, prey or predator behavior, and environmental conditions (Hassell 1978).

Lotka-Volterra predator-prey ordinary differential equation models modified with a type III functional response (Figure 25; Long *et al.* 2012), and parameterized to represent a predator-prey system which included the blue crab *Callinectes sapidus* and the soft-shell clam *Mya arenaria* (Lipcius and Hines 1986), exhibit predator-prey oscillations and a low-density refuge for both predators and prey. Dynamics between the two species are altered when structured habitat is present, and under a scenario of acidification (Figure 26). In respect to predator-prey dynamics in the base scenario (Figure 26a), adding structured habitat increases the number of both predators and prey supported by the low-density refuge in a type III functional response, largely due to a lower encounter rate (Chapter 3; Figure 26b). Acidification increased encounter rate in this predator-prey system, but this was countered by an observed decrease in search time (Chapter 5; Figure 26b). However, acidification also increased the magnitude of oscillations, which decreases stability and increases the opportunity for populations to drop below some low-density threshold beyond which the population cannot recover. See Supplementary Table 22 for model parameter values and additional information.

APPENDIX III

Detailed methods and results for functional response for armor versus avoidance species.

Individuals of the soft-shell clam (*Mya arenaria*, thin-shelled deep infaunal) and ribbed mussels (*Geukensia demissa*, aggregative epifaunal) were exposed to blue crab *Callinectes sapidus* predation in a mesocosm experiment conducted in the Seawater Research Laboratory at the Virginia Institute of Marine Science, VA, USA. Mesocosm tanks of 40 cm x 70 cm were heated to 26-27 °C and aerated throughout the experiment. Tanks were filled with 25 cm sand and 25 cm filtered water from the York River.

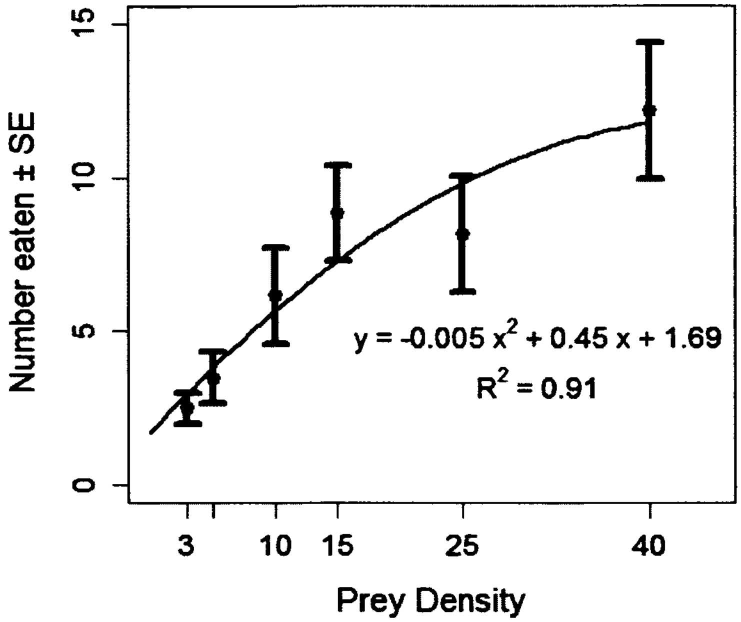
Juvenile *M. arenaria* and *G. demissa* (20-40 mm shell length) were collected from the York River and held in flow-through tanks until the beginning of the experiment. *Callinectes sapidus* were collected from the York River via baited crab pot. All crabs were acclimated to the lab for 1 week or longer and fed fish or bivalve meat three times a week. It was not possible to use a different crab for each trial due to space requirements, nor was it possible to use each crab the same number of times due to losses throughout the experiment. Crabs were used between one and three times, and crabs were randomly assigned to trials so there was no bias inherent in the re-use of crabs.

