

Variation in top-down and bottom-up control of marine bivalves at differing spatial scales

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At large spatial scales (>1 km), the forces structuring marine communities are diverse and include oceanographic, geological, and human processes, as well as availability of regional species pools. Few studies in marine and estuarine systems have examined the joint effects of predation (top-down) and food availability (bottom-up) in controlling populations at these scales. We compared the relative influence of top-down and bottom-up factors to population abundance of the infaunal clam *Macoma balthica* in two ecosystems differing in spatial extent by an order of magnitude: the York River, 50 km long, and the Rhode River, 5 km long. In both rivers, two habitat types could be differentiated by either high or low density of *Macoma*. In the York, *Macoma* abundance was tenfold greater upriver than downriver, predator abundance was greater in the high clam density habitat (i.e. upriver), and predation was only evident where clams were dense (i.e. upriver, where food availability for predatory crabs was elevated). In this large-scale system, predators were apparently unable to travel between upriver and downriver habitats where food availability differed. Moreover, sedimentary carbon (i.e. food for deposit-feeding clams) was significantly greater in the high clam-density habitat; this is consistent with the hypothesis that bottom-up factors principally dictate clam density, and moreover, that clam density drives predator density. In the Rhode River, a smaller-scale system, predators could easily move among habitats differing in clam density. *Macoma* abundance and predator abundance were both threefold greater in mud than sand. In contrast, predation intensity was higher in sand than mud, consistent with a hypothesis of top-down control. As in the large-scale system, sedimentary carbon was significantly greater in the high clam-density habitat (i.e. mud). In this smaller scale system, both top-down and bottom-up factors contributed to habitat-specific patterns in clam population abundance. Hence, in this marine benthic ecosystem, bottom-up control was important at both large and small spatial scales, whereas top-down control was only important at the smaller spatial scale.

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Introduction

The cause of spatial and temporal variation in community structure and abundance has been the focus of much recent ecological work. The relative importance of physical and biotic factors in regulating community patterns can vary with spatial scale (Menge and Olson, 1990; Levin, 1992; Hewitt *et al.*, 1997; Legendre *et al.*, 1997). Whereas at large spatial scales bottom-up forces are most important, top-down factors dominate at

local scales (Hairston *et al.*, 1960; Fretwell, 1977, 1987; Oksanen *et al.*, 1981; Menge and Sutherland, 1987; Menge and Olson, 1990; Power, 1992; Menge *et al.*, 1996). For example, at the local scale (from centimetres to tens of metres), wave-exposed and protected benches at a single rocky intertidal site had similar chlorophyll *a* concentrations, but differences in predation were discernible (Menge *et al.*, 1997), suggesting control of community structure solely by top-down forces at small spatial scales. In contrast, at a larger

scale (i.e. two sites spanning tens of kilometres), a difference in primary productivity (i.e. chlorophyll *a* concentration) accounted for variation in community structure; bottom-up forces apparently structured the community at this scale (Menge *et al.*, 1997). In addition, the size of the ecosystem can affect the transfer of productivity through the food web when movements of predators differ by scale. For example, at small scales (tens of metres), predators may be able to move between sites differing in food availability, whereas at large scales (tens of kilometres), such movements may not be possible (Menge *et al.*, 1996; Seitz, 1996).

The nature of the ecosystem also affects the prominence of top-down vs. bottom-up effects. For example, in freshwater systems, the effect of top-down control only penetrates one or two trophic links away from the predator (Brett and Goldman, 1996). Similarly, the effect of bottom-up control (i.e. nutrient enhancement) only permeates to the next trophic level, beyond which the effects are dampened (Brett and Goldman, 1996, 1997). Similarly, in marine pelagic systems, top-down or bottom-up effects are generally only realized one trophic level away from the manipulation. For example, nutrient additions generally lead to increases in phytoplankton biomass and carnivores reduce herbivore biomass, but there is a weak coupling between phytoplankton and herbivores (Micheli, 1999). In marine benthic systems, few studies have examined top-down and bottom-up control simultaneously (Posey *et al.*, 1995; Menge *et al.*, 1996). Improved understanding of consumer-resource dynamics, particularly in productive marine systems, would aid management of important upper-trophic-level fisheries (Micheli, 1999) and improve our understanding of the joint effects of top-down and bottom-up factors in marine systems.

