

## The roles of predation and postlarval transport in recruitment of the soft shell clam (*Mya arenaria*)

Heather L. Hunt<sup>1</sup> and Lauren S. Mullineaux

Biology Department, MS 34, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, 02543

### Abstract

Rates of mortality and transport of newly settled benthic invertebrates can be very high and potentially have profound effects on patterns of recruitment. We used the soft shell clam *Mya arenaria* as a model organism to compare the magnitude of rates of postlarval transport and predation on juveniles. We hypothesized that there is a critical size below which spatial variation in abundance of juvenile *Mya* is hydrodynamically controlled and above which abundance is mainly influenced by mortality, particularly due to epibenthic predators. To test this hypothesis, we examined transport and predation of early juvenile *Mya* in Barnstable Harbor, Massachusetts, USA. A caging experiment demonstrated that exclusion of epibenthic predators had a large impact on the density and size distribution of juvenile *Mya* within a few weeks of settlement and disproportionately affected juveniles of >2-mm shell length. Enclosure of the green crab *Carcinus maenas* changed the size distribution of *Mya* but did not significantly affect abundance. We attributed the effect of predator exclusion primarily to juvenile green crabs and fish. Current meter measurements suggested that tidal currents were strong enough to cause bedload transport of sediment and *Mya*. Measurement of gross and net rates of transport of *Mya*, using bedload traps and pans of defaunated sediment, confirmed that juveniles up to 5-mm shell length were routinely redistributed by tidal currents, particularly during spring tides. The number of postlarval *Mya* transported varied among sites and dates and was significantly related to ambient density of *Mya* and sediment flux. The loss of *Mya* during the caging experiment was compared to the rate of net flux of *Mya* due to transport during an intermediate tide. This comparison suggested that the loss due to predation was considerably larger than the flux due to transport for individuals >2 mm, but that rates of the two processes were more similar for individuals <2 mm. These experiments indicate that, while predation is likely the ultimate factor controlling abundance and size of juvenile *Mya* at this site, transport often redistributes individuals, at least at the scale of a tidal flat (10s to 100s of m).

Our understanding of recruitment variability of benthic marine invertebrates and its role in population and community dynamics has increased considerably over the last 20 years. Studies often have assumed that recruitment patterns reflect patterns of larval supply or settlement, although there has been increasing recognition of the importance of the early postsettlement period. Patterns set up at the time of settlement may have little effect on the distribution and abundance of adults because newly settled invertebrates usually

are subject to high rates of mortality (reviewed by Gosselin and Qian 1997; Hunt and Scheibling 1997). In soft-bottom habitats, in particular, macroinfauna remain mobile as juveniles, further modifying patterns of distribution and abundance (reviewed by Günther 1992; Armonies 1994). Knowledge of early postsettlement events is critical in understanding patterns of recruitment and the mechanisms that generate them.

Rates of mortality can be extremely high within the first few days to weeks after settlement (reviewed by Olafsson et al. 1994; Hunt and Scheibling 1997). Mortality patterns of early juveniles cannot necessarily be predicted from those of adults because vulnerability to different sources of mortality typically varies with size (see also Juanes 1992). Juvenile macrofauna generally live close to the sediment surface and are often particularly vulnerable to predation by epibenthic organisms (reviewed by Hunt and Scheibling 1997). For example, exclusion of predators in caging experiments often results in increased abundance of juvenile bivalves (Reise 1978; Virnstein 1979; Holland et al. 1980; Botton 1984; Hines et al. 1990). Juvenile macrofauna also are vulnerable to ingestion by deposit feeders (e.g., Elmgren et al. 1986) and to predation by meiofauna (Watzin 1983, 1986). Adult infauna can cause mortality of newly settled macrofauna by bioturbation of the sediments (e.g., Peterson 1977).

Postlarval dispersal also can be important in determining patterns of recruitment of macroinfauna. Changes in spatial distribution with age have been attributed to postlarval dispersal (e.g., polychaetes, Tamaki 1987; bivalves, Günther 1991). Postlarval individuals frequently are important in re-

<sup>1</sup> Current address: Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Rd., New Brunswick, New Jersey 08901 (hunt@imcs.rutgers.edu).

### Acknowledgments

We are particularly grateful to Aaron Stepler, Tom Marcotti, and the rest of the Town of Barnstable's Division of Natural Resources for providing transportation to the field sites and assistance with field work. The Upper Ocean Processes group from the Physical Oceanography Department, WHOI, loaned us the FSI current meters. Field assistance from Kristin France and sample processing by Archie McLean also were invaluable in completing this project. Stace Beaulieu, Lara Gulmann, Anna Metaxas, Susan Mills, and BLee Williams provided help in the field. We also thank Anna Metaxas and two anonymous reviewers for helpful comments on the manuscript. H.L.H. was supported by a postdoctoral fellowship from the National Sciences and Engineering Research Council of Canada (NSERC). The research was supported by a grant from the Rinehart Coastal Research Center at Woods Hole Oceanographic Institution and by the NOAA National Sea Grant College Program Office, under Grant NA86RG0075, Woods Hole Oceanographic Institution Sea Grant Project R/B-142. This is contribution number 10215 from Woods Hole Oceanographic Institution.

colonization after disturbance (e.g., Baggerman 1953; Commito et al. 1995a). For bivalves, transport of juveniles can occur through passive erosion and transport as bedload (e.g., Emerson and Grant 1991; Commito et al. 1995a,b) or active resuspension and byssal drifting (e.g., Sigurdsson et al. 1976; Beukema and de Vlas 1989; Armonies 1992). Commito et al. (1995a) found that postlarval *Gemma gemma* quickly recolonized natural and simulated horseshoe crab pits by passive transport, resulting in recovery to background densities within 1 d. Linkage of populations after settlement through postlarval dispersal may have important consequences for their dynamics.

Gaining a greater understanding of the relative importance of different factors influencing the dynamics of populations and communities is critical, but most studies in soft-bottom habitats concentrate on a single process (Constable 1999). The relative importance of early postsettlement mortality and postlarval transport in determining patterns of recruitment is presently unknown. Juveniles of the soft shell clam *Mya arenaria* live close to the sediment surface (Zwarts and Wanink 1989) and are vulnerable both to predation (Kelso and Wanink 1982; Blundon and Kennedy 1982a) and to bedload transport (Emerson and Grant 1991; Roegner et al. 1995; Dunn et al. 1999). In this study, we examined the effects of epibenthic predators on recent settlers in a caging experiment and measured rates of transport of juvenile *Mya* in bedload traps. Predation and transport were examined at the same sites in the same year, allowing us to assess the relative importance of the two processes. We hypothesized that there is a critical size below which juvenile clams are greatly susceptible to transport in tidal flows (and thus spatial variation in abundance is hydrodynamically controlled) and above which abundance and distribution of juveniles is determined by mortality from epibenthic predators. This hypothesis was based on our predictions that the rate of postlarval transport decreases with increasing size as *Mya* burrow deeper in the sediment (Zwarts and Wanink 1989) and their larger size makes them less susceptible to transport once eroded (effect of particle size on erosion threshold, e.g., Miller et al. 1977). We also predicted that juvenile clams must reach a threshold size before they become vulnerable to epibenthic predators. At large sizes, *Mya* may attain a refuge from predators due to depth of burial or size, although its relatively thin shell may not provide protection against crushing by large predators (Blundon and Kennedy 1982a,b; Ebersole and Kennedy 1995).

## Methods

**Study site**—This study was carried out on intertidal flats in Barnstable Harbor, Massachusetts, USA, on the north side of Cape Cod. Barnstable Harbor is a shallow bay with a large tidal range (mean = 2.9 m, spring = 3.4 m) and strong tidal currents with maximum velocities of 50 to 80 cm s<sup>-1</sup> during flood tide (described in Ayers 1959). At low tide, the harbor is characterized by narrow channels, numerous bars, and extensive sandflats. Three intertidal flats, Thatch Island and Green Point on the north side of the harbor and Calves Pasture on the south side, were chosen as field sites. These sites

also were used in prior studies of *Mya* recruitment (Marcotti and Leavitt 1997; Dunn et al. 1999 and unpubl. data). The study sites were in the midintertidal zone and were aerially exposed for an average of 6 to 10 h per day. The flats are comprised of fine sand with a median grain size of 125–150  $\mu\text{m}$  at Calves Pasture, and 150–180  $\mu\text{m}$  at Thatch Island and Green Point. Organic content of the sediment was 2% at Calves Pasture and 0.8% at the other two sites. Commercial and recreational digging of *Mya* occurs at Thatch Island and Calves Pasture, but not at Green Point, where *Mya* is less abundant. In 1998 and 1999 (Hunt unpubl. data), *Mya* was the most abundant bivalve at Thatch Island and Calves Pasture but was less abundant than *Gemma gemma* at Green Point. Several types of polychaetes, including *Streblospio benedicti* and other spionids, *Mediomastus californianus*, *Glycera dibranchiata*, *Nereis* sp., phyllodocids, and cirratulids, were common components of the macrofauna. A similar faunal assemblage is described in more detail by Sanders et al. (1962) and Green and Hobson (1970), who characterized the fauna of sand flats in Barnstable Harbor.

**Cage experiment**—To examine effects of epibenthic predators (e.g., the green crab *Carcinus maenas*, fish such as the mummichog *Fundulus heteroclitus*) on the abundance of recently settled clams, a caging experiment was set up at the Thatch Island and Calves Pasture sites, where recently settled (<500  $\mu\text{m}$ ) *Mya* were abundant during the previous summer and fall (1998; unpubl. data). The experiment at Calves Pasture was compromised by artifacts due to a high rate of accumulation of macroalgal and *Spartina* debris within the cages. As a result, we will not present the data from that site.

