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Consumer versus resource control and the importance of habitat heterogeneity for estuarine bivalves

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The relative influence of consumers (top down) and resources (bottom up) on the distribution and abundance of organisms remains a key question in ecology. We examined the relationships between consumer and resource variables along a productivity gradient for a dominant predator–prey interaction in a marine soft-sediment system. We 1) quantified density and size of the clam *Macoma balthica* (prey species) in six replicate sites at each of four habitat types (shallow mud, deep mud, muddy sand and detrital mud) in the Rhode River, Chesapeake Bay. We selected one habitat type of high food availability and clam density (shallow mud) and another of low food availability and clam density (muddy sand) for manipulative experiments. Then, we 2) measured *M. balthica* survival and growth through transplants, 3) measured food availability as sedimentary organic carbon content, 4) quantified predator density, and 5) calculated predator foraging efficiency in the two habitat types. Clam density in the four habitat types differed and was related to sedimentary carbon availability and predator density. One of the habitats, detrital mud, appeared to be a population sink because it only held juvenile *Macoma* that never survived to reproductive age. *Macoma* size and growth, and predator (mainly blue crab *Callinectes sapidus*) densities were positively correlated with productivity and were higher in shallow mud than muddy sand. In contrast, *Macoma* mortality, local 'interaction strength', and predator foraging efficiency were lower in the productive habitat (shallow mud). Thus, predation intensity was inversely correlated with productivity (food availability); consumer and resource effects differed by habitat type; and, at a relatively small spatial scale, consumer and resource forces jointly determined population dynamics in this soft-sediment marine system.

A key issue in community ecology deals with the relative influence of consumers (predation and herbivory) and resources (nutrients or food) upon the distribution of populations among habitats (Hunter and Price 1992, Power 1992, Trussell et al. 2006). Much of our understanding about the roles of biotic and physical processes in driving benthic community structure comes from the extensive work in marine rocky intertidal habitats (reviewed by Menge and Menge 2013). In marine ecosystems, there has been an emphasis on population dynamics within habitats and across regional spatial scales, but less frequently among different habitats (Dekker and Beukema 2007). Habitat heterogeneity can affect the abundance and distribution of benthic infauna by affecting relative recruitment and predation (Menge and Sutherland 1987, Heck and Crowder 1991, Seitz et al. 2001). Moreover, the productivity within a habitat can affect the strength of top–down versus bottom–up forces (Worm et al. 2002, Burkepile and Hay 2006). A system with a gradient in productivity is ideal for testing the relative effects of top–down and bottom–up forcing, as we expect differences based on the available resources. Determining the relative influence of consumers and resources across habitat types will become more important against the backdrop of climate change in human-dominated ecosystems with reduced numbers of higher-level consumers (Jackson et al. 2001) and altered nutrient inputs (Worm and Lotze 2006). Herein, we focus on variation and dynamics among subpopulations in contrasting habitats along a gradient of food availability (productivity), and we use as a test species a dominant marine clam with a heterogeneous distribution and population structure in various habitats. Specifically, we test predictions about the importance of consumers and resources to the distribution and abundance of bivalves at the local scale.

Consumer or resource control

Both resources and consumers play important roles in most systems, yet questions remain regarding the relative and interaction strengths of resource and consumer control (Worm et al. 2002, Trussell et al. 2006, Gruner et al. 2008). In terrestrial systems, there is a bottom–up template over which top–down dynamics act (Hunter and Price 1992), but in diverse systems, consumer effects may be dampened by the complexity of interactions among species (Strong 1992). In meta-analyses of marine systems, the interaction of the two forces depends on the underlying productivity of the system (Worm et al. 2002, Burkepile and Hay 2006), yet variability in the patterns across systems calls for additional

studies of the interactions of the two forces (Gruner et al. 2008). Therefore, studies in estuarine systems with varying productivity should elucidate unique features of consumer and resource control.

Spatial scales are germane to our understanding of the processes governing ecosystems (Thrush et al. 1997, Gripenberg and Roslin 2007, Menge et al. 2011). Coastal benthic ecologists have generally focused on the structuring of marine benthic communities at the local scale, examining the interactions of biological processes with physical stress gradients (Menge et al. 1997, Ysebaert et al. 2002). Recently the focus has shifted to broader spatial and temporal scales (e.g. the relationship between physical oceanography, nutrients, productivity, and community structure; Menge et al. 2011, Menge and Menge 2013). Because of the use of small spatial scales (Paine 2010), marine studies incorporating both consumer and resource effects among differing habitat types are uncommon.

Although the spatial scale of a study can determine the processes that appear to control community structure (Gripenberg and Roslin 2007, Menge et al. 2011), some generalities concerning the importance of top–down and bottom–up factors at various spatial scales have emerged. Earlier conceptual models posited that bottom–up forces are most important at large spatial scales, whereas top–down factors tend to dominate at local scales (Hairston et al. 1960, Oksanen et al. 1981, Fretwell 1987). For example, at the local scale (cm to 10s of m), variation in food availability (chl a) was undetectable, but differences in predation were discernible (Menge et al. 1997), suggesting control of community structure solely by consumers. In contrast, at a larger scale (i.e. two sites spanning 10s of km), a difference in primary productivity (chl a) accounted for variation in community structure; bottom–up forces apparently structured the community (Menge et al. 1997). Furthermore, the transfer of productivity through the food web depends on the scale of the investigation; at small scales (10s of m), predators may be able to move among sites differing in food availability (Navarette and Manzur 2008, Hines et al. 2009, Witman et al. 2010), whereas at large scales (>10s of km), such movements may not be possible (Menge et al. 1997, Thrush et al. 1997, Mitchell and Lima 2002, Seitz 2011). The generality of hypotheses relating scale to consumer or resource control remains untested in many systems.

In marine systems, predation in part controls community structure (Beal 2006, Paine 2010), with its influence generally increasing unimodally along gradients in productivity (Menge et al. 1997, Seitz 2011, Menge and Menge 2013). In addition, a system with low productivity may only have sufficient nutrients to support primary producers and a sparse assemblage of consumers. A combination of consumers and resources likely drives community structure in marine, freshwater and terrestrial habitats with the relative influence of these forces varying according to the specific characteristics of the food web (Posey et al. 1995, Frederiksen et al. 2006). By examining controlling factors in separate habitats, it will be possible to formulate a theoretical understanding of how the factors vary across differing habitat types and across the broader ecosystem (Beal 2006).

Experimental system: *Macoma balthica* in Chesapeake Bay

Macoma balthica is an infaunal bivalve (up to 45 mm shell length) distributed in muddy and sandy sediments along both coasts of the temperate North Atlantic and Pacific Oceans (Beukema and Meehan 1985) that plays an important role in both North American and European benthic systems (Beukema et al. 2010, Long et al. 2014). *Macoma balthica* is distributed across a wide range of shallow, soft-sediment habitats, which differ in the quality of nutrients and food, and thus the magnitude of primary productivity and secondary production via bottom–up control (Posey et al. 1995).

In Chesapeake Bay, *M. balthica* is a deposit feeder and facultative suspension feeder (Beukema and Cadée 1991), which can burrow to 30 cm in depth (Hines and Comtois 1985, Hines et al. 1990). This species either deposit feeds by using its siphon to scrape diatoms and benthic algae from the sediment surface, or it suspension feeds by inhaling algae from the water column via siphons extended to the sediment surface (Lin and Hines 1994). The degree of suspension or deposit feeding depends on current flow and intraspecific competition (Beukema and Cadée 1991). Settlement of *M. balthica* occurs in two pulses, a weak fall–winter pulse and a strong spring peak; abundance decreases through summer due to intense predation (Hines et al. 1990). Burial deeper than 15 cm (Blundon and Kennedy 1982) and residence in low-density patches (Eggleston et al. 1992, Seitz et al. 2001, Long et al. 2014) can provide relative refuges from predation for large juvenile and adult clams.

Epibenthic consumers of *M. balthica* such as spot *Leiostomus xanthurus*, croaker *Micropogonias undulatus*, waterbirds and blue crab *Callinectes sapidus* are dispersed along the Atlantic and Gulf coasts of North America and are abundant throughout Chesapeake Bay (Horwood and Goss-Custard 1977, Hines et al. 1990, Lipcius et al. 2007). In the Chesapeake Bay system, clams can constitute up to 50% of the crab's diet (Hines et al. 1990, Seitz et al. 2011), and adult blue crabs are the main predators of whole adult clams. Diet of adult blue crabs consists mainly of bivalve molluscs and mollusc siphons, predominantly *M. balthica*, in addition to polychaetes, crabs and fish (Hines et al. 1990, Hines 2007, Lipcius et al. 2007). Feeding efficiency and prey capture by blue crabs vary with prey availability, predator density and habitat complexity (Blundon and Kennedy 1982, Mansour and Lipcius 1991), as do other predator–prey interactions (Janssen et al. 2007). Spot, croaker, and hogchoker may consume whole juvenile clams near the sediment surface or nip the siphons of adult clams (Skilleter and Peterson 1994).

Survival and abundance of *M. balthica* in lower Chesapeake Bay are partially driven by predation at small spatial scales of 0.1–1 km (Hines et al. 1990, Eggleston et al. 1992), though the influence of predation as a structuring force varies over spatial scales on the order of 2–50 km (Menge et al. 1997, Beal 2006). The effects of nutrients or food availability (Seitz 2011) and environmental stress (Beukema et al. 2010) may affect the role of predation at these larger spatial scales. Additionally, diseases such as the parasite *Perkinsus marinus*

or *P. chesapeaki* may have effects on bivalve populations, but the evidence for control by disease is scant (Reece et al. 2008).

Our objective was to use a relatively small-scale system to determine the relative roles of consumers and resources in a dominant clam of the established, late-succession community. We quantified density and size structure of *M. balthica* in prevalent habitat types (shallow mud, deep mud, muddy sand and detrital mud) and then selected habitat types where *M. balthica* was in high and low density and where food availability was high and low (shallow mud and muddy sand, respectively). Subsequently, we experimentally tested growth and survival of *M. balthica* in field manipulations, and quantified food availability, predator density, and predator foraging efficiency in the habitat types. We hypothesized that the density of *M. balthica* was related to both food availability (bottom–up force) and predation (top–down force) in this relatively small-scale system.