In Chesapeake Bay, the infaunal clam *Macoma balthica* is a deposit feeder and facultative suspension feeder that can burrow to 30 cm deep (Hines *et al.*, 1990). Settlement occurs in two pulses (autumn-winter and spring), with abundance decreasing in late summer in conjunction with intense predator activity (Hines *et al.*, 1990). *Macoma* is a biomass dominant and contributes substantially to trophic transfer through the benthic-pelagic food web (Holland *et al.*, 1987; Baird and Ulanowicz, 1989). The blue crab *Callinectes sapidus* plays a crucial role in energy transfer in estuaries (Baird and Ulanowicz, 1989), serving as both prey and consumer, and is abundant and actively foraging from late spring through autumn in Chesapeake Bay (Hines *et al.*, 1990). Gut contents consist mainly of bivalve molluscs and mollusc siphons, predominantly *Macoma*, in addition to polychaetes, other crabs, and fish (Mansour, 1992; Ebersole and Kennedy, 1995).

To evaluate the relative influence of top-down and bottom-up factors on population density of the infaunal

clam, *Macoma balthica*, in two ecosystems differing in scale by an order of magnitude, we used two systems, the York River (50 km long) and the Rhode River (5 km long) in Chesapeake Bay. In the York River, two river zones (upriver and downriver) separated by 30 km were compared in terms of *Macoma* density, clam survival, food availability for clams, and predator density. In this large-scale system, predators do not easily migrate between the two zones investigated. Thus, we hypothesized that predation might not be equally important in both river zones.

For the Rhode River, we quantified density of *Macoma* in two habitat types, shallow mud (hereafter "mud") and shallow muddy sand (hereafter "sand"). We then experimentally tested survival of *Macoma* in field manipulations, and quantified food availability and predator density in the two habitat types. Depending on the outcomes of the manipulative and mensurative experiments, we were able to determine the relative roles of top-down and bottom-up factors to the system. We hypothesized that the density of *Macoma* was related to both food availability (bottom-up force) and predation (top-down force) in this relatively small-scale system where predators could easily move between both habitat types.

To compare the influence of top-down and bottom-up control between habitats differing in clam density, there are theoretical predictions for habitat-specific sedimentary food availability, predator abundance, and proportional mortality. Specifically, we would expect that under bottom-up control alone, food availability would be greatest in the high clam-density habitat [Figure 1(a)], but predator abundance or proportional mortality would be, at a minimum, equal between habitats or possibly greater in the high clam density habitat [Figure 1(a)]. In contrast, if clam patterns were dictated by top-down control alone, we would expect that food would be equally or less abundant in the high clam-density habitat, but predator abundance would be equal, higher, or lower, and proportional mortality would be lower in the high than in the low clam-density habitat [Figure 1(b)]. Finally, if both bottom-up and top-down control were important, we would expect higher food availability along with uncertain predator abundance and lower proportional mortality in the high clam-density habitat [Figure 1(c)]. Based on the relative magnitude of these factors, we can draw conclusions about top-down or bottom-up control in a given system.

This publication compares previous work conducted at two spatial scales, large (York River; R.D.S. and R.N.L., unpublished) and small (Rhode River; R.D.S., R.N.L., and A. H. Hines, unpublished). Our unique contribution is a synthesis of the influence of spatial scale on the relative magnitude of top-down and bottom-up control in a marine benthic system.