The predators manipulated in our enclosure treatments (juvenile green crabs, *Carcinus maenas*, and adult hermit crabs, *Pagurus longicarpus*) were chosen based on the literature and on their consumption rates of 1.4–1.5-mm *Mya* in laboratory experiments (unpubl. data). Fish such as the mummichog *Fundulus heteroclitus* and other small estuarine fish (sticklebacks, flounder, pipefish) also were considered to be potentially important predators, but they could not be enclosed in cages in the intertidal zone. The moon snail *Polinices duplicatus*, which is a predator of large juvenile *Mya* in Barnstable Harbor (Edwards and Huebner 1977; Wiltse 1980), was not used in an enclosure treatment because *P. duplicatus* of the sizes ( $\geq 13$  mm) present in the summer during our study did not feed on 1.5- or 2-mm *Mya* in laboratory experiments (unpubl. data). Several other species of invertebrates are known to be predators of *Mya* in other systems, but were not abundant at our study sites (also see *Discussion, Predation*). Although we focused on the effects of epibenthic predators in the present study, a companion study (K. France and H. Hunt unpubl. data) has addressed the effects of infaunal predators. Potential effects of infaunal predators are evaluated in the Discussion.

At Thatch Island, we set up five replicates (0.25 m<sup>2</sup> in area each) of each of five treatments: exclusion cage, control cage (with access holes for predators), hermit crab enclosure, juvenile green crab enclosure, and uncaged plot. Each enclosure contained one juvenile (ca. 2-cm carapace width [CW]) green crab, *Carcinus maenas*, or one adult hermit

crab, *Pagurus longicarpus*, resulting in a density of  $4 \text{ m}^{-2}$ . This density, the minimum possible for this cage size, was chosen to avoid unnaturally high predator densities (see *Discussion, Predation*). Cage frames were constructed of PVC pipe (1.25-cm diameter) and were covered on the top and sides with plastic netting (4-mm mesh size) secured with cable ties. Cages were 30 cm high and were buried 15 cm into the sediment to avoid erosion under the bottom edges; the two cages in which erosion occurred were excluded from analysis. Control cages had two rectangular ( $5 \times 10 \text{ cm}$ ) holes on each side, at the sediment surface, and four square ( $10 \times 10 \text{ cm}$ ) holes on the top to allow movement of predators through the cage. Green crabs occasionally were observed inside cage controls. The exclusion and enclosure cages were sampled through openings in two corners on the top of the cage, which were secured by Velcro fasteners and cable ties when not in use. Uncaged plots were marked with PVC posts.

The experiment was set up on 18 June 1999, 1 week after monitoring indicated a peak of abundance of recently settled ( $<500 \mu\text{m}$ ) *Mya*. The experimental area was  $15 \text{ m} \times 5 \text{ m}$  and oriented lengthwise in the direction of tidal flow. Each treatment was randomly allocated to each of five experimental units within each of five blocks. Blocks were used to distribute replicates in the along-stream and across-stream directions, although geographical constraints prevented the blocking from being fully balanced in both directions. Block was not included as a factor in the analysis because within-block replicates were not collected. Cages and uncaged plots were separated by 1.5 to 2 m in the along-stream direction and by at least 1 m in the across-stream direction. The top 2 cm of sediment in each plot were plowed by fingers to search for potential predators (crabs, moon snails), which were removed, and the density of the mud snail *Ilyanassa obsoleta* was adjusted to 38 per experimental unit (152 per  $\text{m}^2$ , the average of the density measured at this site over the summer of 1998; unpubl. data). Densities of *I. obsoleta* at Thatch Island were extremely variable in space and time, and previous research indicated that *I. obsoleta* can increase postlarval transport of *Mya* and change abundance of juveniles in the field (Dunn et al. 1999). To determine the abundance of *Mya*, one sediment core sample (diameter, 6.5 cm; depth, 2 cm) was collected from each cage and uncaged plot at the start of the experiment, and weekly for the following 3 weeks. Samples were randomly positioned using a grid with  $10 \times 10 \text{ cm}$  sections, but were at least at least 10 cm away from the cage walls to avoid edge effects. The core depth of 2 cm was selected to collect *Mya*  $<10 \text{ mm}$  shell length (SL) (Zwarts and Wanink 1989). The experiment ended when the cages disappeared on 10 or 11 July, most likely due to vandalism.

To enumerate the clams, the sediment samples first were sieved on a  $180\text{-}\mu\text{m}$  (diameter) mesh, preserved in 80% ethanol, and stained with Rose Bengal. Before sorting, samples were sieved through nested  $500\text{-}\mu\text{m}$  and  $180\text{-}\mu\text{m}$  sieves. Animals in the  $180\text{--}500\text{-}\mu\text{m}$  fraction were separated from most of the sand by swirling the sample in water and decanting the lighter supernatant fraction containing the animals. This process was repeated several times for each sample. Both the  $500\text{-}$  and  $180\text{-}\mu\text{m}$  fractions were examined under a binocular

microscope, all bivalves were counted, and *Mya* were measured in  $100\text{-}\mu\text{m}$  size classes using an ocular micrometer.

The initial variation in abundance of *Mya* (18 June) among the five cage and plot treatments was examined using one-way ANOVA. The data were log transformed prior to analysis to satisfy the assumption of homogeneity of variances, as indicated by Cochran's test (significance level  $\alpha = 0.05$ ). Because the same plots and cages were sampled each week, abundances of *Mya* in the 3 weeks following the setup of the experiment were examined using repeated measures ANOVA. There was one between-plot factor, treatment (five levels), and one within-plot factor, date (three levels). The Greenhouse-Geisser statistic was used to adjust the probabilities of the within-plot factor to compensate for any lack of compound symmetry of the covariance matrix (Systat 7.0). Planned post hoc comparisons were done using *t*-tests. To test for any cage artifacts, abundance in control cages was compared to that in uncaged plots. To test for the effect of predator exclusion, the abundance of *Mya* in exclusion cages was compared to that in control cages. The effect of the enclosure treatments was tested by comparing densities among green crab enclosures, hermit crab enclosures, and exclusion cages. Mean size frequency distributions of *Mya* on day 21 were compared among treatments using Kolmogorov-Smirnov tests.

Epibenthic predators also may have indirect effects on clams by consuming their infaunal predators and/or competitors. We addressed this question by enumerating the abundance of all polychaetes  $>500 \mu\text{m}$  in the cores collected on day 14. Polychaetes were identified to family, and one-way ANOVA was used to compare the abundance among treatments for each of the common families.

*Survey of predator densities*—Surveys of mobile epifaunal predators (crabs, fish, moon snails) were done by snorkeling at high tide on 19 July (Thatch Island, flooding tide), 21 July (Calves Pasture, ebbing tide), and 9 August 1999 (Thatch Island and Calves Pasture, ebbing tide). On each sampling date, two snorkelers swam along each of three,  $2 \times 30 \text{ m}$  belt transects, each snorkeler surveying a 1-m wide area. These belt transects were centered in the area where the caging experiments had been located and oriented in the along-stream direction. Snorkelers swam against the current to avoid disturbing the unsurveyed area. Since small individuals may not have been counted accurately in the surveys, crabs collected in bedload traps (see *Postlarval Transport*) also were used as an index of predator abundance.

*Current meter measurements*—We deployed a Falmouth Scientific Inc. (FSI) three-dimensional acoustic current meter on each of the three tidal flats for 24 h on three separate dates. The objective of these measurements was to characterize currents at each site over a range of tidal conditions, including neap (20 October 1998) and spring (7 November 1998 and 29 September 1999) tides. The final current meter deployment was synoptic with measurements of clam transport. The current meters were anchored by an aluminum post buried in the sediment and four stainless steel guy wires. The current meter's sensors were 22 cm above the sediment surface. Data were averaged over 1-min intervals. Current

speed ( $u$ ,  $\text{cm s}^{-1}$ , at height  $z$  above bottom) was converted to boundary shear velocity  $u_*$  using the relationship that, in the logarithmic region of a depth-limited boundary layer,  $U(z) = (u_*/\kappa) \ln(z/z_0)$ , where  $\kappa$  is a constant ( $= 0.40$ ) and  $z_0$  is the roughness height (cm), estimated to be 0.04 cm for sand (Soulsby 1990). This value for  $z_0$  was selected because the sediment at the sites generally was flat. The observed topography was limited to widely spaced pits (presumably from predator foraging) and occasional ripples that developed only during spring tides. However, shell fragments were common at the Green Point site and this added roughness may have resulted in a moderate (i.e., 20%) underestimation of  $u_*$  at this site. Estimates of  $u_*$  were useful for comparison to laboratory flume experiments on erosion of newly settled clams (Dunn et al. 1999). The flume measurements showed that an increase in  $u_*$  from 1.0 to 1.4  $\text{cm s}^{-1}$  resulted in a sharp increase in the erosion rate of small (1.8 mm SL) *Mya*.