Material and methods

Study sites

This study was conducted in the Rhode River, a sub-estuary in upper Chesapeake Bay (Fig. 1). The main axis of the Rhode River has been studied extensively (Hines et al. 1990); long-term data exist on *Macoma balthica* and other infaunal species for five of the sites included in our study (Eggleston et al. 1992, Seitz et al. 2001). The Rhode River is shallow (on average < 4 m) and relatively small (5 km long), though it includes multiple habitat types (i.e. subtidal mud flats, marshes, muddy sand and sand flats, submerged aquatic vegetation, coarse woody debris) within this limited spatial extent. Most of these habitats contain *M. balthica* patches linked by dispersal. In particular, *M. balthica* is commonly found in four major types of subtidal habitats: 1) shallow mud flats – typically in coves down-estuary from tidal creeks fringed by marshes in still waters, at 1–2 m depths; 2) shallow
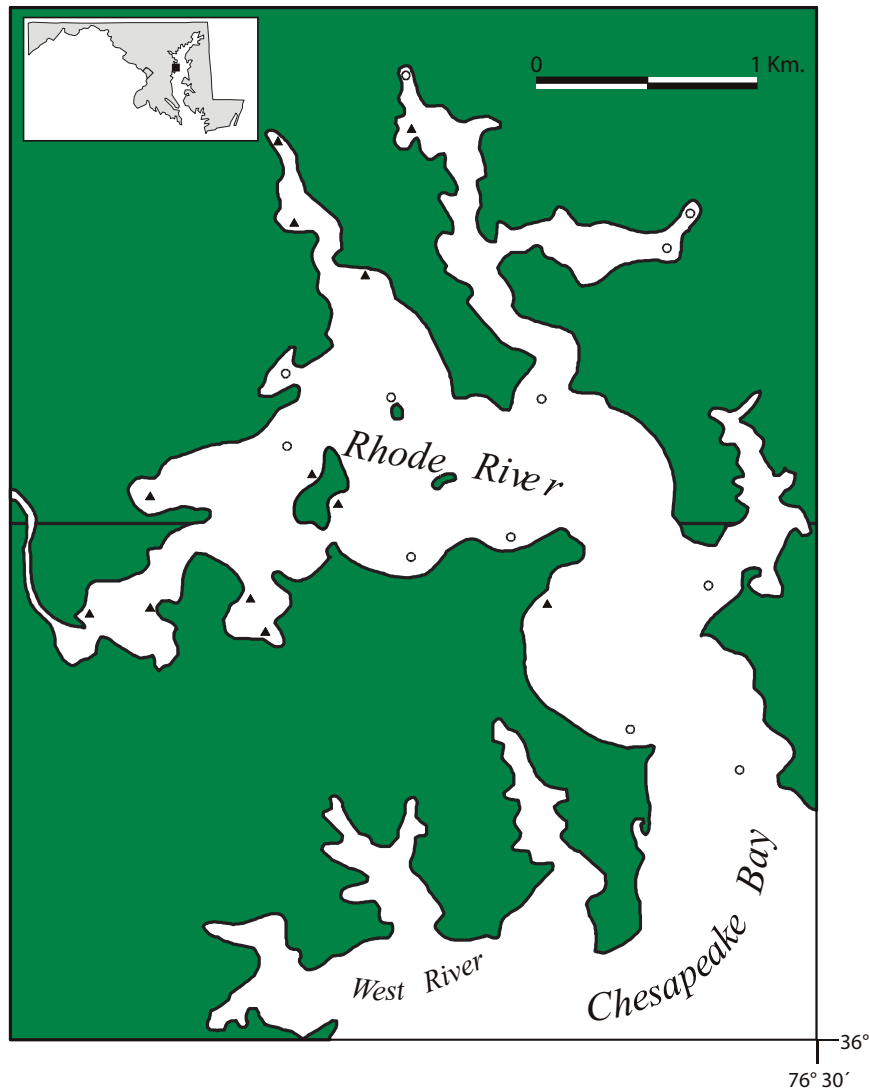

Figure 1. Map of the Rhode River with 24 sampling and experimental sites. Inset of Maryland with a filled box indicating the location of the Rhode River in the upper Chesapeake Bay. Triangles – sites used for survival and growth experiments as well as mensurative sampling; circles – sites used only for mensurative sampling.

muddy sands – along shoreline beaches farther down-estuary from the tidal creeks in faster-moving waters, at 1–2 m depths (approximately 16% coarse sand, 56% medium sand and 28% fine sand; Lin and Hines 1994); 3) deep channel muds – muds in the main channel of the Rhode River, at 3–6 m depths; and 4) shallow detrital muds – near the mouths of tidal creeks or along the shore bordering marshes, usually at 0.5–1.5 m depths with a heavy layer of detritus on the sediment surface and sediments composed predominantly of silt and clay.

From the accessible sites encompassing these habitat types, we selected six of each type for the mensurative sampling and field experiments. Except for five sites that were selected due to the available long-term data (Eggleston et al. 1992), the remaining 19 sites of 24 total were selected using computer-generated random coordinates from a grid overlaying the various sediment types throughout the river. Because of the physical similarity among shallow mud, deep mud, and detrital mud (Fig. 2), and the extreme difference between each of these three habitats and muddy sand, only shallow-mud and muddy-sand sites were chosen for more detailed manipulative experiments comparing growth of and predation on *M. balthica*.

Food availability and sediment features

Sediment nutrient content (carbon, hydrogen, nitrogen – CHN) was determined by collecting 1–2 cm of surface sediment with a 3-cm-diameter core. Sediments were stored in a freezer, defrosted, weighed, dried (48 h at 160°C), ground with an automatic grinder, mechanically homogenized and combusted at 924°C in a CHN analyzer. For ANOVA statistical analysis of carbon and nitrogen, one detrital mud sample was eliminated due to high sand content, leaving the degrees of freedom at 3 and 19. Sediment grain size was measured using wet sieving and pipetting of the top 3–5 cm of surface sediment collected with a 5-cm-diameter core.

Quantity of detritus was determined at the 24 sites in December, when the level of detritus did not fluctuate greatly. We took a 0.008 m² core at the sediment surface at each site near each suction sample, sieved it on a 500 μm sieve, elutriated the detritus from remaining sand or gravel, completely dried the sample (48 h at 60°C), and weighed the dried material to the nearest 0.1 g.

Bivalve density and size structure

Macoma balthica density was quantified on 14–28 July 1997 at six sites in each of the four different habitat types, yielding 24 sampling sites (Fig. 1), and later at a subset of sites in two habitats (eight shallow muds and four muddy sands) used for manipulative experiments on 22–24 August 1997. A suction device (Eggleston et al. 1992) was used to sample bivalves from a cylinder of 0.46 m diameter (0.17 m² area) to a depth of ~40 cm. A sample at each of the 24 sites was suctioned into a 1 mm mesh bag and subsequently sieved on a 1 mm mesh sieve. Bivalves in the sample were identified and counted; length (anterior to posterior) was measured with calipers to 0.1 mm.

Macoma balthica density was contrasted among habitat types using a one-way ANOVA model with habitat type
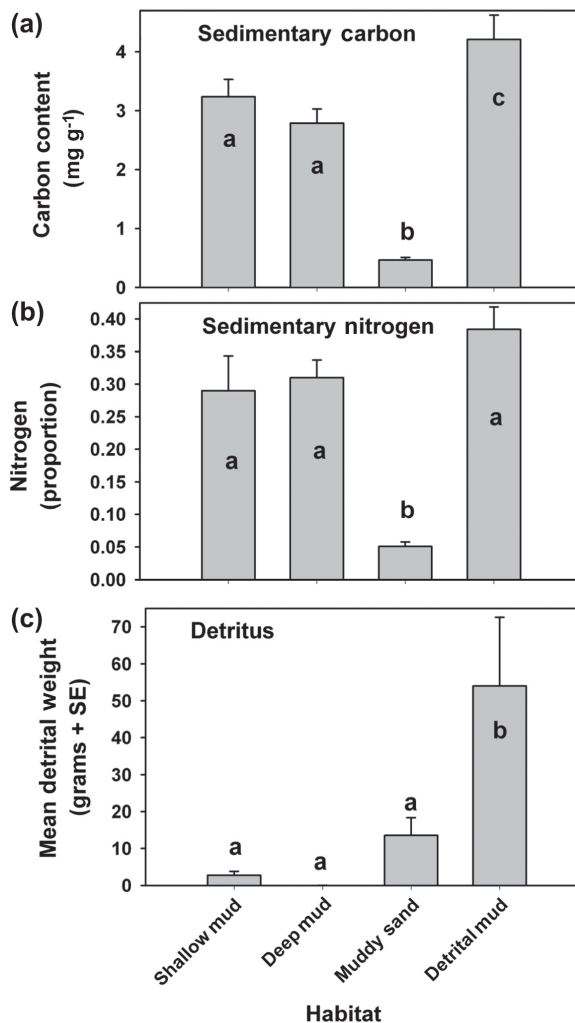

Figure 2. Sedimentary features. (a) Mean sedimentary organic carbon (+ SE) and (b) mean sedimentary nitrogen (+ SE) from surface sediments in four habitats: shallow mud, deep mud, muddy sand and detrital mud, from July 1997. (c) Mean detrital content (+ SE) from surface sediments in four habitats from December 1998. Habitat types with same letter do not differ significantly (SNK test, p > 0.05).

as a fixed factor having four levels (shallow mud, muddy sand, detrital mud and deep mud) and six replicate sites per habitat. When significant differences were detected, SNK/Tukey multiple comparison tests were used to evaluate the source of the difference. Heterogeneity of variance between levels of the factor was eliminated by log or square-root transformation, when necessary.

Using density samples, the size structure of each subpopulation of *M. balthica* was evaluated with site-specific size–frequency histograms. Cohorts were easily identified by breaks between the modes of the size–frequency histograms. Typically, two cohorts were evident, juveniles and adults, for which density was analyzed separately and similar to that for total population density.

Mean clam size per site was also derived from the site-specific juvenile and adult density samples. These were analyzed separately with ANOVA models in the same manner as for density. No adult clams were found in detrital

mud habitats; therefore, adult size comparisons were only conducted for the three remaining habitats. Additionally, sites containing fewer than four adult clams (two sand sites) or fewer than four juvenile clams (several sites) were not included in the size comparisons (degrees of freedom 2 and 13 for adult comparisons).