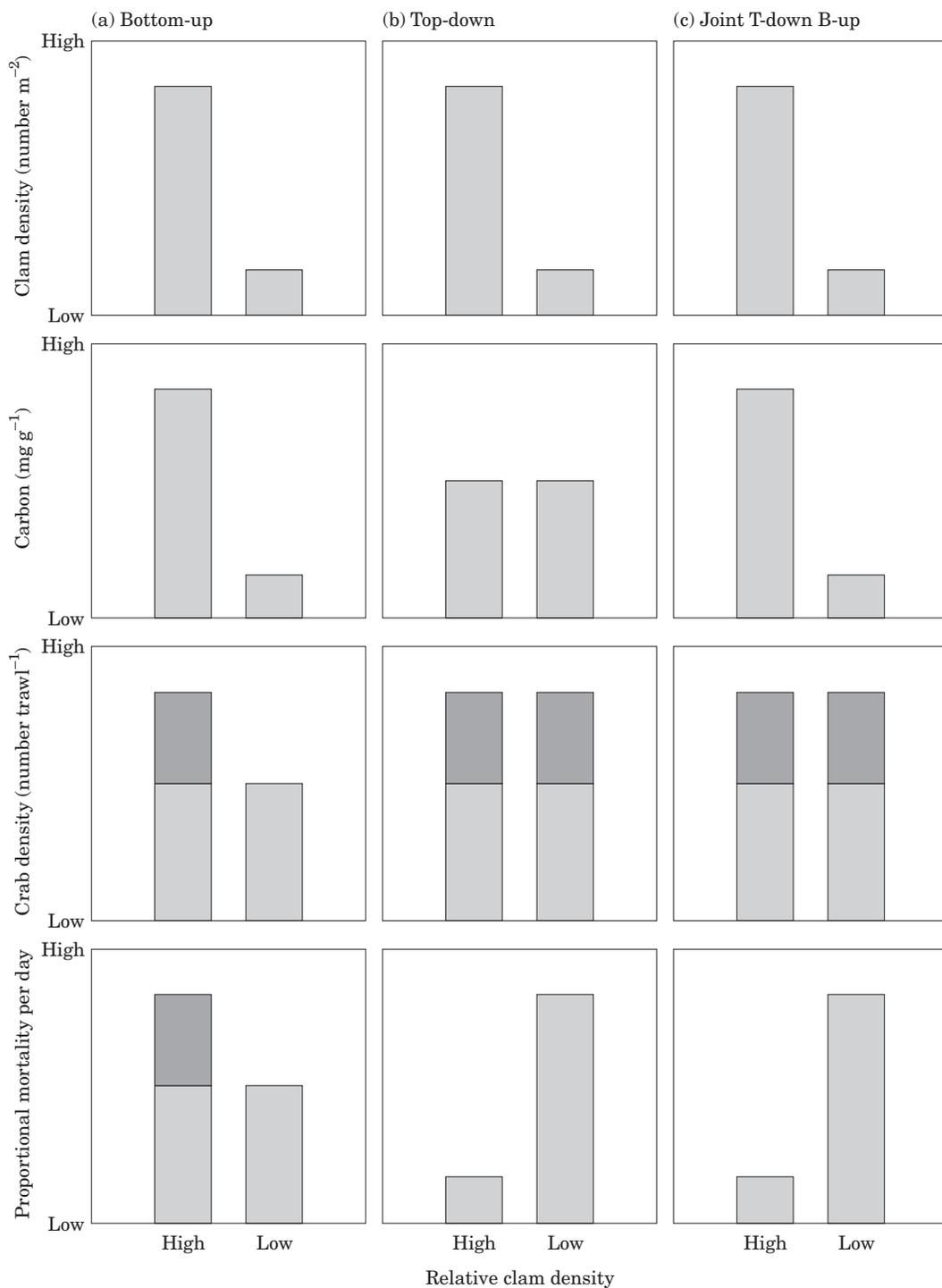


Figure 1. Theoretical predictions for the relative magnitudes of various factors between high and low clam-density habitats under (a) solely bottom-up control, (b) solely top-down control, and (c) joint bottom-up and top-down control. Light shading indicates one possible scenario and darker shading a second one; either possibility is viable.

Materials and methods

Study areas

This study was conducted in two tributaries of Chesapeake Bay: the York and Rhode rivers (Figure 2). The York River is a 50 km long tributary in lower Chesapeake Bay, whereas the Rhode River, in upper Chesapeake Bay, is approximately 5 km long.

In the York River, four sites were randomly chosen in muddy-sand sediments (1–2-m depth) in each of two zones differing by salinity and location, the “upriver” lower-mesohaline zone (S=5–10), and the “downriver” upper-mesohaline zone (S=15–20). Upriver sites were approximately 40 km from the mouth of the York River and located near West Point, whereas downriver sites were approximately 8 km from the mouth, near Gloucester Point [Figure 2(a)].

In the Rhode River, *Macoma* is commonly found in four major types of subtidal habitats, shallow mud flats, shallow muddy sands, shallow detrital muds, and deeper channel muds. From the accessible sites encompassing these habitat types, we selected six of each type for the mensurative sampling and field experiments. Four mud and four sand sites in 5–10 salinity were chosen for detailed manipulative experiments comparing *Macoma* density, growth, and predator-induced mortality.

Natural clam density and food availability

Similar methods were used in both the York and Rhode rivers with some differences in the time and duration of the experiments, as noted below. We assumed that temporal differences among years were inconsequential. In the York, natural ambient clam density was compared between upriver and downriver zones at each of the four sites per zone before and after a transplant experiment on 22–24 July 1995. In the Rhode, ambient clam densities were estimated and compared between two habitat types (mud and sand) on 22–24 August 1997. Either a PVC frame marking a 0.25 m² plot (York) or a cylinder of 0.17 m² surface area (Rhode) was used to excavate natural clams to 30–40 cm deep using a suction dredge (Orth and van Montfrans, 1987; Eggleston *et al.*, 1992). The samples were suctioned into a bag of 1-mm mesh and subsequently sieved on a screen of the same mesh. All clams were identified and enumerated, and shell length (SL, anterior to posterior) was measured with calipers accurate to 0.1 mm.

In the York, clam density between upriver and downriver zones was compared using the mean density from two paired plots at each site using a one-way Analysis of Variance (ANOVA) model. Similarly in the Rhode, mean ambient clam density from two paired plots at each site was compared between mud and sand habitats using a one-way ANOVA. Dependent variables were

log-transformed to meet assumptions of normality and homogeneity of variance when necessary (Underwood, 1997).