**Postlarval transport**—Cylindrical sediment traps were installed flush with the sediment surface on each of the three tidal flats to provide direct estimates of the flux of clams and sediment transported as bedload or falling out of suspension in the water column. These bedload traps were based on the design of Emerson (1991) and were similar to those used by Commito et al. (1995b) and Turner et al. (1997). The traps were cut from PVC pipe (outer diameter 4.8 cm, inner diameter 3.6 cm, depth 60 cm) with an aspect ratio of 17 : 1. The bottom of each trap was sealed with a rubber stopper for easy removal of its contents. After the first deployment, a piece of galvanized metal mesh (4 mm) was placed inside each trap and 10 cm from the bottom to prevent any crabs that entered the traps from preying on clams accumulated on the bottom. Each trap was held inside an outer sleeve (outer diameter 6.0 cm, inner diameter 5.2 cm, depth 65 cm) by an o-ring in a groove machined on the outer surface of the trap. The outer sleeve allowed for easy deployment and removal of the trap without disturbing the surrounding sediment. Between 27 and 30 July, five outer sleeves were positioned at each of the three study sites, emptied of sediment, and capped. At the start of each trap deployment, the sleeves were uncapped and a trap filled with filtered seawater was placed inside each sleeve, flush with the sediment surface.

To measure the net transport of *Mya* (balance of immigration and emigration), we deployed pans (constructed of PVC, 15.2 cm diameter, 4 cm deep), filled with defaunated sediment and buried flush with the sediment surface (as in Turner et al. 1997). Sediment for the pans was collected at each study site in May 1999 when densities of juvenile *Mya* were low. The sediment was frozen and then sieved through a 500- $\mu\text{m}$  mesh sieve to remove shell fragments and dead macrofauna. Any previously frozen *Mya* remaining in the defaunated sediment could be differentiated from new individuals because the frozen *Mya* were gaping and contained very little flesh. When the pans were collected from the field, only the top 1 cm of sediment was retained and preserved because the volume of sediment was large, and our previous experience with burrowing of small clams indicated that they rarely occurred deeper.

Transport sampling was carried out shortly after the completion of the caging experiments on three dates selected to differ in tidal range: 2 and 19 August and 29 September 1999 (caging and transport experiments were conducted sequentially because of the labor involved). The first deployment was on a neap tide with a predicted tidal range of 2.19 m (19–20 August), while the other two deployments were on spring tides with ranges of 3.54 m (29–30 September) and 3.12 m (2–3 August). Mean wind conditions (obtained from NOAA for Hyannis, located approximately 5 km away) on the three sampling dates were similar, ranging from 3.3 to 3.7  $\text{m s}^{-1}$ , and were close to monthly averages for August (3.8  $\text{m s}^{-1}$ ) and September (3.4  $\text{m s}^{-1}$ ). On each sampling date, five bedload traps and five pans were deployed at each of the three sites for 24 h. Additionally, on each date that the traps and pans were collected, five cores (diameter, 6.5 cm; depth, 2 cm) were collected from each site to measure the ambient density of juvenile ( $< 10$  mm) *Mya*. Each ambient core was taken from a ca. 1  $\text{m}^2$  plot, randomly chosen from a visually estimated grid covering the site. During the 29–30 September sampling, a current meter also was deployed at each site (see *Methods, current meters*). The traps, pans, ambient cores, and current meters were deployed within the same area of the sites where the caging experiment and previous descriptive sampling (Hunt unpubl. data) was carried out. To enumerate the clams, the ambient cores and samples from the traps and pans were processed in the same manner as the cores from the caging experiment. After the clams were removed, the sediment from the bedload traps was dried at 78°C for 24 h and then weighed.

Two-way ANOVA was used to examine spatial and temporal variation in abundance of *Mya* collected in the traps, pans, and ambient cores. Each data set was analyzed separately. Site was a random factor (three levels), while date was considered a fixed factor because the sampling dates were selected to represent particular tidal heights: weak spring tide (2–3 August), neap tide (19–20 August), and strong spring tide (29–30 September). However, the sampling was not designed to specifically test the effect of tidal height because tidal heights were not replicated. Prior to ANOVA, the raw data were log or log ( $x + 1$ ) transformed to satisfy the assumption of homogeneity of variances, as assessed by Cochran's tests. Post hoc comparisons were made using Student-Newman-Keuls (SNK) tests. We anticipate that clams are transported by the same processes as similarly sized sediment. Thus, we expected clam transport to correspond to sediment flux and the proportional abundance of clams in ambient sediment. To test this hypothesis, we examined the correlation between transport of clams into the bedload traps and the product of sediment flux and ambient density of clams. Data were averages for each site on each sampling date.

## Results

**Predation**—At the start of the caging experiment on 18 June, mean density of clams at Thatch Island was 29,600  $\text{m}^{-2}$  (Fig. 1) and did not differ significantly among the caging treatments (Table 1). Repeated measures ANOVA (Table

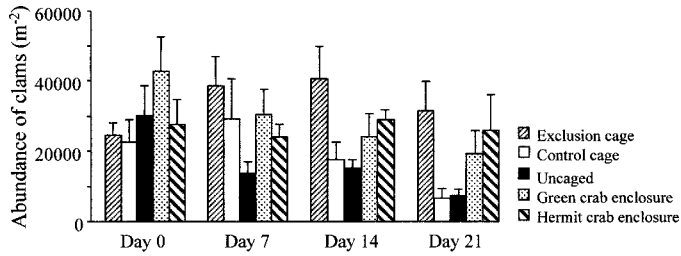


Fig. 1. Mean ( $\pm 1SE$ ,  $n = 5$ ) density ( $m^{-2}$ ) of *Mya* in exclusion and control cages, uncaged plots, and green crab and hermit crab enclosures at Thatch Island at the start of the caging experiment (day 0, 18 June 1999), and 7, 14, and 21 days later.

1) indicated that, after the start of the experiment, the abundance of clams differed among the five caging treatments and among sampling dates (days 7, 14, and 21), but that there was no significant interaction between date and treatment. The abundance of clams decreased from day 7 to day 21. Clam abundance differed significantly between exclusion cages and partial cages ( $t = 2.46$ ,  $df = 12$ ,  $0.01 < p < 0.05$ ), indicating a strong effect of complete cages. On day 21, clam abundance in complete cages was similar to initial values at day 0 but close to five times the abundance in partial cages. The lack of a significant difference in abundance between partial cages and uncaged plots ( $t = 0.88$ ,  $df = 12$ ,  $p > 0.20$ ) indicated that there was no net effect of a cage structure (Table 1). There were no significant differences among the three cage treatments (complete exclusion cage, green crab inclusion, hermit crab inclusion), indicating that enclosure of a green crab or a hermit crab had no net effect on clam abundance (Exclusion vs. hermit,  $t = 1.36$ ,  $df = 12$ ,  $0.10 < p < 0.20$ ; Exclusion vs. green crab,  $t = 1.59$ ,  $df = 12$ ,  $0.10 < p < 0.20$ ; Hermit vs. green crab,  $t = 0.22$ ,  $df = 12$ ,  $p > 0.50$ ). Given the observed variability in clam abundance and an  $\alpha = 0.05$ , analysis of statistical power indicated that only large differences in clam abundance between treatments could be detected (minimum detectable effect size: 16,896 ind  $m^{-2}$ ). The nonsignificant differences between treatments ranged from 10% (Hermit crab vs. green crab) to 73% (Exclusion vs. green crab) of the minimum

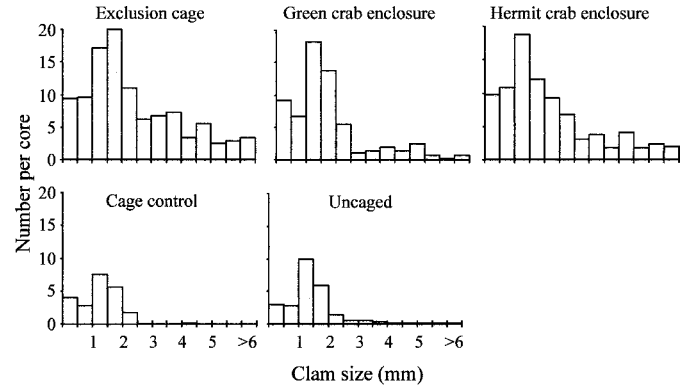


Fig. 2. Size frequency distributions (shell length, SL, in 0.5-mm size classes) of *Mya* in each of the caging treatments at the end of the experiment (day 21). Data are abundances per core (diameter 6.5 cm), averaged across treatments.

detectable difference. Median size of clams increased from 0.4–0.5 mm on June 18 to 0.6–0.9 mm after 1 week. Two weeks after the start of the experiment, median size was 1.3–1.4 mm in the exclusion cages and 1.1–1.2 mm in the other treatments. At the end of the experiment, exposure to predators (partial cages, uncaged plots) had decreased the density of clams of all size classes but had a disproportionately greater effect on the abundance of individuals  $>2$  mm SL (Fig. 2). Median size of clams in exclusion cages was 1.8–1.9 mm, whereas that in control cages was 1.2–1.3 mm. No individuals  $>4.5$  mm were collected from the partial cages or uncaged plots, whereas  $>10\%$  of clams in the exclusion cages were in this size range. At the end of the experiment, size distributions differed significantly between exclusion and control cages (Kolmogorov-Smirnov test,  $D = 0.37$ ,  $n_1 = 105$ ,  $n_2 = 22$ ,  $p < 0.05$ ) and between the exclusion and green crab inclusion treatments ( $D = 0.22$ ,  $n_1 = 105$ ,  $n_2 = 64$ ,  $p < 0.05$ ). The size distribution of clams did not differ significantly between the exclusion and hermit crab inclusion treatments ( $D = 0.11$ ,  $n_1 = 105$ ,  $n_2 = 86$ ,  $p > 0.05$ ), between the green crab and hermit crab inclusion treatments ( $D = 0.22$ ,  $n_1 = 64$ ,  $n_2 = 86$ ,  $p > 0.05$ ), or between the

Table 1. Analysis of density of *Mya* during the predation experiment at Thatch Island. Initial densities of *Mya* (log transformed) on day 0 of the experiment, 18 June, were compared among treatments (predator exclusion, partial cage, green crab enclosure, hermit crab enclosure, uncaged plots) with one-way ANOVA. Densities on days 7, 14, and 21 were analyzed with repeated measures ANOVA. Treatment was a fixed, between-plot factor, and date was a fixed, within-plot factor. The  $p$  value was adjusted by the Greenhouse-Geisser statistic ( $\epsilon = 0.853$ ).