Mortality and growth

We used field transplant experiments to examine habitat-specific survival and growth in the two most extensive habitat types: shallow mud and muddy sand. Bivalves were collected in the Rhode River using a suction sampler and held overnight in open-seawater tanks. In our analysis of bivalve density and size structure by habitat, *M. balthica* in the size group 14–20 mm shell length (SL) were collected in shallow muds, but not muddy sands, suggesting that differential growth or survival produced the disparity between the two habitats. Therefore, *M. balthica* were selected from the upper end (14–20 mm SL, mean 15.53 ± 0.10 mm) of the small cohort (6–23 mm SL) for the transplant experiments to test if size-specific predation produced the disparity in size frequencies between habitats.

Eight shallow-mud and four muddy-sand sites were used in the manipulative experiments beginning on 1 August 1997. We included more shallow-mud than muddy-sand sites due to the higher variance in mean size and density of *M. balthica* in the former. Each site contained two plots, an uncaged and a caged plot. Each plot consisted of a 0.5×0.5 m area where 10 adult *M. balthica* were marked, measured, and transplanted into the sediment (among ambient clams). This density of marked clams (40 m^{-2}) was approximately equal to mean densities in shallow-mud habitats in August. To measure growth, clam shells were blotted dry and marked individually with a number (1–10) using a blue permanent marker. Clams were buried foot-down ~5 cm below the sediment surface, taking care to leave the surrounding sediment intact. Clams were spaced evenly in each plot, which was marked with a frame deployed over two stakes ~2 m apart. After transplanting the clams, the frame was removed, leaving only two stakes, each about 0.75 m from the plot edges. This procedure minimized predator attraction and structural artifacts that might produce treatment-specific bias. All plots were covered with a predator-exclusion cage for an acclimation period of 40–48 h; in previous studies, 24–36 h was sufficient for clams to achieve a stable burial depth and for the disturbance to stop attracting crabs (Eggleston et al. 1992). The cages were made of 13 mm hardware mesh and were pushed approximately 10 cm into the sediment; each cage roof was raised approximately 10 cm above the sediment surface.

After acclimation, cages were removed from half of the plots (uncaged treatment), left on the other half (caged), and all plots were untouched prior to retrieval 20–22 d later. At the end of the exposure period, contents of all caged and uncaged plots were extracted to a depth of ~40 cm using a suction sampler with a 1-mm mesh collection bag fitted to the outflow. Both marked and unmarked (ambient) *M. balthica* and other clams were enumerated and measured. Marked broken shells and umbos were indicative of crab predation, whereas marked intact shells with no live individual indicated physical mortality, handling mortality, or starvation. Ambient *M. balthica* density in each plot was measured and compared between habitats.

Mortality and 'local' interaction strength of *M. balthica* were quantified. Local interaction strength is defined as the number of animals missing and presumed eaten per day per site (Connolly and Roughgarden 1999). In studies with differing clam densities, proportional mortalities are more informative than number of animals consumed per day because of subtle changes at low densities (Eggleston et al. 1992, Seitz et al. 2001). Therefore, in our study, mortality and local interaction strength were quantified as the proportional mortality plot^{-1} day^{-1} (sensu Paine 1992). Data for proportional mortality plot^{-1} were converted to plot^{-1} day^{-1} to standardize across plots with slightly different exposure periods (20–22 days). Mortalities of marked *M. balthica* from caged plots were subtracted from those in uncaged plots because caged and uncaged plots were paired in the experimental design and caged plots were used to account for handling mortality. Thus, proportional mortality was determined as [proportion of dead uncaged clams – proportion of dead caged clams] similar to Paine's (1992) assessment of grazer-induced changes in algal populations using the following equation: (treatment density – control density)/(control density).

Mortality of caged marked clams indicated handling mortality, physical mortality and efficiency of clam recapture. Although cage artifacts such as mortality due to sedimentation, low flow or low food delivery would also be encompassed in control mortality, such artifacts were not significant in similar caging experiments (Seitz 2011). Proportional mortality of caged control clams did not differ between mud (mean $= 0.03$ day^{-1}, SE $= 0.01$) and sand (mean $= 0.025$ day^{-1}, SE $= 0.0125$; ANOVA, F $= 0.06$, DF $= 1, 10$, p $= 0.813$), indicating that mortality from physical stress between the habitat types would not confound estimates of predator-induced mortality. Proportional mortality was arcsine, square-root transformed when necessary to attain normality and homogeneity of variance (as determined by Cochran's test).

Growth was quantified as the mean size increase in shell length of marked *M. balthica* plot^{-1} day^{-1} over the 20-22 d exposure. Growth data were not transformed, as variances were homogeneous. Growth rate and proportional mortality were analyzed using ANOVA models with habitat type as a fixed factor of two levels (shallow mud and muddy sand).

Ambient *M. balthica* within experimental and control plots were enumerated and measured. Density and size structure of clams were compared with a split-plot ANOVA using the log-transformed density of total ambient clams m^{-2} from control and experimental plots as the dependent variable, habitat type (mud and sand) as a fixed between-subjects factor, treatment (control and experimental) as a fixed within-subjects factor, and site as a random factor nested within habitat.

Predator density and foraging efficiency

Predator density in shallow water was quantified by trawling at the terminus of the field experiments on 26 August 1997. At each of four muddy-sand and four shallow-mud sites,

demersal fishes and crabs were collected with a 4.9 m semi-balloon otter trawl (3 m wide mouth, 5 cm mesh net body, and 7 mm mesh cod end). During the daytime, one 2-min tow was taken parallel to shore at ~1 m depth at each site near the experimental transplant (tidal currents were minimal and presumably did not affect capture rates). Although gear avoidance by predators can reduce the numbers of predators caught in trawl gear, all sizes of predators are caught with almost equal efficiency except for extremely small individuals that can escape through the mesh; trawl efficiency for most predators including large crabs is ~22% (Homer et al. 1980). The small predators that were not estimated efficiently were not large enough to consume whole large clams of the size we used in our transplant experiments and were therefore not relevant to this analysis. We estimated that each 2-min trawl sampled a 120 m² area (3 × 40 m), using GPS positions at the beginning and end of each trawl. Animals in each trawl were identified, counted, and measured (fish: total length, crabs: carapace width) and compared using an ANOVA model with habitat type as a two-level (shallow mud and muddy sand) fixed factor. Data were log-transformed when necessary to meet assumptions of normality and homogeneity of variance (Cochran's test).

Habitat-specific foraging efficiency (i.e. per capita local "interaction strength," sensu Paine 1992) of the blue crab at each site for which we had both crab density and clam proportional mortality data was calculated as:

foraging efficiency = (number of clams eaten m⁻² day⁻¹)/
(crab density m⁻²)

where number of clams eaten m^{-2} day^{-1} = proportional mortality day^{-1} (from the survival experiments) × ambient density m^{-2}, and crab density = number of crabs caught per trawl divided by 120 (the area covered by each trawl), multiplied by a 4.55 correction factor to account for the 22% trawl efficiency.

Recruitment

In April–May 1998, *M. balthica* recruitment was monitored at each of the six replicate sites in the four habitat types. A suction device with a 1 mm mesh bag fitted to the outflow was used to sample bivalves from a cylinder of 0.46 m diameter (0.17 m² area) to a depth of ~40 cm. Two samples were taken at each site and a mean was taken for comparison of density by habitat using a one-way ANOVA. *Macoma balthica* were measured to 0.01 mm with calipers, or if less than 2 mm SL, clams were measured with an ocular micrometer under a microscope.

Habitat-specific consumer regulation of clam density

We examined consumer regulation of prey using clam densities from field experiments, mortality-rate calculations, and published literature values for a low-density refuge. We estimated the potential of field predators (assumed to be mostly crabs, which was confirmed by trawling results) in each of the two experimental habitats (shallow mud and muddy sand) to regulate clam populations by using initial clam densities in July and proportional mortalities d⁻¹ from

the manipulative field experiments through August. Habitat-specific instantaneous mortality rates (i) were calculated as $i = \log_e$ (finite rate of survival) $= \log_e$ (1 − proportional mortality d⁻¹) and used with the density values as an initial population size (N_0) in the equation $N_t = N_0 e^{-it}$ to solve for values of N_t at $t = 0$ to 100 (the predation period during our study, Julian days 195–295, or 14 July to 22 October). The overall predation period extends from 1 May to 1 November, with a steep decline in predation rates after 1 October (Hines et al. 1990). Thus, predation is likely negligible after the endpoint of our study, although it was one week short of the typical predation period. Calculated values of N_t were compared to published density estimates for a low-density refuge from predation in *M. balthica* (20–40 m⁻², Eggleston et al. 1992). We assumed that consumer regulation of clams occurred if the calculated value of N_t decreased below the upper limit of low-density refuge before the end of the predation period (approximately 1 November, Hines et al. 1990). If clam densities never reached the low-density refuge, then we concluded that clams were not regulated by predators (though this conclusion depends on the amount of time measured).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4ht96> (Seitz et al. 2016).

Results

Food availability and sediment features

Food resources for clams and nutrient availability differed among the four habitats: sedimentary carbon was greatest in detrital mud, and greater in shallow and deep mud than in muddy sand (Fig. 2a; ANOVA, F = 34.95, DF = 3, 19, p < 0.001, SNK test); nitrogen was lower in the muddy-sand habitat than all three others (Fig. 2b; ANOVA, F = 17.19, DF = 3, 19, p < 0.001, SNK test). Additionally, detritus was greater in the detrital mud habitat than the other three (Fig. 2c; ANOVA, F = 6.75, DF = 3, 20, p = 0.003); the scent of hydrogen sulfide was prominent in the detrital mud habitats, though sulfide content of the sediments was not measured. Hence, carbon and nitrogen concentrations were greater in shallow mud than muddy sand, the two habitats used for measurements of clam growth. Moreover, carbon content and *Macoma balthica* density were positively related amongst shallow-mud, deep-mud and muddy-sand habitats (*M. balthica* density = 61.7 + 63.9 × carbon; R² = 0.35, p = 0.009), the habitats with little detritus.