As *Macoma balthica* is a facultative deposit feeder, food availability was quantified as sedimentary organic carbon. Sedimentary carbon was determined by collecting 1–2 cm of surface sediment with a 3-cm-diameter core at each site. Sediments were stored in a freezer, defrosted, weighed, dried, prepared, and later combusted in a standard CHN analyser (see details of methods in Seitz *et al.*, 2001b).

Proportional mortality of clams

In the York, we tested the effect of predation by epibenthic crabs on *Macoma balthica* in two river zones with three sets of experiments using transplants of clams in summer 1995. Large adult clams were used in transplant trial 1 (mean size 25.5 mm), whereas small (mean 13.7 mm) and large (mean 24.5 mm) clams were transplanted at each site in subsequent trials. There was no difference in predation attributable to size, so both clam sizes were pooled for subsequent analyses. Trial 1 was conducted from 17–24 July 1995, trial 2 from 9–18 August, and trial 3 from 15–25 August. Clam sizes used in the experiments were based on random samples of clams collected from sediments in the area of the experimental plots. Proportional mortality in the high- and low-density habitats from each trial was compared with a two-way ANOVA using trial and habitat as factors.

In the Rhode, *Macoma* were selected (14–20 mm SL, mean 15.53 ± 0.10 mm) from the new cohort (6–23 mm SL) for the transplant experiments. Eight mud and four sand sites were used in the manipulative experiments; we included more mud than sand sites because of the higher variance in mean size and density of *Macoma* in the former. Each site contained two plots, an experimental (uncaged) and a control (caged) plot. Each plot consisted of a 0.5 m × 0.5 m (0.25 m²) area where 10 adult *Macoma* were marked, measured, and transplanted into the sediment among ambient clams. The transplant experiments in the York were conducted from 17 July–18 August 1995 and those in the Rhode from 1–23 August 1997. Although the dates of experiments were slightly different, all experiments were conducted during the high predation period during the middle of summer, so we assume that there was no considerable temporal variation in predation. This assumption was confirmed when we found no significant effect of time on proportional mortality in the York River experiments (Table 1).

In the Rhode River, habitat-specific growth of *Macoma* was also compared with marked and measured transplanted clams. Growth was quantified as the mean size increase (SL) of marked *Macoma* plot⁻¹ d⁻¹ over