		<i>df</i>	MS	<i>F</i>	<i>p</i>
Initial densities	Treatment	4	0.055	0.75	0.57
	Error	20	0.074		
Days 7, 14, 21					
	Between plots				
	Treatment	4	$1.37 \times 10^9$	3.025	0.045*
	Error	18	$4.52 \times 10^8$		
Within plots	Date	2	$6.45 \times 10^8$	6.84	0.005†
	Date $\times$ Treatment	8	$8.72 \times 10^7$		
	Error	36	$9.43 \times 10^7$		

\*  $p \leq 0.05$ .

†  $p \leq 0.01$ .

Table 2. Mean ( $\pm$ SE,  $n = 3$ ) density ( $m^{-2}$ ) of *Carcinus maenas* observed in snorkeling surveys on 19 and 21 July, and 9 August 1999 and mean ( $\pm$ SE,  $n = 5$ ) abundance (individuals trap $^{-1}$  d $^{-1}$ ) of juvenile *C. maenas* in bedload traps on 2–3 and 19–20 August, and 29–30 September. *C. maenas* collected in bedload traps were  $<30$  mm in carapace width. No snorkeling surveys were done at Green Point.

	Site	Density ( $m^{-2}$ ) from survey			Abundance (trap $^{-1}$ d $^{-1}$ ) from traps		
		19 Jul	21 Jul	9 Aug	2–3 Aug	19–20 Aug	29–30 Sep
Green crabs	Thatch Island	0.03 $\pm$ 0.01	nd	0.03 $\pm$ 0.01	1.5 $\pm$ 0.9	0.6 $\pm$ 0.2	1.0 $\pm$ 0.3
	Calves Pasture	nd	0.04 $\pm$ 0.01	0.03 $\pm$ 0.01	1.4 $\pm$ 0.2	0.2 $\pm$ 0.2	0.8 $\pm$ 0.4
	Green Point	nd	nd	nd	2.8 $\pm$ 0.8	0.8 $\pm$ 0.5	1.2 $\pm$ 0.6
Hermit crabs	Thatch Island	0.3 $\pm$ 0.09	nd	0.12 $\pm$ 0.03	0.8 $\pm$ 0.8	0	0.8 $\pm$ 0.5
	Calves Pasture	nd	0.04 $\pm$ 0.01	0.02 $\pm$ 0.01	0.4 $\pm$ 0.4	0	0.4 $\pm$ 0.2
	Green Point	nd	nd	nd	7.3 $\pm$ 2.7	0	2.4 $\pm$ 0.7

cage control and uncaged plots ( $D = 0.06$ ,  $n_1 = 22$ ,  $n_2 = 25$ ,  $p > 0.05$ ).

To determine whether epibenthic predators influenced the abundance of species other than *Mya*, we examined polychaetes in the core samples from day 14 and compared them among treatments using ANOVA. In these samples, the abundance of spionids ( $F_{4,14} = 0.38$ ,  $p = 0.82$ ) and the capitellid *Mediomastus* sp. ( $F_{4,14} = 0.06$ ,  $p = 0.99$ ) did not differ between treatments. The abundance of phyllodocids (probably *Eteone* sp.) differed among caging treatments ( $F_{4,14} = 3.36$ ,  $p = 0.04$ ). Phyllodocid abundance was significantly greater in exclusion cages (mean = 2,511  $m^{-2}$ ) than in the other treatments (mean = 894  $m^{-2}$ ), which did not differ significantly (SNK,  $p < 0.05$ ).

Mean density of green crabs observed in snorkeling surveys during daylight was 0.03  $m^{-2}$  at Thatch Island and 0.04  $m^{-2}$  at Calves Pasture (Table 2). Fish (probably Atlantic silversides, *Menidia menidia*) were observed on only one occasion. Accumulation of juvenile ( $<30$  mm) crabs in the bedload traps was high, up to 1.5 individuals d $^{-1}$  at Thatch Island, 1.4 individuals d $^{-1}$  at Calves Pasture, and 2.8 individuals d $^{-1}$  at Green Point (Table 2). These small juvenile green crabs were not observed by the snorkelers. These crabs may not have been active during the day or may have been

too small to detect. Mean density of hermit crabs in snorkeling surveys was greater at Thatch Island (0.2  $m^{-2}$ ) than at Calves Pasture (0.03  $m^{-2}$ ) (Table 2). Hermit crab accumulation was up to 0.8 individuals d $^{-1}$  at Thatch Island, 7.3 individuals d $^{-1}$  at Green Point, and 0.4 individuals d $^{-1}$  at Calves Pasture (Table 2).

*Postlarval transport*—Current speed at the study sites varied over the tidal cycle and was lowest at slack high tide and greatest during early flood and ebb tide (Fig. 3). Current speeds were lower during a neap tide (maximum = 34.2, 44.6, and 45.1  $cm\ s^{-1}$  at Calves Pasture, Thatch Island, and Green Point, respectively, on October 1998) than during two spring tides (November 1998, maximum = 48.1, 57.5, and 49.4  $cm\ s^{-1}$  at Calves Pasture, Thatch Island, and Green Point, respectively; September 1999, maximum = 43.2, 54.3, and 42.9  $cm\ s^{-1}$ , respectively). Spring tides generated shear velocities,  $u_*$ , of up to 3.5  $cm\ s^{-1}$  ( $U_{22} = 58\ cm\ s^{-1}$ ). Tidal current speeds were similar among sites, although speeds during flood tide were considerably more variable at Thatch Island than at the other two sites. Our current meter data revealed that a substantial proportion of observed velocities exceeded 22  $cm\ s^{-1}$  (indicated by a dashed line on Fig. 3), which corresponded to the  $u_*$  that caused significant erosion of 1.8-mm SL *Mya* in a prior laboratory flume experiment (Dunn et al. 1999). The percentage of observed shear velocities greater than 1.4  $cm\ s^{-1}$  was 63–77% on 7 November 1998, 44–65% on 29 September 1999, and 20–49% on 21 October 1998. Based on these results, we predict that a sizeable component of the population of early juvenile *Mya* should be eroded and transported semidiurnally by tidal currents in Barnstable Harbor, particularly during spring tides.

Mean gross sediment flux into the bedload traps ranged up to 73  $kg\ dry\ weight\ m^{-2}\ d^{-1}$  (Fig. 4). One bedload trap at Thatch Island completely filled with sand 29–30 September and was excluded from analysis, which did not affect the qualitative outcome. A significant interaction was detected between site and date (Table 3). At Thatch Island and Calves Pasture, sediment flux was significantly greater on 29–30 September than on the other dates, which did not differ significantly from one another (SNK,  $p < 0.05$ ). At Green Point, sediment flux was significantly greater on 2–3 August and 29–30 September (which did not differ significantly from one another) than on 19–20 August (SNK,  $p <$

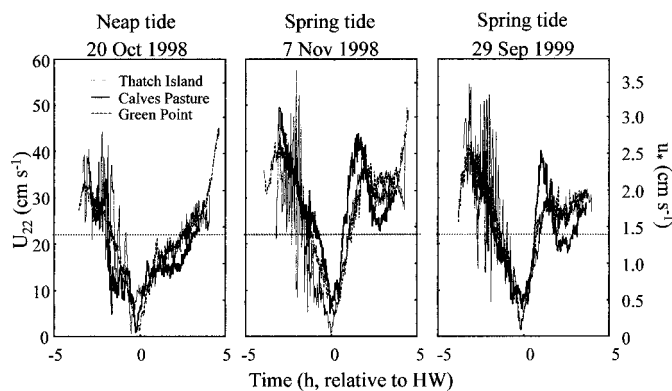


Fig. 3. Current speeds ( $cm\ s^{-1}$ ) recorded over a tidal cycle on a neap tide, 20 October 1998, and on two spring tides, 7 November 1998 and 29 September 1999, at Thatch Island, Green Point, and Calves Pasture. Data are presented as free stream velocity (22 cm above bottom) and converted to shear velocity ( $u_*$ , see Methods for the relationship between the two values). The dotted line indicates  $u_* = 1.4\ cm\ s^{-1}$ .