Bivalve density and size structure

Various bivalve molluscs were collected, including mainly the thin-shelled tellinids *Macoma balthica* and *M. mitchelli*, which collectively were over 95% of the clams collected. Other clams in the samples included the soft-shell clam *Mya arenaria*, brackish-water hard clam *Rangia cuneata* and stout razor clam *Tagelus plebeius*.
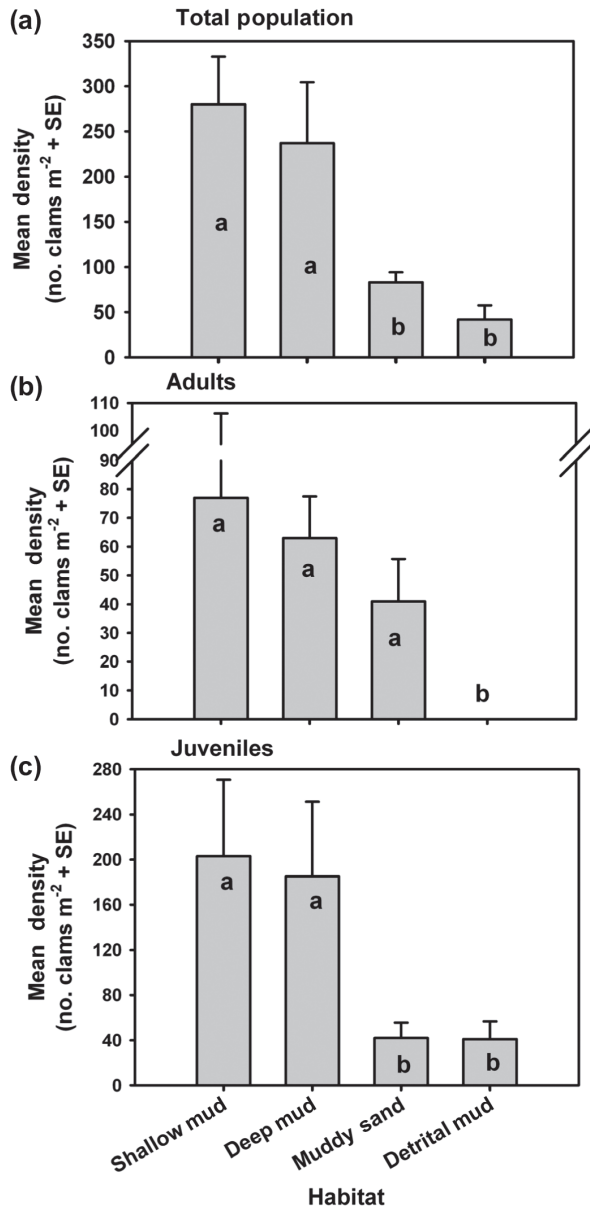
Figure 3. Mean densities (+ SE) of *Macoma balthica* from six replicate sites in each of four habitats: shallow mud, deep mud, muddy sand and detrital mud, in the Rhode River for (a) total population (both cohorts combined), (b) adults; clams > 23 mm SL (shell length), and (c) juveniles; clams < 23 mm SL. Data collected July 1997. Habitat types with same letter do not differ significantly (SNK test, p > 0.05).
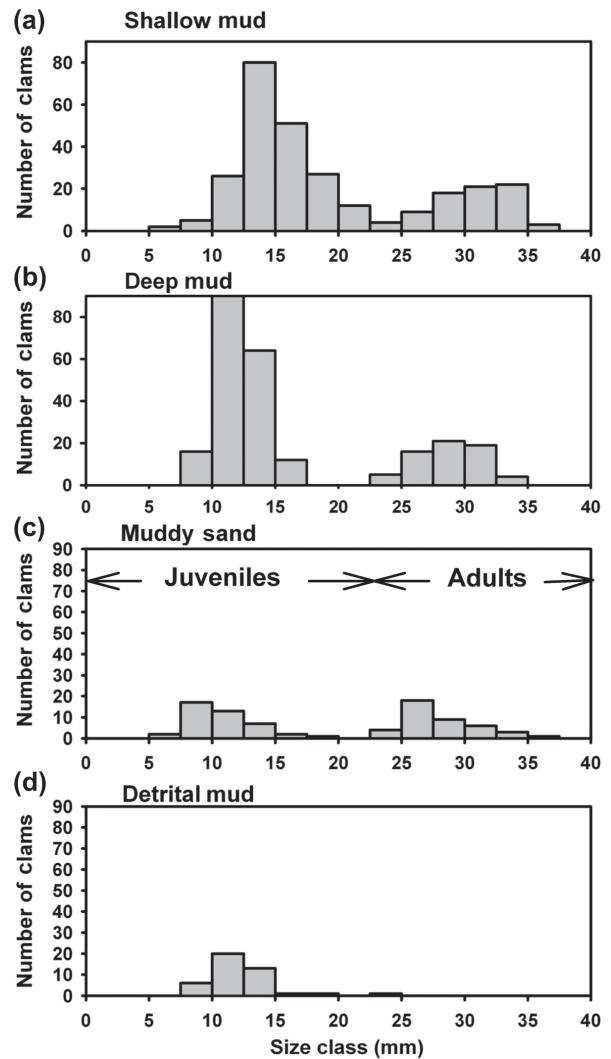

Figure 4. Size structure of *Macoma balthica* subpopulations compiled from (a) shallow mud, (b) deep mud, (c) muddy sand, and (d) detrital mud. Note the presence of two modes, juveniles and adults, separated at approximately 23 mm SL (shell length) in all habitats except detrital mud.

Density of *M. balthica* differed by habitat type (Fig. 3a; ANOVA with log-transformed data, F = 10.37, DF = 3, 20, p < 0.001); densities in shallow mud and deep mud were fivefold greater than those in detrital mud and muddy sand (SNK test, p < 0.05). Two size classes were apparent in the size-frequency distributions from most habitats (Fig. 4). We defined juvenile *M. balthica* (age 0 year class) as those < 23 mm shell length (SL), which had not reached their first reproductive season in the fall (Honkoop and van der Meer 1997), and adults (age 1 + year classes) as those > 23 mm SL. Despite the presence of juveniles, there were no adults in detrital mud, but the other three habitats had similar

adult densities (Fig. 3b; ANOVA on log-transformed adult densities, F = 1.41, DF = 2, 15, p = 0.274). Juvenile density was higher in deep and shallow muds than in muddy sand and detrital mud (Fig. 3c; ANOVA on 2/3-root-transformed juvenile densities, F = 3.16, DF = 3, 20, p = 0.047, SNK test).

To further compare densities between two of the habitats (shallow mud and muddy sand), densities of ambient *M. balthica* in plots used for the manipulative experiments were examined before manipulation. Total density was nearly ten-fold higher in shallow mud than muddy sand (Fig. 5) (split-plot ANOVA; Table 1a), and there was no difference between experimental and control treatments (Table 1a). Adult clams were five times denser in shallow mud than muddy sand (Table 1b), and juvenile clams were nine times denser in shallow mud than muddy sand (Table 1c). The difference in density of ambient clams between shallow-mud and muddy-sand habitats in experimental plots confirmed the differences between those two habitats seen in
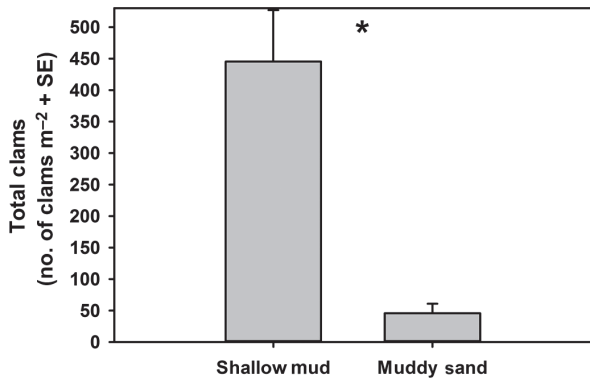
Figure 5. Mean densities (+ SE) of total *M. balthica* pooled from experimental and control plots in two habitats: shallow mud and muddy sand, in the Rhode River. Data collected August 1997. *denotes significant difference between treatments (ANOVA, $p < 0.05$).

density comparisons across the four habitats at the original 24 sampling locations.

Mean size of adult *M. balthica* was only compared among shallow mud, deep mud and muddy sand because detrital mud had no adult clams. Adults were larger in shallow mud than muddy sand, and deep mud was not different than either of the other two habitats (Fig. 6a; ANOVA; $F = 7.10$, $DF = 2$, 13, $p = 0.008$, Tukey-test). For the juveniles, there was no difference in size among all four habitats (Fig. 6b; ANOVA, $F = 1.34$, $DF = 3$, 20, $p = 0.291$).

Resource control: bivalve growth

The size of all surviving marked *M. balthica* (mean = 16.0 ± 0.16 mm) was greater than that of the initial marked

Table 1. GLM ANOVA split-plot design using the log-transformed density of (a) total ambient clams m^{-2} and (b) adult (> 23 mm) clams m^{-2} and (c) juvenile (< 23 mm) clams m^{-2} from control and experimental plots as the dependent variable, habitat type (mud and sand) as a fixed between-subjects factor, treatment (control and experimental) as a fixed within-subjects factor, and site as a random factor nested within habitat.