Trials were randomly assigned one of two defense tactic treatments, with the choices being either defense presence or absence. Defense tactic "present" bivalves were placed carefully in the sediment, siphon upwards, with even spacing (for *M. arenaria*) or placed in a naturally aggregated clump (for *G. demissa*). Defense tactic "absent" individuals were planted at the surface with a Vexar plastic mesh false bottom to eliminate a burrowing refuge (*M. arenaria*) or planted as individuals removed from aggregates to remove the aggregation refuge (*G. demissa*). Each species was planted at two densities, one low and one medium density, which is sufficient to determine if the functional response of the predator-prey interaction takes the form of type II or III (Lipcius and Hines 1986; Taylor and Eggleston 2000). Low and medium densities for *M. arenaria* were 4 and 16 clams per tank clams per tank (Taylor and Eggleston 2000). Low and medium densities were determined from a pilot study to determine the full functional response curve for *G. demissa* (Supplementary Figure 1), and were 12 and 40 mussels per tank.

At the start of the experiment, one adult male blue crab with a carapace width 100 mm or greater was added to each tank receiving a predator treatment. Bivalves were exposed to blue crab predation for 48 h, as is common for similar mesocosm studies (Eggleston *et al.* 1992). Remaining bivalves were counted upon termination of the experiment. There were six replicates of each defense treatment/density combination, as well as an equal number of mesocosms set up without predators, which served as controls. All treatments were assigned randomly.

Proportional mortality data were analyzed using three-way ANOVA, with density (2 levels: low and medium), species (2 levels: *M. arenaria* and *G. demissa*) and defense (2 levels: presence and absence) as fixed factors, with $\alpha = 0.05$ for main effects and $\alpha = 0.20$ for interaction terms (Underwood 1997). Post-hoc pairwise comparisons were done using Tukey HSD tests. All analyses were completed in R statistical software (R Core Team 2015).

Mya arenaria tended to have higher mortality than *G. demissa* (p = 0.06). Defense-present individuals had on average 22.8% lower mortality than defense-absent individuals (p = 0.03), but the effect of one main effect depended on the conditions of the others. There was no significant main effect of density (p = 0.29). Mortality of *G. demissa* at medium density was lower than other species x density combinations, driving a significant species x density interaction (*G. demissa* x medium-*G. demissa* x low, p = 0.03; *G. demissa* x medium-*M. arenaria* x low, p = 0.16; *G. demissa* x medium-*M. arenaria* x medium, p = 0.01).



Supplementary Figure 1. Functional response curve for ribbed mussels *Geukensia demissa* exposed to blue crab *Callinectes sapidus* predation. Plotted are the mean number of mussels eaten (± 1 SE, n = 6) after exposure to blue crab predation for 24 hours for different initial densities of mussels (prey density). Equation is provided for the fitted hyperbolic function.

Supplementary Table 22. Parameter estimates for the ordinary differential equation predator-prey models. Parameters: *r* is the intrinsic per capita growth rate, *K* is the carrying capacity, *q* is the efficiency with which predators convert prey into new predators, *d* is the death rate, *T* is the time available for foraging, T_h is the handling time, and *b* and *c* are components of the attack rate in a type III functional response. For scenarios representing the provision of complex habitat, the parameter b of attack rate was decreased by a factor of 3.14, which corresponds to similar decreases in encounter rate observed in oyster shell habitat (Chapter 3). For the scenario representing acidification, encounter rate and search time were increased or decreased by a factor of 8.91 or 0.43, respectively, according to proportional changes observed in Chapter 5. References: 1. Brousseau 1978; 2. Abraham and Dillon 1986; 3. Hewitt *et al.* 2007; 4. Lipcius and Hines 1986; 5. Chapter 3; 6. Chapter 5.

Parameter	Description	Estimate (base, in sand)	Estimate (complex habitat)	Estimate (acidification)	Units
r	Intrinsic rate of increase (due to settlement)	1.75[1]	1.75[1]	1.75[1]	yr^{-1}
K	Carrying capacity	200[2]	200[2]	200[2]	prey $\cdot$ m^{-2}
q	Conversion efficiency	0.01	0.01	0.01	g predator $\cdot$ g prey^{-1}
d	Death rate (of predators)	0.9[3]	0.9[3]	0.9[3]	yr^{-1}
T	Time available for foraging	1	1	0.43[6]	yr $\cdot$ yr^{-1} $\cdot$ predator^{-1}
T_h	Handling time	0.001483[4]	0.001483[4]	0.001483[4]	yr $\cdot$ prey^{-1}
b	Component of attack rate in Type III response	26.29743[4]	8.3484[5]	74.4217[6]	yr^{-1}
c	Component of attack rate in Type III response	0.143[4]	0.143[4]	0.143[4]	

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