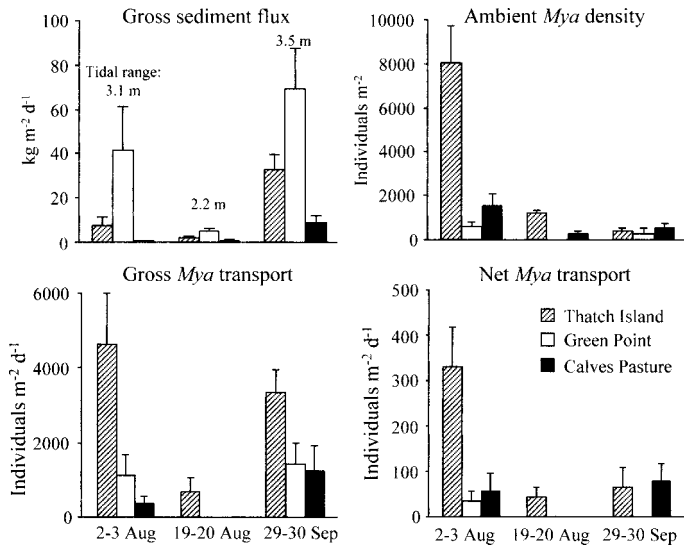


Fig. 4. Mean (+SE,  $n = 5$  for each combination of date and site) gross flux of sediment ( $\text{kg m}^{-2} \text{d}^{-1}$ ) in bedload traps, density ( $\text{m}^{-2}$ ) of *Mya* in the surrounding sediment, and gross and net transport of *Mya* ( $\text{m}^{-2} \text{d}^{-1}$ ) in bedload traps and pans of defaunated sediment, respectively, at Thatch Island, Green Point, and Calves Pasture on 2–3 and 19–20 August and 29–30 September 1999. Estimated tidal heights for each date are indicated on the graph of sediment flux.

0.05). Variation in sediment flux among dates was related to differences in tidal conditions, with lowest values during the neap, and highest during the spring, tides. We attribute this correlation to the increase in current velocities with higher tidal range, as demonstrated in the current meter records. The ranking of the sites for sediment flux was consistent among sampling dates, being greatest at Green Point and smallest at Calves Pasture. However, the magnitude and sta-

tistical significance of differences among sites varied among dates. On 2–3 August, sediment flux differed significantly among all three sites (SNK,  $p < 0.05$ ). On 29–30 September, sediment flux was significantly lower at Calves Pasture than at Green Point and Thatch Island, which did not differ significantly from one another (SNK,  $p < 0.05$ ).

The grain sizes of sediment in the traps were much larger than in the surrounding sediment. For example on 29–30 September, 12 (Calves Pasture) to 34% (Green Point) of the  $>180\text{-}\mu\text{m}$  component from the traps was  $180\text{--}250\ \mu\text{m}$ , whereas 47 (Green Point) to 93% (Calves Pasture) of this component in surrounding sediment was  $180\text{--}250\ \mu\text{m}$ . Most of the large particles collected in the traps, particularly at Calves Pasture, comprised organic debris such as macroalgae and *Spartina*.

Ambient densities of *Mya* were lower during the measurements of postlarval transport (Fig. 4) than during the caging experiment (Fig. 1). Ambient density of *Mya* varied significantly among the three sites (Fig. 4, Table 3) and was greatest at Thatch Island and lowest at Green Point (SNK,  $p < 0.05$ ). Ambient density did not vary significantly among dates, and the interaction between site and date was marginally nonsignificant ( $p = 0.07$ , Table 3).

The gross transport rate of *Mya* into the bedload traps ranged up to  $4,600\ \text{m}^{-2} \text{d}^{-1}$  (Thatch Island, 2–3 August; Fig. 4) and varied significantly among sites and dates (Table 3). There was no significant interaction between site and date (Table 3). The transport of clams into bedload traps was significantly greater on 2–3 August and 29–30 September than on 19–20 August (SNK,  $p < 0.05$ ). Clams were significantly more abundant in traps at Thatch Island than at the other two sites (SNK,  $p < 0.05$ ). We examined the relationship between gross transport of *Mya* into bedload traps and sediment flux and ambient density of *Mya*. There was a strong correlation ( $r = 0.87$ ) between mean gross transport

Table 3. ANOVA of sediment flux in bedload traps, ambient density of *Mya*, and transport of *Mya* into bedload traps and pans of defaunated sediment. Factors are date (2–3 Aug, 19–20 Aug, and 29–30 Sep), a fixed factor, and site (Thatch Island, Green Point, and Calves Pasture), a random factor.

		df	MS	F	p
Sediment flux in traps	Date	2	3.2	12.4	0.019*
	Site	2	2.8	31.9	0.001‡
	Date $\times$ Site	4	0.3	2.9	0.04*
	Residual	32	0.1		
Ambient density	Date	2	10.0	4.4	0.096
	Site	2	13.5	15.0	0.0001‡
	Date $\times$ Site	4	2.2	2.4	0.07
	Residual	35	0.9		
Gross transport of <i>Mya</i> (traps)	Date	2	17.2	32.1	0.003†
	Site	2	13.8	9.0	0.001‡
	Date $\times$ Site	4	0.5	0.3	0.84
	Residual	33	1.5		
Net transport of <i>Mya</i> (pans)	Date	2	3.7	2.6	0.19
	Site	2	5.8	8.3	0.001‡
	Date $\times$ Site	4	1.4	2.0	0.11
	Residual	36	0.7		

\*  $p \leq 0.05$ .

†  $p \leq 0.01$ .

‡  $p \leq 0.001$ .

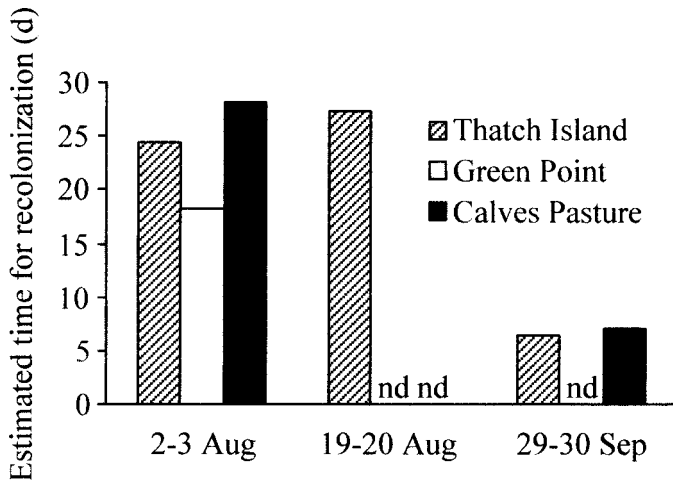


Fig. 5. Estimated time (d) required for *Mya* to recolonize disturbed sediment at Thatch Island, Green Point, and Calves Pasture, based on mean ambient density and net transport of clams on 2–3 and 19–20 August and 29–30 September 1999. Recolonization time was not calculated for dates when no *Mya* were detected in the ambient sediment (nd).

and the product of mean sediment flux and mean ambient density of *Mya*.

Maximum rate of net transport of clams, measured in pans of defaunated sediment, was  $330 \text{ m}^{-2} \text{ d}^{-1}$ , <10% of the gross transport measured in the bedload traps (Fig. 4). However, the patterns of spatial and temporal variation were similar to those observed in the traps. The net transport of clams varied significantly among sites but did not differ significantly between dates, and there was no significant interaction between site and date (Table 3). The abundance of clams in the pans was significantly higher at Thatch Island than at the other two sites (SNK,  $p < 0.05$ ). Net transport was 4–6% of ambient density on 2–3 August and 14–16% on 29–30 September. Net transport was used to estimate the time required for recolonization of a disturbed area to ambient density of *Mya*. Recolonization time was calculated by dividing mean ambient density by mean net transport for each site and sampling date. Estimated recolonization time of *Mya* at Thatch Island and Calves Pasture ranged from 6–7 d (29–30 September) to 24–28 d (2–3 August) (Fig. 5).

We compared the size distributions of *Mya* collected in traps and pans to those of *Mya* in the surrounding sediment from Thatch Island, the site with the largest abundance of *Mya* (Fig. 6). On 2–3 August, the size distribution in the pans at Thatch Island differed significantly from the size distributions in the traps and the ambient sediment (Kolmogorov-Smirnov test;  $D = 0.52$ ,  $n_1 = 30$ ,  $n_2 = 21$ , and  $D = 0.46$ ,  $n_1 = 30$ ,  $n_2 = 134$ , respectively,  $p < 0.05$ ), which did not differ from one another ( $D = 0.21$ ,  $n_1 = 21$ ,  $n_2 = 134$ ,  $p < 0.05$ ). On this date, no clams  $\geq 2$  mm were collected in the pans, and clams  $< 1$  mm were proportionately more abundant in the pans than in the traps or the surrounding sediment. On 29–30 September, there were no significant differences in size distributions among the three sources (traps vs. pans,  $D = 0.47$ ,  $n_1 = 19$ ,  $n_2 = 6$ ; pans vs. ambient,  $D = 0.57$ ,  $n_1 = 6$ ,  $n_2 = 7$ ; traps vs. ambient,  $D =$

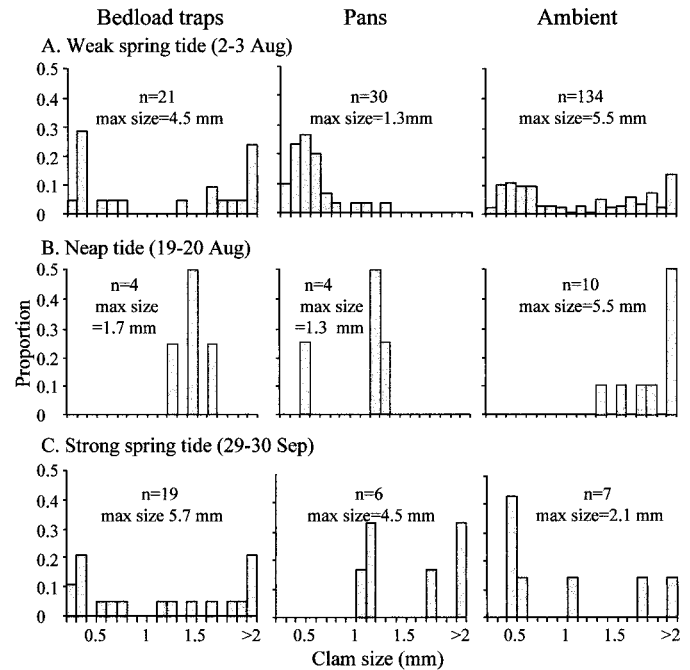


Fig. 6. Size frequency distributions (shell length, in 100- $\mu\text{m}$  size classes) of *Mya* in bedload traps, pans of defaunated sediment, and ambient sediment at Thatch Island on (A) 2–3 August, (B) 19–20 August, and (C) 29–30 September 1999. Data are pooled across replicates within a date. Sample size and maximum clam size are given.