Source of variation	SS	DF	MS	F
(a)				
Habitat type	5.28	1	5.28	19.95***
Site (Habitat type)	2.38	9	0.26	5.11*
Treatment	0.12	1	0.12	2.34ns
Habitat × Treatment		1	0.21	4.23ns
Error	0.22	9	0.05	
(b)				
Habitat type	2.36	1	2.36	10.68**
Site (Habitat type)	1.99	9	0.22	3.78*
Treatment	0.001	1	0.001	0.02ns
Habitat × Treatment	0.006	1	0.006	0.10ns
Error	0.53	9	0.059	
(c)				
Habitat type	5.05	1	5.05	9.27*
Site (Habitat type)	4.90	9	0.54	6.17**
Treatment	0.18	1	0.18	2.01ns
Habitat × Treatment	0.11	1	0.11	1.19ns
Error	0.79	9	0.09	

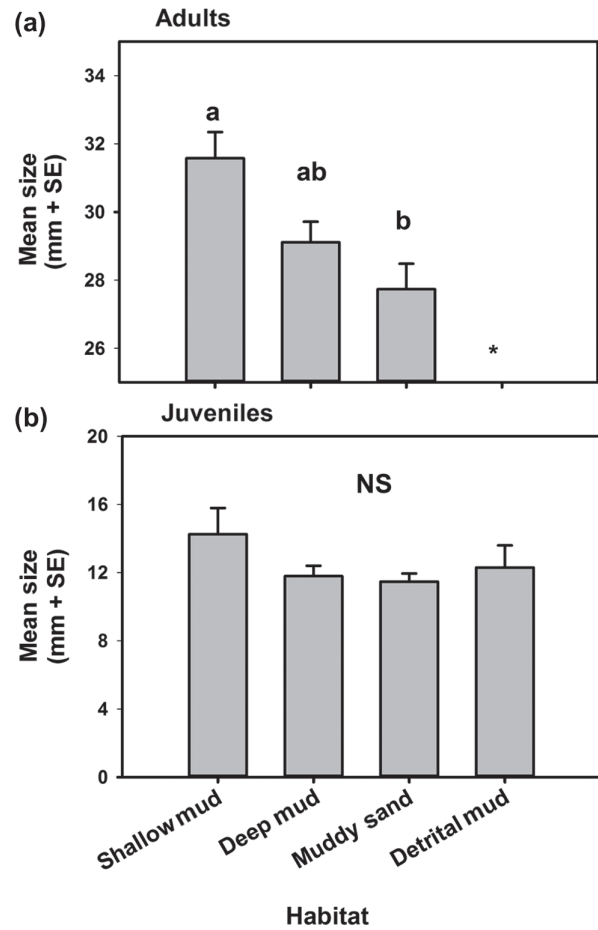***$p < 0.005$, **$p < 0.01$, *$p < 0.05$, ns$p > 0.05$.

Figure 6. Mean *Macoma balthica* size (SL shell length, + SE) in four habitats: shallow mud, deep mud, muddy sand and detrital mud, for (a) adults; clams > 23 mm SL in three habitats: shallow mud, deep mud and muddy sand (* note that no large cohort was present in the detrital mud habitat), and (b) juveniles; clams < 23 mm in four habitats: shallow mud, deep mud, muddy sand and detrital mud. Only sites with more than four small individuals were included in the analysis. Habitat types with same letter or NS do not differ significantly (Tukey test, $p > 0.05$).

clams (mean = 15.5 ± 0.10 mm) (ANOVA, $F = 7.43$, $DF = 1$, 10, $p = 0.007$), indicating that, on average, clams grew during the experimental period. There was no difference in growth between uncaged experimental and caged control plots (split-plot ANOVA, Table 2), suggesting that

Table 2. GLM ANOVA split-plot design using the log-transformed mean growth of clams from control and experimental plots as the dependent variable, habitat type (mud and sand) as a fixed between-subjects factor, treatment (control and experimental) as a fixed within-subjects factor, and site as a random factor nested within habitat.

Source of variation	SS	DF	MS	F
Habitat type	0.13	1	0.13	5.20*
Site (Habitat type)	0.21	8	0.03	6.22**
Treatment	0.01	1	0.01	2.63ns
Habitat × Treatment		1	0.01	0.01ns
Error	0.03	8	0.01	

**$p < 0.01$, *$p < 0.052$, ns$p > 0.052$.

there were no caging differences, no within-site differences, and that sublethal mortality (i.e. siphon-nipping) did not affect growth. Clam growth was greater (Fig. 7a; nested ANOVA, F = 42.34, DF = 1,2, p < 0.025) and sedimentary carbon and nitrogen were four-fold greater in shallow mud than muddy sand (Fig. 7b).

Consumer control: clam mortality, predator density and foraging efficiency

Mean proportional mortality day^{-1} of clams (= local interaction strength) was four-fold higher in muddy sand than shallow mud (Fig. 8a; ANOVA on angularly transformed data, F = 7.08, DF = 1, 10, p = 0.024). In addition to loss of marked clams, the presence of cracked umbos from marked clams (evidence of crab predation on clams) was compared by habitat. The number of marked cracked umbos plot^{-1} day^{-1} was greater by seven-fold in muddy sand than in shallow mud (Fig. 8b; ANOVA, F = 10.35, DF = 1, 10, p = 0.009). The number of marked clams eaten per ambient number available plot^{-1} day^{-1} was lower in shallow mud (0.0038) than in muddy sand (0.056) by nearly an order of magnitude (ANOVA on log-transformed data, F = 11.82, DF = 1, 6, p = 0.014).

In total, 128 epibenthic predators were collected during the day in shallow-water trawls. Predators included the
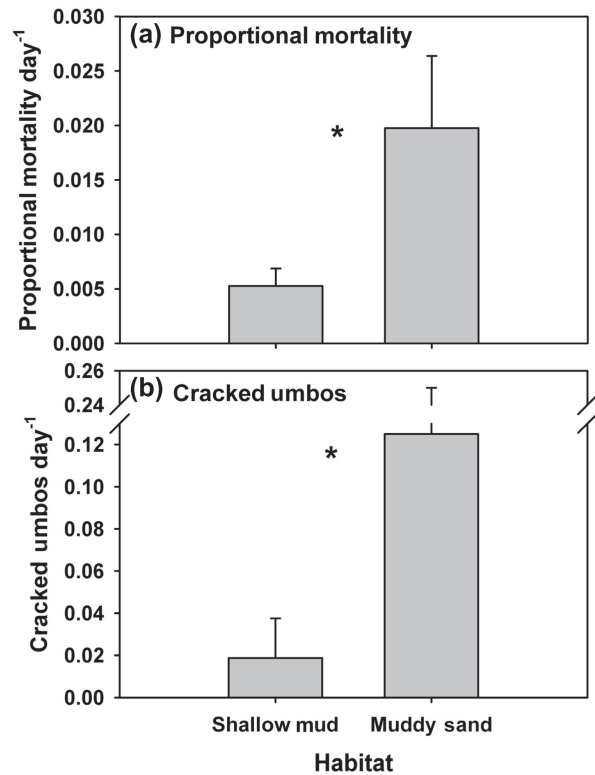
Figure 8. (a) Proportional mortality in number of clams eaten plot^{-1} day^{-1} (+ SE) and (b) no. of cracked umbos plot^{-1} day^{-1} (+ SE) (indicative of predation) for transplanted clams in two experimental habitats: shallow mud and muddy sand, in August. *denotes significant difference between treatments (ANOVA, p < 0.05).

blue crab *Callinectes sapidus* (43.8% of total) and various finfish, such as white perch *Morone americana* (35.9%), spot *Leiostomus xanthurus* (8.6%) and hogchoker *Trinectes maculatus* (3.9%). Nearly three times more crabs were caught in shallow mud than in muddy sand (Fig. 9a) (ANOVA on square-root transformed data, F = 6.16, DF = 1, 6, p = 0.048). The total number of predatory finfish tended to be slightly greater in shallow mud than in muddy sand, but the difference was not significant (ANOVA, F = 0.05, DF = 1, 6, p = 0.837). Crabs tended to be slightly larger in shallow mud (mean 106.8 ± SE 5.3 mm CW) than muddy sand (mean 83.8 ± SE 15.5 mm CW), but this difference was not significant (ANOVA, F = 1.97, DF = 1, 6, p = 0.210). Predator size did not differ between habitats for other predators including white perch (ANOVA, F = 2.81, DF = 1, 5, p = 0.155), spot (ANOVA, F = 0.67, DF = 1, 5, p = 0.445), and hogchoker (ANOVA, F = 1.06, DF = 1, 3, p = 0.380). Moreover, clam density and crab density were positively related (Fig. 10) at the local scale (i.e. 5 km).

Given that blue crabs are the major predators of juvenile and adult whole *M. balthica* in the study system (Hines et al. 1990), and cracked umbos showed evidence of crab predation on our experimental clams, we calculated foraging efficiencies as a function of blue crab density. The availability of clams per crab tended to be higher in shallow mud (4.38 clams crab^{-1}) than muddy sand (3.23 clams crab^{-1}), though this difference was not significant between habitats from four replicate sites of each habitat type where predator
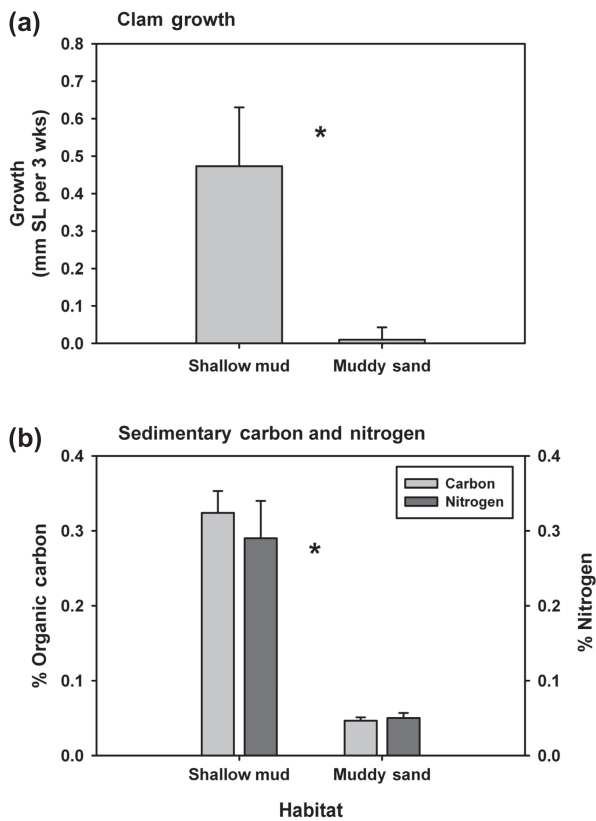

Figure 7. (a) Mean growth of transplanted clams (mm three weeks^{-1} + SE) for two habitats: shallow mud and muddy sand, from pooled control and experimental plots. (b) Mean sedimentary carbon and nitrogen at clam transplant sites in two experimental habitats: shallow mud and muddy sand, in August. * denotes significant difference between treatments (ANOVA, p < 0.05).