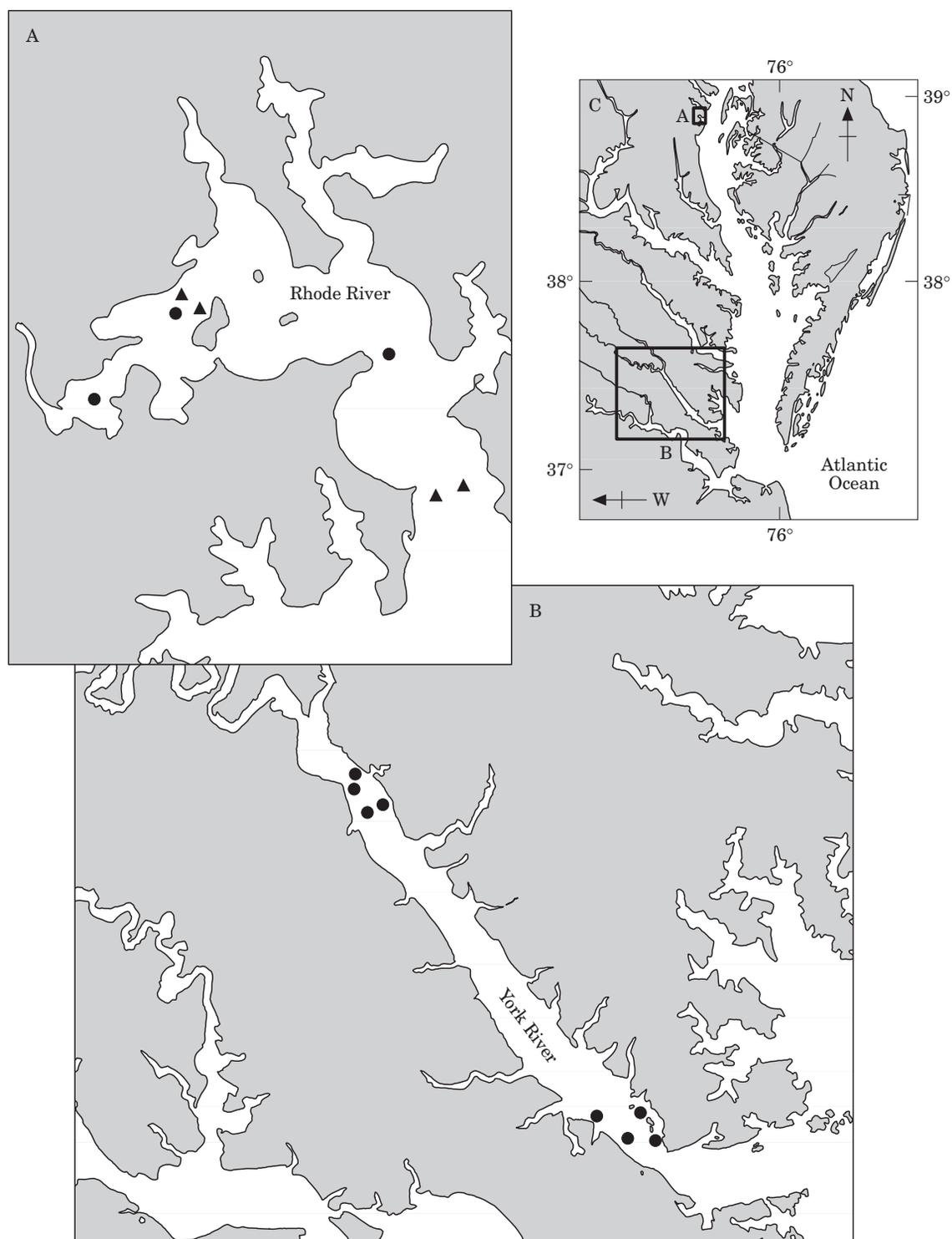


Figure 2. Map of Chesapeake Bay with insets of sampling locations in (a) the Rhode River (5 km) and (b) the York River (50 km). For the Rhode River, dots (predation experiments) and triangles (long-term sampling sites) are a representative subset of the random sampling sites (n=12).

Table 1. Two-way ANOVA using the proportional mortality of transplanted clams from three experimental trials in the York River with habitat (upriver or downriver) and time (trial 1, 2, or 3) as factors. Trial 1 was conducted from 17–24 July 1995, trial 2 from 9–18 August 1995, and trial 3 from 15–25 August 1995.

Source of variation	SS	d.f.	MS	F	p
Habitat	0.212	1	0.212	9.39	0.007
Time	0.034	2	0.017	0.75	0.485
Habitat \times time	0.081	2	0.041	1.80	0.195
Error	0.407	18	0.022		

the 20–22 d exposure period. Growth data were not transformed, as variances were homogeneous.

After clams were transplanted, all plots were covered with a predator exclusion cage (mesh size 13 mm) for an acclimation period of 48 h, a sufficient duration for clams to achieve a stable burial depth (Mansour and Lipcius, 1991; Eggleston *et al.*, 1992). After acclimation, cages were removed from half of the plots (uncaged treatment), left on the other half (caged controls), and all plots were left intact for 9 (York) or 21 days (Rhode). Mortalities were standardized to proportional mortality per day to account for varying exposure periods between different trials and rivers.

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 dredge with a collection bag of 1-mm mesh fitted to the outflow. Both marked and unmarked *M. balthica* and other clams were enumerated. Marked broken shells were noted as indicative of crab predation. Marked shells with no live individual were noted as evidence of physiological or handling mortality. Handling and physiological mortality in controls did not differ by time period in the York (ANOVA, $F=2.48$, $d.f.=23$, $p>0.05$), so all three trials were compared for differences by habitat.

In the York, predation-induced proportional mortality was determined for each site by subtracting the mean number of transplanted clams dead or missing from caged controls (handling mortality) from the number of clams missing for each experimental plot. In the Rhode, mortalities of marked *Macoma* from each caged plot (handling mortality) were subtracted from those in each paired uncaged plot. Thus, proportional mortality at each site was determined as (proportion of dead uncaged clams – proportion of dead caged clams).

Natural abundance of predators

In the York, predator abundance in shallow water was quantified by trawling on 21 and 22 July 1995. At each of the four upriver and downriver sites, demersal fish and crabs were collected with a 4.9-m semi-balloon otter trawl (mouth 3 m wide, net body of 5-cm mesh, and codend of 7-mm mesh). Two tows of 2 min each were

taken parallel to shore at each site, one with the tidal current, and one against the tidal current. The results of both trawls were pooled and analysed as one sample. Thus, four replicate samples were taken in each of the upriver and downriver zones. Although the estimate of predator abundance from trawling can be low owing to gear avoidance by predators (trawl efficiency for most predators is $\sim 22\%$; Homer *et al.*, 1980), all sizes of predators are caught with approximately equal efficiency (Homer *et al.*, 1980). Animals in each trawl were identified, counted, and measured (total length for fish, carapace width for crabs). Similar procedures were used at four sites each in high and low clam-density habitats in the Rhode.