0.24,  $n_1 = 19$ ,  $n_2 = 7$ ;  $p > 0.05$ ). Sample sizes were too small to make comparisons of size distributions for 19–20 August at Thatch Island and for the other sites, but numbers in the  $< 2$ -mm and  $\geq 2$ -mm size classes are presented in Fig. 6 (Thatch Island) and Table 4.

Clams  $\geq 2$  mm SL were not transported into bedload traps or pans at any of the sites on the neap tide (19–20 August) when currents were assumed to be weakest (Table 4). A few individuals in this size category were transported into traps on spring tides (2–3 August and 29–30 September) at each of the sites. Clams  $\geq 2$  mm were transported into pans only on the more intense spring tide (29–30 September), with two individuals at Thatch Island and one at Calves Pasture. These results indicate that although  $\geq 2$ -mm individuals of *Mya* were transported as bedload on each spring tide, net transport occurred only on the more intense of the two. The largest *Mya* collected was a 5.7-mm individual found in a bedload trap at Thatch Island on 29–30 September.

## Discussion

**Predation**—Within 3 weeks, complete cages had dramatic effects on the abundance of recently settled *Mya*. Densities were almost five times higher in exclusion cages than in partial cages or uncaged plots. This significant effect of exclusion cages on *Mya* abundance and the lack of a similar effect in the cage controls suggest that predation had strong effects on *Mya* abundance at the Thatch Island site within 1 month of settlement. In addition to consumption, the effects

Table 4. Number of <2 mm and  $\geq 2$  mm *Mya* collected in bedload traps and pans at Thatch Island, Calves Pasture, and Green Point during a weak spring (2–3 Aug), a neap (19–20 Aug), and a strong spring tide (29–30 Sep).

	Thatch Island		Calves Pasture		Green Point	
	<2 mm	$\geq 2$ mm	<2 mm	$\geq 2$ mm	<2 mm	$\geq 2$ mm
Gross transport						
2–3 Aug (weak spring)	16	5	2	0	2	3
19–20 Aug (neap)	4	0	0	0	0	0
29–30 Sep (strong spring)	15	4	5	2	8	0
Net transport						
2–3 Aug (weak spring)	30	0	5	0	3	0
19–20 Aug (neap)	4	0	0	0	0	0
29–30 Sep (strong spring)	4	2	6	1	0	0

of predators on recently settled clams may have included disturbance-induced mortality or resuspension and transport.

In soft-sediment habitats, caging experiments potentially can have a number of artifacts. By decreasing flow, cages may increase deposition and alter the sedimentary environment (Peterson 1979; Hurlberg and Oliver 1980). We observed no changes in the sediment in cages at Thatch Island, in contrast to a second experiment set up at Calves Pasture that did have large artifacts due to deposition of *Spartina* and macroalgal debris and was excluded from analysis. Changes in flow rate also may influence settlement rate of larvae into cages. We set up our experiment after a settlement peak to avoid initial differences in settler abundance between treatments. A comparison of clam size at the start of the experiment (400–500  $\mu\text{m}$ ) to that typical for settlement and metamorphosis (ca. 200  $\mu\text{m}$ , Loosanoff et al. 1966) and our knowledge of changes in clam size distribution over previous settlement seasons (unpubl. data) suggested that the caging experiment was set up within 1 week of a settlement peak. Cages also may decrease rates of erosion of *Mya* at high flow speeds (Gulmann et al. 2001). However, this process did not appear to affect our results because cage controls did not show the same *Mya* abundance patterns as cages. Partial cages may not be effective controls for complete cages if predators, such as crabs, are attracted to the structure of the cages or do not move through cages. Observations of cages at Thatch Island immediately before the tidal flats were exposed and of those at Calves Pasture by snorkeling showed that crabs did move into cages. We did not observe an accumulation of a large number of crabs in cages, although the abundance of predators may have differed at night. The similarity in *Mya* density between partial cages and uncaged plots suggests that the effects of complete cages were due to predator exclusion and not to caging artifacts. To reject this conclusion, one would need to invoke the existence of two artifacts that exactly cancelled one another out. Two compensating artifacts are possible, but are not the most parsimonious explanation for the patterns observed in the experiment.

Exclusion of epibenthic predators also has the potential to alter the abundance of other infauna, such as polychaetes. An increase in polychaetes can have multitrophic effects since a number of species of polychaetes are predatory (Commito and Ambrose 1985). The abundance of spionid and capitellid polychaetes did not differ between our caging

treatments, but phyllodocids, a family of predatory errant polychaetes, were more abundant in exclusion cages than in the other treatments. Differences in abundance of phyllodocids among treatments did not match the patterns of abundance of *Mya*, which did not differ between any of the complete cage treatments (exclusion, hermit crab, and green crab inclusions). This lack of correspondence of the patterns suggests that phyllodocids were not responsible for the effects of caging on clam abundance. In associated laboratory experiments, K. France (unpubl. data) found no significant effect of phyllodocids, cirratulids, or the capitellid *Mediomastus* from Barnstable Harbor on mortality of 300–450- and 600–800- $\mu\text{m}$  *Mya*. Tube-building spionid polychaetes were not manipulated in her experiment. The sediment cores collected in our caging experiment were only 2 cm deep and would not have effectively sampled any large predatory polychaetes (*Nereis*, *Glycera*). Therefore, we cannot rule out a change in abundance of these genera in complete cages. However, if the abundance of large predatory polychaetes had increased in the absence of predators, it is unlikely that we would have seen such a dramatic increase in clam abundance in complete cages. We conclude that polychaetes probably were not responsible for the effects of exclusion of epibenthic predators on clams.

Our observation that recruitment of *Mya* was greater in exclusion cages than in control cages or uncaged plots is consistent with results of other similar caging studies (Virnstein 1979; Holland et al. 1980; Botton 1984). However, the frequent sampling in the present study provides additional information on the size-specific shift in vulnerability of juvenile clams to predators. Complete cages increased the abundance of all sizes of clams but had a greater effect on individuals  $\geq 2$  mm SL. As a result, clam size distributions differed significantly between exclusion and partial cages. Cages can increase growth rates of bivalves (Peterson and Beal 1989). However, we think that the differences in size distributions between complete cages and the other treatments in our experiment were most likely due to size-selective predation. If cages influenced growth rates of *Mya* in our experiment, we would have expected the size distribution in partial cages to be intermediate to that in complete cages and uncaged plots rather than similar to that in uncaged plots. The scarcity of large juvenile *Mya* outside of protected locations also was demonstrated by other sampling. In weekly sampling from June to October 1998, cov-

ering two settlement peaks, we collected only one juvenile  $>4.5$  mm (4.9 mm) (unpubl. data). In 10-cm deep cores collected after the 1998 settlement season, in November 1998 and May 1999, we found low abundances of 3–6 mm *Mya* and no larger juveniles. In contrast, in the caging experiment, 10% of individuals in complete cages were  $>4.5$  mm after 3 weeks and 3% were  $>6$  mm. Even the PVC posts marking the uncaged plots appeared to provide protection from predators. When we removed the posts in October, we found them filled with 20–30 mm *Mya*. No *Mya* of this size were found in the surrounding sediment. These observations and the data from the caging experiment support the hypothesis that the differences in size distributions between the caging treatments were due to size-selective predation.

There are a number of species of epibenthic predators that may have been responsible for the effect of predator exclusion on *Mya* abundance. In particular, juvenile green crabs likely played an important role in the caging effects observed in the experiment. Inclusion of one juvenile *C. maenas* per cage did not significantly reduce clam abundance, but did affect clam size distribution. Juvenile green crabs in the inclusion cages were usually observed around the edges. If crabs foraged mostly around the edge of the cage, their effect would have been underestimated because sediment samples were collected away from the edges. The density of juvenile green crabs enclosed in the cages ( $4\text{ m}^{-2}$ ) was low compared to other studies (e.g., Richards et al. 1999). Given the high rate of accumulation of juvenile crabs in the bedload traps later in the summer (Table 2), this density may have been lower than natural densities in Barnstable Harbor and may have contributed to the lack of an effect of green crab enclosure on *Mya* density. Juvenile *C. maenas* are important predators of juvenile bivalves in other areas, particularly in Europe (Reise 1979; Scherer and Reise 1981; Jensen and Jensen 1985; Richards et al. 1999). *C. maenas* is an invasive species in North America. Declines in commercial harvests of *Mya* in New England in the 1940s and 1950s have been attributed by some authors to the spread of *C. maenas* north of Cape Cod (e.g., Glude 1955).