(a) Crab abundance

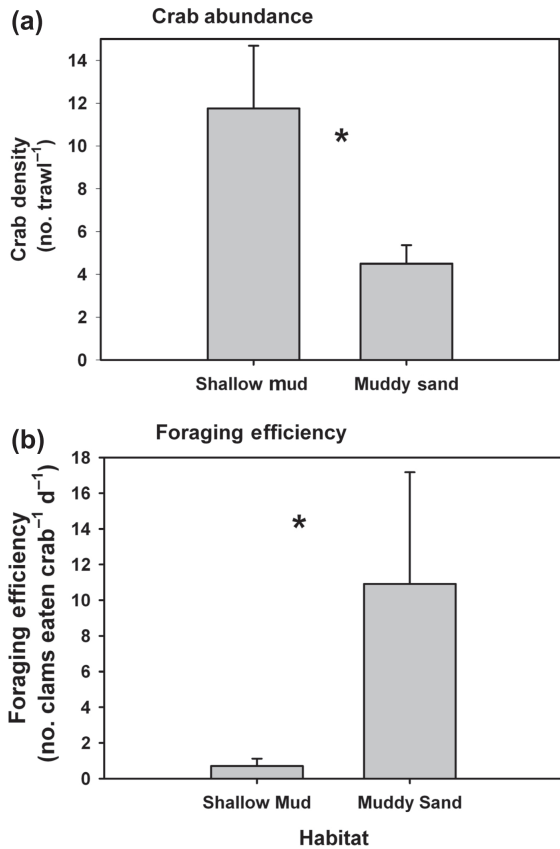
(b) Foraging efficiency

Figure 9. (a) Density of crab predators per trawl (+ SE) from trawls taken near the experimental sites in two habitats: shallow mud and muddy sand. (b) Foraging efficiency of crabs (i.e. per capita interaction strength) in number of clams eaten $crab^{-1}$ day^{-1}. * denotes significant difference between treatments (ANOVA, $p < 0.05$).

data were taken (ANOVA, F = 0.57, DF = 1, 6, p = 0.477). Consumption (= mortality) of clams $crab^{-1}$ day^{-1} was much lower in shallow mud than muddy sand (values standardized for crab and clam densities m^{-2}). Thus, habitat-specific foraging efficiency of crabs on clams (= local per capita interaction strength, sensu Menge et al. 1996) was higher in
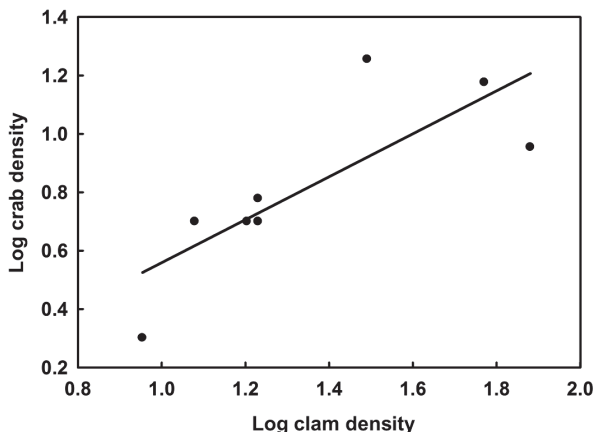

Figure 10. Regression of log crab density versus log ambient clam density from eight habitats where both sets of data were collected. Regression equation: crab density = 0.665 clam $density^{0.736}$ (DF = 1, 6, p = 0.018; $r^2 = 0.63$).

muddy sand than in shallow mud (Fig. 9b; ANOVA on log-transformed data: F = 6.14, DF = 1, 6, p = 0.048). Though alternative prey were not enumerated in this study, the total density and biomass of the infaunal communities are similar between sand and mud habitats of the Rhode River, where only five species differ in biomass by habitat, two of which are the thin-shelled clams *Macoma balthica* and *Mya arenaria* (Hines and Comtois 1985).

Habitat-specific consumer regulation of clam density

The potential for crabs in specific habitats (i.e. shallow mud and muddy sand) to regulate clams (or reduce density) was estimated from clam densities of 280 m^{-2} for shallow mud and 80 m^{-2} for muddy sand in July (Fig. 3a), and proportional mortality day^{-1} of 0.005 in shallow mud and 0.019 in muddy sand from our manipulative experiments in August (Fig. 8a; proportional mortalities corrected for non-predation-induced mortality). During this time frame, crab foraging was greatest (Hines et al. 1990), and thus these estimates represent maximum prey mortality rates. Instantaneous mortality rates (i) were calculated as $i = \log_e$ (1 – proportional mortality day^{-1}) = –0.005 for shallow mud and –0.019 for muddy sand. These values were used, along with density as initial population size (N_0) in $N_t = N_0 e^{it}$, to solve for values of N_t. In shallow mud, clam densities never reached the zone of regulation (i.e. remained above the low-density refuge; 20–40 m^{-2}, Eggleston et al. 1992, Seitz et al. 2001) during the predation period, but in muddy sand, clam densities reached the predation refuge ~two months before the end of the period (~Julian day 235; Fig. 11).

Recruitment and alternative factors affecting clam distributions

We hypothesized that recruitment could potentially contribute to observed habitat-specific densities of *M. balthica*. In 1998, a strong recruitment year for *M. balthica*, April densities of recruits were equivalent in shallow mud, muddy sand, and detrital mud, but higher in deep mud (Fig. 12; ANOVA, F = 14.14, DF = 3, 20, p < 0.001, SNK).

Discussion

This study addressed the effects of both consumer (top–down) and resource (bottom–up) forces on a dominant bivalve in an estuarine soft-sediment community in which heterogeneous habitats differ in productivity. The major findings were that 1) consumers and resources jointly controlled benthic bivalve populations in an estuarine system, 2) consumer processes (i.e. local and per capita interaction strength of predation sensu Paine (1992) and Connolly and Roughgarden (1999)) were not correlated directly with food availability or productivity gradients, and 3) the role of consumer and resource control varied between habitats in the same ecosystem and for the same species. Clam density was positively correlated with resource abundance (sedimentary carbon) across shallow-mud, muddy-sand and deep-mud habitats, consistent with bottom–up control. *Macoma balthica* mortality (= local interaction strength)
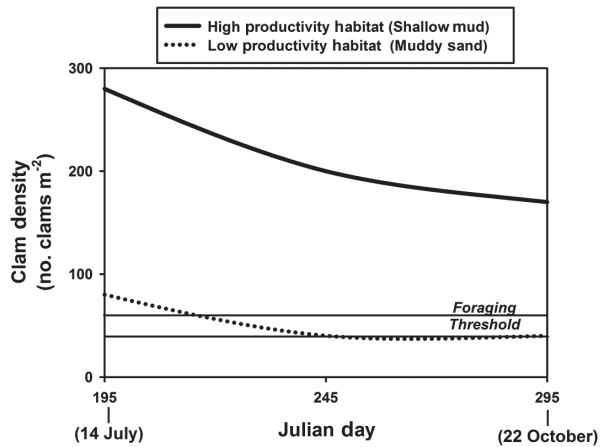
Figure 11. Theoretical examination of the potential for crabs to control clam densities. We used clam densities (derived from field data) at the beginning of the predation season (mid-July, Julian day 195), which decrease due to predator foraging over the next 100 days until Julian day 295 (October 22) and compared these with a low-density refuge zone. Survivorship curves are derived from instantaneous mortality rates calculated from the survival experiments for each habitat type, shallow mud and muddy sand. The low-density refuge zone, or foraging zone (20–60 clams m^{-2}), was derived from lab (Eggleston et al. 1992) and field experiments (Seitz et al. 2001). The top curve (solid line) depicts density in the high-productivity shallow mud habitat; here densities remained above the refuge zone, indicating that predation did not control clam density. The lower curve (dotted line) delineates densities in the low-productivity muddy sand habitat; here densities descend into the low-density refuge zone, suggesting that clam densities are controlled by predators.

and predator foraging efficiency (= local per capita interaction strength) were lower in the more productive habitat (shallow mud) contrary to predictions from productivity models (Oksanen et al. 1981, Menge et al. 1996), possibly due to deeper burial by *M. balthica* in mud habitat. In
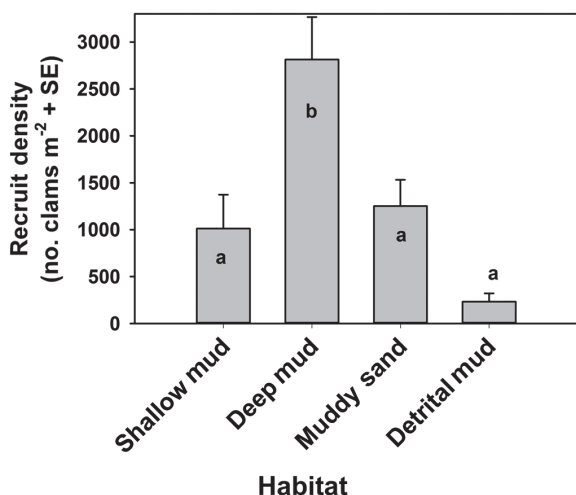

Figure 12. Spring recruitment of *Macoma balthica* from suction samples in April/early May 1998 at the same 24 sites as the initial density samples. Habitats included shallow mud, deep mud, muddy sand and detrital mud. Habitat types with same letter do not differ significantly (SNK test, p > 0.05).

the low-productivity, muddy-sand habitat, clam density declined to a low-density refuge, indicating that predators controlled clam density, whereas clam density in the productive shallow-mud habitat never declined to a low-density, predator-controlled level.

Resource control: clam density and growth

Higher sedimentary carbon and nutrient content in the productive habitat (shallow mud) relative to the low-productivity muddy sand habitat was likely due to the proximity of sources of riverine input (contributing food for deposit-feeding clams) to the shallow-mud sites. In contrast, amplified wave energy and shoreward bank erosion lowered nutrient inputs at muddy-sand sites. The detrital-mud habitat, although closest to riverine inputs, did not have elevated clam density with increased sedimentary carbon levels, probably because of the heightened biological oxygen demand and hydrogen sulfide associated with high detrital content.

The positive correlation of clam density with sedimentary food availability across habitats is consistent with the hypothesis of bottom–up control in both the shallow-mud habitat and in the muddy-sand habitat, as in other systems (Fretwell 1987, Power 1992, Menge et al. 1996, Seitz 2011). As predicted by current theory, and similar to the rocky intertidal zone (Menge et al. 1996), clam density, size and growth were higher in the more productive shallow-mud habitats than in muddy sands. Nutrient loading and transformation into food for marine benthos can increase abundance and biomass of infauna (Posey et al. 1995). Accordingly, in our study, higher food availability for prey in shallow- and deep-mud habitats likely fueled increased clam density, size and growth, as for various species in other ecosystems (Oksanen et al. 1981, Menge et al. 1996). In addition, clams at the productive, muddy sites could bury deeper and achieve a depth refuge from predation (Blundon and Kennedy 1982). Moreover, these patterns are compatible with long-term trends over decades of higher *M. balthica* density in deep muds than muddy sands in the Rhode River (Eggleston et al. 1992, Seitz et al. 2001).