In both rivers, density of crabs was compared between high and low clam-density zones using ANOVA. Log ($x+1$) transformations were used when variances of the raw data were heterogeneous (Cochran's test; Underwood, 1997).

Results

Ambient clam densities showed similar patterns between the two habitat types in both rivers. In the York, clam densities were significantly greater in the muddy upriver sites than in the more sandy downriver sites [Figure 3(a); ANOVA on log-transformed data, $F=8.37$, $d.f.=1, 6$, $p=0.025$]. Similarly, in the Rhode, clam densities were significantly greater in mud than in sand [Figure 3(b); ANOVA on log-transformed data, $F=13.11$, $d.f.=1, 6$, $p=0.011$]. To compare differences in controlling factors by spatial scale within the two study rivers, we used this differential in clam density to characterize two habitats in each river as "high clam density" and "low clam density." Note that the upriver habitat in the York was similar to the mud habitat in the Rhode (i.e. high density), and the downriver habitat was similar to the sand habitat (i.e. low density).

In both York and Rhode rivers, sedimentary organic carbon was significantly greater in the high than in the low clam-density habitat [Figure 3(c) and (d); York ANOVA, $F=12.8$, $d.f.=1, 8$, $p=0.037$, Rhode ANOVA, $F=87.33$, $d.f.=1, 10$, $p<0.001$]. More-