Fish such as mummichogs (Kelso 1979) and flatfish (Pihl 1985) also can be significant predators of juvenile *Mya*. The mummichog *Fundulus heteroclitus* is common in marshes and shallow bays in New England (Werme 1981; Ayvazian et al. 1992) and is a predator of juvenile *Mya* (Kelso 1979). Another killifish, *Fundulus majalis*, is less abundant but is also a predator of small bivalves such as *Gemma gemma* (Werme 1981). We observed few benthic feeding fish (probably Atlantic silversides, *Menidia menidia*) in our limited snorkeling surveys, but fish abundance is likely patchy and will vary with time of day and tidal state. On other occasions, we have collected mummichogs (*Fundulus heteroclitus*), three-spine stickleback (*Gasterosteus aculeatus*), pipefish (*Syngnathus fuscus*), and a flounder in Barnstable Harbor. Both fish and crabs may be more active on unvegetated tidal flats at night than during daylight surveys (e.g., Summerson and Peterson 1984). Also, the snorkeling surveys were carried out 1 week to 1 month after the end of the caging experiment, and predator densities may have differed somewhat from what they had been earlier in the summer.

Epibenthic invertebrates other than *C. maenas* are not

likely to be important predators of *Mya* in Barnstable Harbor. The hermit crab *Pagurus longicarpus* consumed juvenile (1–2 mm) *Mya* in the laboratory (unpubl. data). However, hermit crabs had no effect on *Mya* abundance or size distribution in the caging experiment, even though they were enclosed at densities ( $4\text{ m}^{-2}$ ) greater than those observed at Thatch Island during our snorkeling surveys ( $0.28\text{ m}^{-2}$  on 19 July and  $0.12\text{ m}^{-2}$  on 9 August). The moonshell *Polinices duplicatus*, a predator of large juvenile *Mya* in Barnstable Harbor (Edwards and Huebner 1977; Wiltse 1980), did not feed on 1.5 or 2 mm *Mya* in laboratory experiments (*P. duplicatus*  $>13$  mm; unpubl. data), and we observed few empty shells of juveniles with drill holes, indicative of gastropod predation, in the field. Other potential predators (e.g., birds, juvenile horseshoe crabs, *Crangon*) were rare in Barnstable Harbor during the experimental period (pers. obs.), although birds and horseshoe crabs can be present in substantial numbers at other times of year (T. Marcotti pers. obs.).

Both predator exclusion and enclosure of *C. maenas* had proportionately larger effects on individuals  $\geq 2$  mm SL than on smaller individuals, resulting in significant differences in size distributions between treatments. Predation on bivalves by *C. maenas* is generally size selective (reviewed by Juanes 1992). For example, Richards et al. (1999) found that enclosure of juvenile *C. maenas* in cages changed the size distribution of early juvenile *Cerastoderma edule* and *Macoma balthica* (median size 0.6 to 1 mm). Fish predation on juvenile bivalves also may be size selective. Based on stomach contents, Kelso (1979) found that predation of *F. heteroclitus* on *Mya* was restricted to 2–11-mm SL individuals, and within this size range, size of *Mya* consumed increased with size of fish.

*Postlarval transport*—Based on comparison of current meter data to results of previous flume studies (Dunn et al. 1999; Mullineaux et al. 1999; Gulmann et al. 2001), we predicted that tidal currents would cause bedload transport of sediment and juvenile *Mya* at our study sites, particularly during spring tides. Deployment of bedload traps demonstrated that juvenile *Mya*  $<2$  mm were routinely redistributed by tidal currents, but that *Mya*  $\geq 2$  mm were not transported on a neap tide. Gross transport was greater during a spring tide than during a neap tide, but postlarval transport occurred on each of our three sampling dates. Postlarval transport of *Mya* has been noted in other studies. At another site in Massachusetts, Matthiessen (1960) described temporal changes in the spatial distribution of 2–15-mm *Mya*, which were similar to changes in the distribution of sediments. In Nova Scotia, Canada, Roegner (1996) found that defaunated plots were recolonized by 1–6-mm *Mya*, similar to the size of *Mya* found in our study. Also in Nova Scotia, Emerson and Grant (1991) measured rates of transport of *Mya* using bedload traps. Their study focused on wind-driven resuspension and transport of larger juveniles (mean size 9 mm) in fall and winter storms since tidal currents at their site were not strong enough ( $<10\text{ cm s}^{-1}$  free stream velocity) to resuspend clams. Studies of bedload transport of bivalves have focused on wind-driven transport (Commito et al. 1995b; Turner et al. 1997), although tidal current transport has been described for postlarval *Macoma*

*balthica* drifting using byssal threads (Beukema and de Vlas 1989) and for subtidal bivalves under megatidal conditions (Olivier et al. 1996). The relative importance of tidal transport versus wind-driven transport at a given site presumably depends on a number of factors, including tidal range, wind velocity, direction, fetch, sediment characteristics, and the size and behavior of the juvenile bivalves. Our study reaffirms the importance of postlarval transport for *Mya* and demonstrates that tidally driven transport can be important in the intertidal zone.

Postlarval transport of *Mya* in Barnstable Harbor varied among sites and sampling dates with different tidal ranges. Transport of *Mya* into bedload traps was significantly greater at Thatch Island, where ambient density of *Mya* was greater than at the other sites. Greater peak current speeds at Thatch Island also may have contributed to between-site differences in rates of transport of *Mya*. As we had predicted based on the current meter data, flux of sediment and *Mya* in the traps was significantly lower during a neap tide (19–20 August) than during the other sampling dates. Despite similar current speeds at our three sampling sites, sediment flux varied among sites. These among-site differences in sediment flux may result from differences in other physical characteristics, such as exposure to waves (greatest at Green Point, as estimated visually) and erodability of sediment (most organic and cohesive at Calves Pasture). The linear relationship between transport of *Mya* in bedload traps and the product of sediment flux and clam abundance supports the hypothesis that clams are transported in the same way as similarly sized sediment particles. Commito et al. (1995b), examining wind-driven rather than tidal transport, also found a positive relationship between water velocity, sediment flux, and postlarval dispersal of bivalves. This relationship between postlarval transport and ambient clam density will likely hold in most environments, except where the source population of transported clams is far away, and differs in density from the local sampled population.

Net transport of *Mya* into pans of defaunated sediment was an order of magnitude lower than gross transport measured in bedload traps (Fig. 6a,b and Table 4). This lower rate is not surprising because abundance in the pans reflects both immigration and emigration. Also, only a small proportion of transported individuals are likely to burrow into the sediment and remain at a particular location. The time required for a disturbed area to be recolonized was estimated from net transport and ambient density of *Mya*. The estimated recolonization time was 1–4 weeks, comparable to the results of Roegner (1996), who found a recolonization time of 2–6 weeks for *Mya* on tidal flats in Nova Scotia. These estimates of recolonization rates indicate that postlarval transport results in regular turnover and redistribution of clams in Barnstable Harbor. Our estimates are conservative because they were calculated from net transport and because rough, disturbed sediment may trap more transported clams than the smooth sediment in our pans.

On spring tides, *Mya*  $\geq 2$  mm were transported into bedload traps in roughly the same relative abundances as they occurred in ambient sediments (Fig. 6). This size correspondence between clams in traps and ambient clams is consistent with the findings of Commito et al. (1995a) for *Gemma*

*gemma*. However, the  $\geq 2$ -mm size class was absent among *Mya* transported into traps on a neap tide. Furthermore, this size class was absent from the pans, except for a few individuals transported on the most intense tide sampled. This decrease in transport with size is likely due to the clams' burrowing behavior and susceptibility to erosion. As *Mya* increase in size, their siphon length and, therefore, maximum potential burial depth increases (Blundon and Kennedy 1982a; Zwarts and Wanink 1989), and they are less likely to become exposed by sediment erosion to the sediment–water interface. If *Mya* individuals do become exposed to the interface, larger ones are expected to be less susceptible to erosion. A decrease in erosion rate of *Mya* with increasing clam size has been observed in flume studies (Dunn et al. 1999; Mullineux et al. 1999; Gulmann et al. 2001). Size distributions differed significantly between traps and pans on a weak spring tide (2–3 August) but not on a strong spring tide (29–30 September). This difference between dates probably results from differences in the collection of particles between traps and pans. Bedload traps will collect particles moving along the bottom as bedload throughout the tidal cycle, and both traps and pans will collect particles dropping out of suspension when velocities decrease at slack high tide. If clams  $\geq 2$  mm were resuspended and transported in the water column on a strong spring tide but not on a weak spring tide, we would expect clams  $\geq 2$  mm in pans on 29–30 September but not on 2–3 August.

*Predation and transport: exploring their relative importance to recruitment*—By conducting the predation and transport experiments at the same sites during the same summer, our goal was to assess the relative importance of the two processes. As an example, we estimated the loss of *Mya* per day resulting from predation during the caging experiment and compared it to the net transport rate on 2–3 August (Fig. 7). We selected this particular date for transport because it occurred during intermediate tidal conditions and shortly after the completion of predation experiment when ambient densities of *Mya* were similar to those in July. Loss from predation was calculated from the difference in density between exclusion and control cages at the end of the caging experiment. Net transport per day was calculated from the sediment pans; these values are positive because the pans were initially unoccupied. Because clam densities in the ambient sediments decreased over the course of the experiments, and transport varies with ambient density, we adjusted the transport value on 2–3 August to correspond to densities midway through the predation experiment. *Mya*  $< 2$  and  $\geq 2$  mm SL (up to ca. 5 mm SL) were examined separately because the caging experiment suggested a sharp increase in vulnerability of *Mya* to predation around this size.