Growth of bivalves is often related to ambient food supply (Beukema and Cadée 1991). Growth of *M. balthica* in our system was greater in shallow mud, where increased sedimentary carbon translated to higher food availability for this facultative deposit feeder (Beukema and Cadée 1991) and larger size, thus allowing deeper burial and escape from predation. Growth in the two habitats did not differ with caging treatment and therefore was not confounded with habitat-specific siphon nipping by predatory fish (Skilleter and Peterson 1994), which also did not differ in density between the two habitats. Enhanced suspension feeding in muddy-sand habitats with higher water flow could lead to faster growth and the associated deeper burial (siphons do not extend out onto the sediment surface), thereby enhancing survival of *M. balthica* (Lin and Hines 1994). In our study, clam growth was lower in the higher-flow muddy-sand habitat, suggesting that clams were not profiting from suspension feeding to overcome deficiencies in food available for deposit feeding.

Substantial increases in growth and size of *M. balthica* can translate into increases in reproductive output because fecundity in *M. balthica* increases linearly with body mass and exponentially with length (Honkoop and van der Meer 1997). Moreover, fewer and smaller eggs are often produced under unfavorable conditions, such as low food availability (Honkoop and van der Meer 1997). Hence, larger clams in high-productivity habitats could produce a much larger fraction of the larval pool for the total population encompassing all habitat types. This suggests that shallow-mud habitats serve as "source" habitats (sensu Pulliam 1988, Lipcius and Ralph 2011, Long et al. 2014) for other sub-habitats serving as "sinks" with interconnected larval transport. In particular, the detrital-mud habitat lacked adult clams, yet it harbored high densities of juvenile clams, and the muddy-sand habitat had very high juvenile mortality and correspondingly low adult densities. We suggest that detrital-mud habitats are population sinks for *M. balthica*, similar to deep-mud habitats in larger rivers where *M. balthica* recruitment is high, yet no juveniles survive to reproduce due to seasonal anoxia (Long et al. 2014).

Consumer control: predation and foraging efficiency

High clam density in deep- and shallow-mud habitats was not only associated with favorable habitat quality, allowing large adults of high fecundity to survive (Honkop and van der Meer 1997), but in shallow mud, high density was also associated with lower predation-induced mortality. Contrary to model predictions (Fretwell 1987, Oksanen et al. 1981), clam mortality was lower in the more-productive habitat (shallow mud) than in the less-productive habitat (muddy sand). The lower mortality was due to decreased predator foraging efficiency, rather than decreased predator density or size. In shallow-mud habitats, more prey items were available per predator, thus, each predator consumed a smaller fraction of the total available.

Several alternatives explain why predator foraging efficiency was reduced in shallow mud. First, decreased efficiency of predators (e.g. crabs) in shallow mud may have been because clams bury deep in these sediments (Hines and Comtois 1985), rendering them less susceptible to predation (Blundon and Kennedy 1982, Hines et al. 1990, Eggleston et al. 1992). Second, in shallow-mud habitats, excess prey may have swamped predators (Menge and Menge 2013). Third, mutual interference with conspecific predators (e.g. crabs) is greater in areas of high prey density, likewise leading to reduced foraging efficiency (Mansour and Lipcius 1991, Clark et al. 1999). Whatever the mechanism, in the Rhode River, there was low predation-induced mortality in shallow mud, and clam densities remained above a low-density refuge. This implies that the distribution of *M. balthica* was more influenced by bottom–up than top–down forces in that habitat. In contrast, in muddy sand, predators cropped clam densities down to a low-density refuge (Eggleston et al. 1992, Seitz et al. 2001), such that top–down regulation operated in that habitat.

Predator densities were positively correlated with densities of *M. balthica*, consistent with resource control, similar to rocky intertidal habitats where invertebrate abundance is driven by productivity across spatial scales of 100 + meters (Menge et al. 1996, 1997). Likewise, in the York River, a large-scale Chesapeake Bay tributary (50 km long), density of both predators and prey were greater at upriver locations where productivity was higher compared to downriver locations (Seitz 2011), as in other large-scale systems where predators cannot easily move among habitats (Mitchell and Lima 2002).

Potential spillover exploitation

Although the concept of "exploitation ecosystems" (sensu Oksanen 1990), or "spillover exploitation" was not directly tested, it is a likely explanation for the patterns observed in this system. In linked habitats where a relatively productive habitat occurs, exploitation tends to 'spill over' to a less-productive habitat when certain criteria are met (Oksanen 1990). These criteria include (a) at least two distinct habitats with differing productivity, (b) consumers that readily migrate between the habitats, (c) a high-productivity habitat with a carrying capacity to support an excess of consumers, and (d) a low-productivity habitat that is not capable of supporting the resident consumers. Consumers may choose a less-productive habitat temporarily where they would not persist in isolation (Fretwell 1987), and exploitation spills over from the more-productive habitat to the less-productive habitat (Holt 1985). These consumers may utilize the less-productive habitats either because their foraging efficiency is greater, there is less mutual interference with other predators (Mansour and Lipcius 1991), or they feed opportunistically as they travel to more productive habitats (Clark et al. 1999).

Several features of our system fit the criteria for spillover exploitation: (a) the shallow-mud habitat had greater sedimentary productivity than the muddy-sand habitat; (b) crabs tracked with ultrasonic tags migrate easily between habitats of varying quality in the Rhode River (Hines et al. 1995, 2009); (c) the density of clams to support predation was much higher in shallow-mud versus muddy-sand habitats; and (d) alternative benthic prey do not differ substantially between the two habitats in the Rhode River (Hines and Comtois 1985). More specifically, "spillover exploitation" explains the inverse relationship between proportional mortality and productivity in the Rhode River system; when conspecifics are at high densities, blue crabs may disperse into prey-impoverished patches to minimize agonistic encounters. Moreover, crabs in sand habitats tended to be slightly smaller than those in mud habitats and therefore may have been driven there by larger conspecifics.

Spillover exploitation has been documented in aquatic and terrestrial herbivore–plant interactions (Oksanen 1990, Power 1992). Though not explicitly described as "spillover exploitation," other authors have demonstrated predator migrations and differential feeding among habitats of distinct productivity or prey availability (Navarette and Manzur 2008, Witman et al. 2010). In larger-scale systems, spillover exploitation may be precluded when habitats differing in productivity are widely separated and thereby inaccessible to migrating consumers (e.g. the York River, Seitz 2011).

Recruitment and alternative factors affecting clam distributions

Although both consumers and resources partially dictated patterns in clam density and distribution, variation in recruitment to various habitats did not. Recruitment of invertebrate larvae can be highly dependent on currents in estuaries, and a higher larval supply in muds than muddy sands would potentially contribute to increased densities in shallow muds. In the Rhode River, *M. balthica* recruitment is generally greater to shallow-mud than to muddy-sand habitats (Eggleston et al. 1992), but this was not the case in our study.

Secondary dispersal to shallow mud or marsh habitats is a second explanation for the habitat-specific differences in *M. balthica* densities. This hypothesis is supported by two sets of observations. First, postlarval and juvenile *M. balthica* can undergo post-settlement migration; they occur commonly in the plankton, either as byssal-drifting postlarvae (Beukema 1993) or as buoyant juveniles (Armonies 1996). Second, the higher organic carbon in shallow mud as compared to muddy sand provides high-quality habitat to which post-settlement clams could migrate. As a caveat, tidal currents are generally slow in the Rhode River, so postlarval clams might not be able to drift very far. Differences in physical stress among habitats could also dictate densities, though clam mortality did not differ between control (caged) plots among the different habitat types, arguing against this alternative.

Models of co-limitation by predators and resources

In the Rhode River, both consumers and resources drove clam densities in the community, but consumers were not as important in our productive habitat. Food availability was important in increasing clam growth and density in the more-productive habitat, whereas predation was more important in reducing clam densities in the less-productive habitat. This may be because, in this small-scale system, habitats are linked and predators can move easily among all habitats (Clark et al. 1999, Hines et al. 2009). This allows predators to spill over into less-productive habitats, especially due to the aggressive and territorial nature of the main predator in this system, the blue crab. This conclusion is in accord with Menge and Olson's (1990) suggestion that predation is more important at small scales (e.g. the Rhode River) than large scales, as in fresh water streams (Power 1992), and it supports the conclusion that productivity dictates the relative importance of consumers or resources (Worm et al. 2002).

The idea of control by joint effects of top–down and bottom–up forces has yielded mixed results for marine systems. In rocky intertidal habitats, predation increases with productivity (Menge et al. 1996, 1997). In productive systems, energy is sufficient to support both herbivores and carnivores, consequently increasing the importance of predation in community regulation. In this case, nutrient or productivity levels apparently determine trophic complexity (Menge and Olson 1990), and increased productivity elevates the importance of predation in community regulation (Oksanen et al. 1981). In a meta-analysis across marine, freshwater and terrestrial systems, consumer versus resource control in plant communities depended on ecosystem type and producer diversity (Hillebrand et al. 2007). Thus, the effects of top–down and bottom–up forces cannot be viewed in isolation if we strive for a complete understanding of forces structuring communities (Menge et al. 1997, Worm et al. 2002).

The unique contribution of this study is in demonstrating the joint effects of consumer and resource control of a marine bivalve in a small-scale estuarine system with varying productivity. Moreover, we document that both predation and food availability can be important in this relatively small-scale system (5 km long), in accord with previous predictions regarding scale (Menge and Olson 1990, Worm et al. 2002). Moreover, the interconnected habitats appear to function as a source–sink metapopulation (sensu Lipcius and Ralph 2011) due to the varying magnitude of productivity and predation across habitats. Finally, the effects of consumer and resource control can be habitat-specific within a relatively small spatial scale. In summary, in this soft-sediment estuarine system, 1) consumers and resources jointly determined population dynamics, 2) predation intensity was inversely related to primary productivity; 3) the interconnected habitats likely function as a *M. balthica* source–sink metapopulation; and 4) consumer and resource effects differed according to habitat heterogeneity.