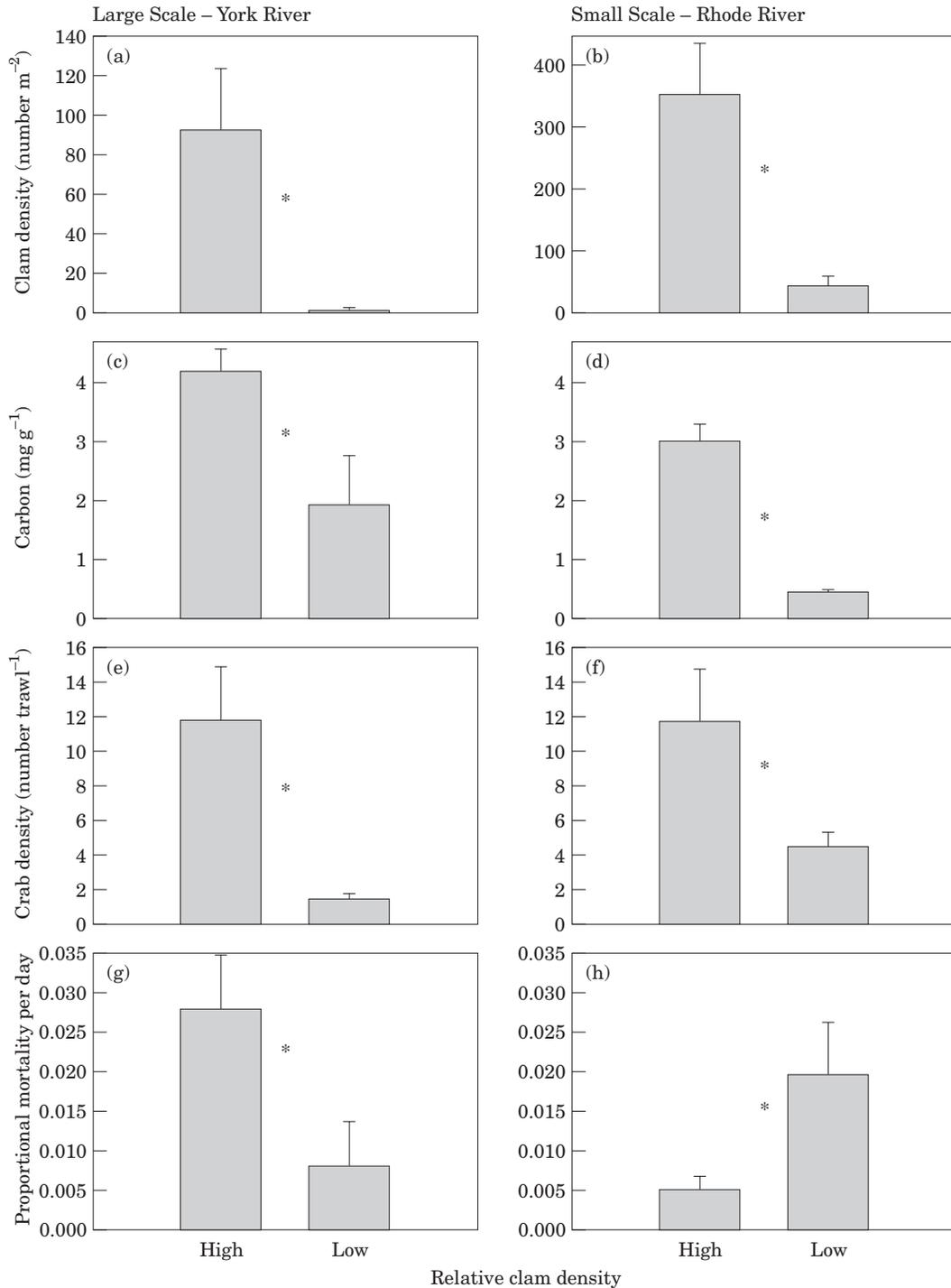


Figure 3. Comparison between habitats of “high” and “low” clam density showing clam density in (a) the York, and (b) the Rhode, sedimentary carbon in (c) the York, and (d) the Rhode, crab density in (e) the York, and (f) the Rhode, and proportional mortality in (g) the York, and (h) the Rhode. All panels show mean plus standard error (the number of samples contributing to data points are given in the text).

over, *Macoma* growth in the Rhode was significantly greater where sedimentary carbon was highest, in the high clam-density habitat (R.D.S., R.N.L., and A. H. Hines, unpublished data: nested ANOVA, $F=42.34$, d.f.=1, 2, $p<0.025$).

In both rivers, crab densities were greatest in the high clam-density habitats [Figure 3(e) and (f); York ANOVA, $F=10.89$, d.f.=1, 6, $p=0.016$; Rhode ANOVA on log-transformed data, $F=5.94$, d.f.=1, 6, $p=0.05$]. In contrast, the pattern in proportional mortality between habitat types differed by river. In the York River, proportional mortality was significantly greater in the high clam-density habitat across three trials [Figure 3(g); Table 1] and did not explain higher clam densities in that habitat. In contrast, in the Rhode River, proportional mortality was significantly greater in the low clam-density habitat [Figure 3(h); ANOVA, $F=6.42$, d.f.=1, 6, $p=0.042$]. Therefore, clam density, sedimentary organic carbon, and predator density were all higher in the muddier habitats. In contrast, proportional mortality was elevated in the muddier upriver habitat in the York, but reduced in the mud habitat in the Rhode.

Discussion

We used clam densities in two distinct habitat types within each of two rivers to define “high-density” and “low-density” habitats, and we compared the contribution of top-down and bottom-up factors to the maintenance of those clam densities. In the York River, at a large spatial scale (50 km), *Macoma balthica* density was orders of magnitude greater in muddy upriver than sandy downriver habitats. At a much smaller scale (5 km), *Macoma* density in the Rhode River was seven times greater in mud than in sand habitats. Sedimentary carbon (i.e. food for the facultative deposit-feeding clams), and growth rate were significantly greater in the high-density habitats. This suggests that bottom-up control was at least partially responsible for differential clam densities between habitats at both large and small spatial scales. Comparisons were made between the locations differing in spatial scale in different years, but all experiments were conducted during the high predation period during the middle of summer, so we assumed that there was no considerable temporal variation in predation.

Bottom-up factors are critical to freshwater populations (McQueen *et al.*, 1989), and there is evidence for food enhancement leading to higher primary consumer densities in marine systems (Pearson and Rosenberg, 1978; Kendall *et al.*, 1995; Frid *et al.*, 1996; Beukema and Cadée, 1997). In addition, the importance of predation in marine systems is appreciated (Paine, 1980; Menge and Sutherland, 1987), although most studies citing its influence have been conducted at the local scale

(Menge *et al.*, 1997). Nonetheless, the interaction of food availability and predation in driving abundance and distribution of marine organisms is neither well studied nor recognized (Menge *et al.*, 1996; Micheli, 1999).

Blue crabs are the major predators of adult clams in Chesapeake Bay (Hines *et al.*, 1990), and therefore crabs were initially hypothesized to be responsible for lower clam densities in certain habitats. Contrary to the prediction, crab density was significantly greater in habitats with high clam densities in both rivers, although predation-induced mortality of clams differed by river (i.e. spatial scale). In the York River, proportional mortality of clams was greatest in the high clam-density habitat, indicating that predation did not drive the difference in clam densities between the two habitats, and therefore that top-down control was not considerable. The patterns in this habitat correspond to the theoretical predictions for bottom-up control alone [Figure 1(a)]. The two habitats that varied in clam density were separated by approximately 30 km, and crabs could not readily migrate between these habitats (Mansour, 1992; Hines *et al.*, 1995). Crabs apparently congregated where their main food source (i.e. clams; Hines *et al.*, 1990) was in greatest abundance, yet crab predation in that zone was not extreme enough to drive clams to low densities.

Conversely, in the Rhode River, proportional mortality was greatest in the low clam-density habitat, although crab density was significantly greater in the high clam-density habitat. At this smaller spatial scale, predators could readily migrate between habitats that vary in prey abundance (Hines *et al.*, 1995), but crabs had greater foraging efficiency in the low clam-density habitat (R.D.S., R.N.L., and A. H. Hines, unpublished data). At this small scale, high predation contributed to lower clam densities in sand habitats, indicating that top-down control was important in determining spatial patterns in density across habitats. The patterns in this small-scale system corresponded to theoretical predictions for joint top-down and bottom-up control [Figure 1(c)].

The most likely mechanism underlying reduced foraging efficiency in the high clam-density mud habitat in the Rhode River is mutual interference among crabs (Mansour and Lipcius, 1991; Clark *et al.*, 1999). In this habitat, although there is plentiful prey, agonistic interactions among crabs may cause difficulty in feeding when crab densities are high. At this small spatial scale, a crab encountering a conspecific in the high clam-density habitat (mud) could easily migrate to the nearby low clam-density habitat (sand) to feed with less interference. Once there, although clams are lower in density, crabs may be able to search uninhibited to encounter the sparsely distributed clams. Alternatively, the lower proportional mortality in the high clam-density habitat

could be a result of swamping of predators by prey (R.D.S., R.N.L., and A. H. Hines, unpublished data).

We recognize that differences in recruitment often account for variation in infaunal densities between habitats (Gaines and Roughgarden, 1985; Underwood and Fairweather, 1989; Menge, 1991). In our systems, however, recruitment was no greater in the high clam-density habitats than in the low-density habitats in the York or Rhode rivers. In contrast, recruitment was lower to habitats where adult densities were high than to habitats where adult densities were low (R.D.S. and R.N.L., unpublished data; R.D.S., R.N.L., and A. H. Hines, unpublished data), indicating that recruitment was not responsible for observed differences in adult clam densities. In addition, some of the variation in clam density between locations in the York River can be explained by salinity, but a much greater percentage is due to differences in sedimentary carbon (Seitz *et al.*, 2001b).

Although top-down and bottom-up processes apparently drove the spatial patterns in distribution of *Macoma*, population regulation by density-dependent predation is a likely underlying mechanism. There is a density-dependent (i.e. sigmoid) relationship between predator-induced mortality and prey density for *Macoma* (Eggleston *et al.*, 1992; Seitz *et al.*, 2001a), whereby proportional mortality rises from low to moderate *Macoma* density and subsequently declines again at high density owing to predator satiation at approximately 100 m^{-2} .

If we examine proportional mortality of *Macoma* with prey density in our sites, mortality was lowered at low and high prey densities, as demonstrated for *Macoma* in other laboratory (Eggleston *et al.*, 1992) and field studies (Seitz *et al.*, 2001a). At low clam densities, where clam populations are regulated by a predator's functional response (see Seitz *et al.*, 2001a), predation tends to minimize spatial variation in density; therefore top-down control would not be expected, as observed in the York River. In contrast, where one habitat has high clam densities ($>100 \text{ clams m}^{-2}$) and one habitat has intermediate densities, then the lack of population regulation by a predator's functional response at moderate to high prey densities leads to a greater differential in density between spatially separated zones; therefore, top-down control is expected, as observed in the Rhode River. Moreover, although there may be population regulation through density dependence, this process does not explain why some habitats support different densities of clams before predation alters them. In these cases, bottom-up control most likely determines the spatial template of prey density before the effects of predation are realized because recruitment does not produce similar spatial patterns. Hence, the magnitude and importance of top-down control will depend on the predator's functional response and initial prey densities,

which we suggest are determined at least in part by bottom-up control.

In summary, at the large spatial scale (i.e. the York River), bottom-up factors were most significant in driving clam densities, whereas at a small spatial scale, both bottom-up and top-down factors drove clam densities. This is in agreement with Menge and Olson's (1990) theory suggesting that bottom-up factors are more important at larger spatial scales. Few marine examples have compared top-down and bottom-up factors at large and small scales, although Menge *et al.* (1996) suggested similar structuring forces in a rocky intertidal habitat.

A comparison of the joint effects of top-down and bottom-up factors on community structure is more common in freshwater systems than in marine systems; for freshwater systems, bottom-up factors are generally more influential than top-down factors (McQueen *et al.*, 1989). For soft-sediment systems, numerous studies highlight the dominance of predation (see review in Wilson, 1991), but these studies are typically at the local scale (tens to hundreds of metres). Herein, we have presented the first recognition that spatial extent is critical in determining the relative importance of top-down and bottom-up control in marine soft-bottom systems. Our unique comparison of driving forces in marine soft-sediment bivalves at differing spatial scales may serve as a model for other soft-sediment populations.

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