References

Armonies, W. 1996. Changes in distribution patterns of 0-group bivalves in the Wadden Sea: Byssus-drifting releases juveniles from the constraints of hydrography. – J. Sea. Res. 35: 323–334.

Beal, B. F. 2006. Relative importance of predation and intraspecific competition in regulating growth and survival of juveniles of the soft-shell clam, *Mya arenaria* L., at several spatial scales. – J. Exp. Mar. Biol. Ecol. 336: 1–17.

Beukema, J. J. 1993. Successive changes in distribution patterns as an adaptive strategy in the bivalve *Macoma balthica* (L.) in the Wadden Sea. – Helgol. Meeresunters 47: 287–304.

Beukema, J. J. and Meehan, B. W. 1985. Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. – Mar. Biol. 90: 27–33.

Beukema, J. J. and Cadée, G. C. 1991. Growth rates of the bivalve *Macoma balthica* (L.) in the Wadden Sea during a period of eutrophication: relationships with concentrations of pelagic diatoms and flagellates. – Mar. Ecol. Prog. Ser. 68: 249–256.

Beukema, J. J. et al. 2010. Long-term variability in bivalve recruitment, mortality and growth and their contribution to

fluctuations in food stocks of shellfish-eating birds. – Mar. Ecol. Prog. Ser. 414: 117–130.

Blundon, J. A. and Kennedy, V. S. 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. – J. Exp. Mar. Biol. Ecol. 56: 67–81.

Burkepile, D. E. and Hay, M. E. 2006. Herbivore vs nutrient control of marine primary producers: context-dependent effects. – Ecology 87: 3128–3139.

Clark, M. E. et al. 1999. Intraspecific interference among foraging blue crabs *Callinectes sapidus*: interactive effects of predator density and prey patch distribution. – Mar. Ecol. Prog. Ser. 178: 69–78.

Connolly, S. R. and Roughgarden, J. 1999. Theory of marine communities: competition, predation and recruitment-dependent interaction strength. – Ecol. Monogr. 69: 277–296.

Dekker, R. and Beukema, J. J. 2007. Long-term and large-scale variability in productivity of the tellinid bivalve *Macoma balthica* on Wadden Sea tidal flats. – Mar. Ecol. Prog. Ser. 337: 117–134.

Eggleston, D. B. et al. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. – Mar. Ecol. Prog. Ser. 85: 55–68.

Frederiksen, M. et al. 2006. From plankton to top predators: bottom–up control of a marine food web across four trophic levels. – J. Anim. Ecol. 75: 1259–1268.

Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? – Oikos 50: 291–301.

Gripenberg, S. and Roslin, T. 2007. Up or down in space? Uniting the bottom–up versus top–down paradigm and spatial ecology. – Oikos 116: 181–188.

Gruner, D. S. et al. 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. – Ecol. Lett. 11: 740–755.

Hairston, N. G. et al. 1960. Community structure, population control and competition. – Am. Nat. 94: 421–425.

Heck, K. L., Jr. and Crowder, L. B. 1991. Habitat structure and predator–prey interactions in vegetated aquatic systems. – In: Bell, S. S. et al. (eds), Habitat structure. The physical arrangement of objects in space. Chapman and Hall, pp. 281–299.

Hillebrand, H. et al. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. – Proc. Natl Acad. Sci. USA 104: 10904–10909.

Hines, A. H. 2007. Ecology of juvenile and adult blue crabs. – In: Kennedy, V. et al. (eds), Biology and management of the blue crab. Maryland Sea Grant Press, pp. 564–573.

Hines, A. H. and Comtois, K. 1985. Vertical distribution of estuarine infauna in sediments of central Chesapeake Bay. – Estuaries 8: 251–261.

Hines, A. H. et al. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. – Mar. Ecol. Prog. Ser. 67: 105–126.

Hines, A. H. et al. 1995. Movement patterns and migrations in crabs: telemetry studies of juvenile and adult behavior in *Callinectes sapidus* and *Maja squinado*. – J. Mar. Biol. Ass. UK 75: 27–42.

Hines, A. H. et al. 2009. Facilitation, interference, and scale: the spatial distribution of prey patches affects predation rates in an estuarine benthic community. – Mar. Ecol. Prog. Ser. 385: 127–135.

Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. – Theor. Popul. Biol. 28: 181–208.

Homer, M. et al. 1980. Quantitative approaches towards characterizing estuarine fish populations and communities. – Am. Fish. Soc. Proc. 4th Annu. Meeting, pp. 39–99.

Honkoop, P. J. C. and van der Meer, J. 1997. Reproductive output of *Macoma balthica* populations in relation to winter-temperature and intertidal-height mediated changes of body mass. – Mar. Ecol. Prog. Ser. 149: 155–162.

Horwood, J. W. and Goss-Custard, J. D. 1977. Predation by the oystercatcher, *Haematopus ostralegus* (L.), in relation to the cockle, *Cerastoderma edule* (L.), fishery in the Burry Inlet, South Wales. – J. Appl. Ecol. 14: 139–158.

Hunter, M. D. and Price, P. W. 1992. Playing chutes and ladders: bottom–up and top–down forces in natural communities. – Ecology 73: 724–732.

Jackson, J. B. C. et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. – Science 293: 629–638.

Janssen, A. et al. 2007. Habitat structure affects intraguild predation. – Ecology 88: 2713–2719.

Lin, J. and Hines, A. H. 1994. Effects of suspended food availability on the feeding mode and burial depth of the Baltic clam, *Macoma balthica*. – Oikos 69: 28–36.

Lipcius, R. N. and Ralph, G. M. 2011. Evidence of source–sink dynamics in marine and estuarine species. – In: Liu, J. et al. (eds), Sources, sinks and sustainability. Cambridge Univ. Press, pp. 361–381.

Lipcius, R. N. et al. 2007. Post-settlement abundance, survival, and growth of postlarvae and young juvenile blue crabs in nursery habitats. – In: Kennedy, V. and Cronin, E. (eds), Biology and management of the blue crab. Maryland Sea Grant Press, pp. 535–564.

Long, W. C. et al. 2014. Individual, population and ecosystem effects of hypoxia on a dominant benthic bivalve in Chesapeake Bay. – Ecol. Monogr. 84: 303–327.

Mansour, R. A. and Lipcius, R. N. 1991. Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams. – Mar. Ecol. Prog. Ser. 72: 239–246.

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

Menge, B. A. and Menge, D. N. 2013. Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions. – Ecol. Monogr. 83: 283–310.

Menge, B. A. and Olson, A. M. 1990. Role of scale and environmental factors in regulation of community structure. – Trends Ecol. Evol. 5: 52–57.

Menge, B. A. et al. 1996. Control of interaction strength in marine benthic communities. – In: Polis, G. A. and Winemiller, K. O. (eds), Food webs: integration of pattern and dynamics Chapman and Hall, pp. 258–274.

Menge, B. A. et al. 1997. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. – Limnol. Oceanogr. 42: 57–66.

Menge, B. A. et al. 2011. Linking long-term, large-scale climatic and environmental variability to patterns of marine invertebrate recruitment: toward explaining "unexplained" variation. – J. Exp. Mar. Biol. Ecol. 400: 236–249.

Mitchell, W. A. and Lima, S. L. 2002. Predator–prey shell games: large-scale movement and its implications for decision-making by prey. – Oikos 99: 249–259.

Navarette, S. A. and Manzur, T. 2008. Individual- and population-level responses of a keystone predator to geographic variation in prey. – Ecology 89: 2005–2018.

Oksanen, T. 1990. Exploitation ecosystems in heterogeneous habitat complexes. – Evol. Ecol. 4: 220–234.

Oksanen, L. et al. 1981. Exploitation ecosystems in gradients of primary productivity. – Am. Nat. 118: 240–261.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. – Nature 355: 73–75.

Paine, R. T. 2010. Macroecology: does it ignore or can it encourage further ecological syntheses based on spatially local experimental manipulations? – Am. Nat. 176: 385–393.

Posey, M. et al. 1995. Top–down vs bottom–up control of benthic community composition on an intertidal tideflat. – J. Exp. Mar. Biol. Ecol. 185: 19–31.

Power, M. E. 1992. Habitat heterogeneity and the functional significance of fish in river food webs. – Ecology 73: 1675–1688.

Pulliam, H. R. 1988. Sources, sinks and population regulation. – Am. Nat. 132: 652–661.

Reece, K. S. et al. 2008. Molecular epizootiology of *Perkinsus marinus* and *P. chesapeaki* infections among wild oysters and clams in Chesapeake Bay, USA. – Dis. Aquat. Org. 82: 237–248.

Seitz, R. D. 2011. Gradient effects on structuring of soft-bottom infauna: *Macoma balthica* and predation, recruitment and food availability. – J. Exp. Mar. Biol. Ecol. 409: 114–122.

Seitz, R. D. et al. 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. – Ecology 82: 2435–2451.

Seitz, R. D. et al. 2011. Diet selectivity of juvenile blue crabs (*Callinectes sapidus*) in Chesapeake Bay. – Int. Comp. Biol. 51: 598–607.

Seitz, R. D. et al. 2016. Data from: Consumer versus resource control and the importance of habitat heterogeneity for estuarine bivalves. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.4ht96>.

Skilleter, G. A. and Peterson, C. H. 1994. Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica* and interactions between competition and siphon cropping. – Oecologia 100: 268–278.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. – Ecology 73: 747–754.

Thrush, S. F. et al. 1997. The sandflat habitat: scaling from experiments to conclusions. – J. Exp. Mar. Biol. Ecol. 216: 1–9.

Trussell, G. C. et al. 2006. Depth-specific differences in growth of the reef sponge *Callyspongia vaginalis*: role of bottom–up effects. – Mar. Ecol. Prog. Ser. 323: 149–158.

Witman, J. D. et al. 2010. Coupling between subtidal prey and consumers along a mesoscale upwelling gradient in the Galapagos Islands. – Ecol. Monogr. 80: 153–177.

Worm, B. and H. K. Lotze. 2006. Effects of eutrophication, grazing, and algal blooms on rocky shores. – Limnol. Oceanogr. 51: 569–579.

Worm, B. et al. 2002. Consumer versus resource control of species diversity and ecosystem functioning. – Nature 417: 848–851.

Ysebaert, T. et al. 2002. Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. – Mar. Ecol. Prog. Ser. 225: 79–95.