The comparison in Fig. 7 shows that the calculated loss rate due to predation was similar to the transport rate for the smaller ( $< 2$  mm) size class but that the transport rate decreased substantially for the larger ( $\geq 2$  mm) size class. These results suggest that the loss or gain of *Mya* at a particular site results from both hydrodynamic transport and predation for small individuals but is dominated by predation for larger ( $\geq 2$  mm) ones. The quantitative details of this comparison are specific to the dates on which the predation

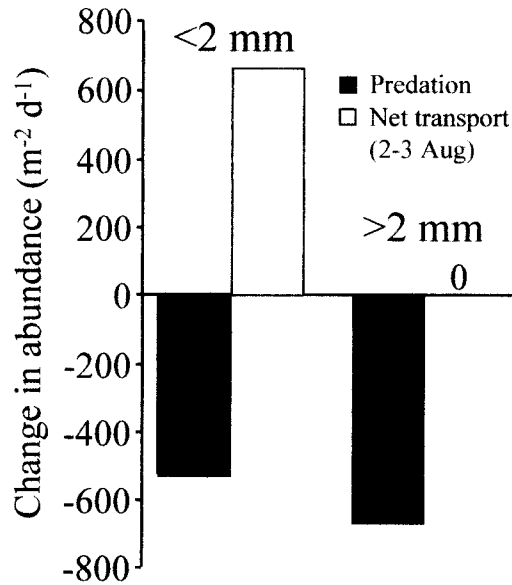


Fig. 7. Change in abundance of <2- and  $\geq 2$ -mm *Mya* ( $m^{-2} d^{-1}$ ) at Thatch Island due to predation during the caging experiment (18 June to 9 July) and to net transport on a weak spring tide (2–3 August). The effect of predation was estimated from the difference in abundance of clams between predator exclusion and partial cages on 9 July. Net transport was adjusted to account for differences in ambient density of *Mya* between the midpoint of the predation experiment and the date of the transport measurements. Displayed net transport for 2–3 August = (measured transport)  $\times$  (average of densities on days 7 and 14 of the predation experiment) / (density on 2–3 August).

(18 June to 9 July) and transport (2–3 August) studies were conducted, but the qualitative pattern (i.e., a decrease with clam size in the importance of transport relative to predation) appears general over time. No net transport of larger ( $\geq 2$  mm) *Mya* was observed during a weak spring (2–3 August) or a neap tide (19–20 August), and individuals of this size experienced net transport only on a strong spring tide (Table 4). Temporal variation in predation rates on <2-mm and  $\geq 2$ -mm clams can be examined by calculating the weekly loss rates of each size class during the predation experiment. In each week, loss due to predation of <2-mm clams was consistently 3% per day of the density in the exclusion cages. In contrast, weekly loss rates of  $\geq 2$ -mm clams varied as ambient densities changed: loss rates decreased from 10% per day in week 1, when densities in exclusion cages were  $180 m^{-2}$ , to 5% per day in week 3 as the clams grew and density of  $\geq 2$ -mm clams in exclusion cages increased to  $14,600 m^{-2}$ . Although predation of  $\geq 2$ -mm clams varied over time, losses due to predation always were considerably greater than the rates of transport.

A comparison of predation and postlarval transport must be interpreted carefully because predation results in a loss of clams whereas transport is a bidirectional flux (immigration and emigration) and potentially could result in either loss or gain. Because we used defaunated sediment in our net transport measurements, we constrained transport to be a gain, representing an area that acted as a sink to transported clams. Within a coastal embayment such as Barnstable Har-

bor, some locations may serve as sinks of postlarval migrants, others as sources, and still others may experience little net change in densities, despite substantial gross fluxes. Our intent herein was not to generalize from the specific balance of predation and transport found at Thatch Island, but rather to demonstrate the change in this balance as clams age and grow. This change occurred because flux of juvenile clams due to predation increased for clam sizes  $\geq 2$  mm, whereas flux due to transport decreased.

At the scale of the bay, predation probably has a greater effect than transport on the abundance and size of juvenile *Mya*. Most of the postlarval transport in Barnstable Harbor will redistribute individuals within the bay or within a tidal flat (tens to hundreds of meters). Postlarval transport may redistribute the effects of localized predation by exporting *Mya* recruits from areas where predation is low. Consequently, abundance of juvenile *Mya* will depend on predator abundance at the scale of the Harbor, but not necessarily at scales of tens of meters or less. The results of this study demonstrate that both predation and transport play important roles during the early postsettlement period for *Mya arenaria*. Our integrative approach, examining both processes at the same sites during the same year, allowed us to examine how the relative importance of these two processes changed through the early postsettlement stage of the clam's life cycle. This study highlights the necessity of gaining a greater understanding of the role and relative importance of early postsettlement processes in determining patterns of recruitment of benthic invertebrates.

## References

- ARMONIES, W. 1992. Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. *Mar. Ecol. Prog. Ser.* **83**: 197–206.
- . 1994. Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. *Helgol. Meeresunters.* **48**: 299–320.
- AYERS, J. C. 1959. The hydrography of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.* **4**: 448–462.
- AYVAZIAN, S. G., L. A. DEEGAN, AND J. T. FINN. 1992. Comparison of habitat use by estuarine fish assemblages in the acadian and virginian zoogeographic provinces. *Estuaries* **15**: 368–383.
- BAGGERMAN, B. 1953. Spatfall and transport of *Cardium edule* L. *Arch. Neerl. Zool.* **10**: 315–342.
- BEUKEMA, J. J., AND J. DE VLAS. 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. *Mar. Ecol. Prog. Ser.* **52**: 193–200.
- BLUNDON, J. A., AND V. S. KENNEDY. 1982a. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.* **65**: 67–81.
- , AND ———. 1982b. Mechanical and behavioral aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. *J. Exp. Mar. Biol. Ecol.* **65**: 47–65.
- BOTTON, M. L. 1984. The importance of predation by horseshoe crabs, *Limulus polyphemus*, to an intertidal sand flat community. *J. Mar. Res.* **42**: 139–161.
- COMMITO, J. A. 1982. Effects of *Lunatia heros* predation on the population dynamics of *Mya arenaria* and *Macoma balthica* in Maine, USA. *Mar. Biol.* **69**: 187–193.
- , AND W. G. AMBROSE. 1985. Multiple trophic levels in soft-bottom communities. *Mar. Ecol. Prog. Ser.* **26**: 289–293.

- , C. A. CURRIER, L. R. KANE, K. A. REINSEL, AND I. M. ULM. 1995a. Dispersal dynamics of the bivalve *Gemma gemma* in a patchy environment. *Ecol. Monogr.* **65**: 1–20.
- , S. F. THRUSH, R. D. PRIDMORE, J. E. HEWITT, AND V. J. CUMMINGS. 1995b. Dispersal dynamics in a wind-driven benthic system. *Limnol. Oceanogr.* **40**: 1513–1518.
- CONSTABLE, A. J. 1999. Ecology of benthic macro-invertebrates in soft-sediment environments: A review of progress towards quantitative models and predictions. *Aust. J. Ecol.* **24**: 452–476.
- DUNN, R., L. S. MULLINEAUX, AND S. W. MILLS. 1999. Resuspension of postlarval soft-shell clams *Mya arenaria* through disturbance by the mud snail *Ilyanassa obsoleta*. *Mar. Ecol. Prog. Ser.* **180**: 223–232.
- EBERSOLE, E. L., AND V. S. KENNEDY. 1995. Prey preferences of blue crabs *Callinectes sapidus* feeding on three bivalve species. *Mar. Ecol. Prog. Ser.* **118**: 167–177.
- EDWARDS, D. C., AND J. D. HUEBNER. 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. *Ecology* **58**: 1218–1236.
- ELMGREN, R., S. ANKAR, B. MARTELEUR, AND G. EJDUNG. 1986. Adult interference with postlarvae in soft sediments: The *Pontoporella-Macoma* example. *Ecology* **67**: 827–836.
- EMERSON, C. W. 1991. A method for the measurement of bedload sediment transport and passive faunal transport on intertidal sandflats. *Estuaries* **14**: 361–371.
- , AND J. GRANT. 1991. The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. *Limnol. Oceanogr.* **36**: 1288–1300.
- GLUDE, J. B. 1955. The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. *Trans. Am. Fish. Soc.* **84**: 13–26.
- GOSSELIN, L. A., AND P.-Y. QIAN. 1997. Juvenile mortality in benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* **146**: 265–282.
- GREEN, R. H., AND K. D. HOBSON. 1970. Spatial and temporal structure in a temperate intertidal community, with special emphasis on *Gemma gemma* (Pelecypoda: Mollusca). *Ecology* **51**: 999–1011.
- GULMANN, L. K., L. S. MULLINEAUX, AND H. L. HUNT. 2001. Effects of caging on transport of postlarval soft-shell clams (*Mya arenaria*). *J. Shellfish Res.* **20**: 135–142.
- GÜNTHER, C.-P. 1991. Settlement of *Macoma balthica* on an intertidal sandflat in the Wadden Sea. *Mar. Ecol. Prog. Ser.* **76**: 73–79.
- . 1992. Dispersal of intertidal invertebrates: A strategy to react to disturbances of different scales? *Neth. J. Sea Res.* **30**: 45–56.
- HINES, A. H., A. M. HADDON, AND L. A. WIECHERT. 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.
- HOLLAND, A. F., N. K. MOUNTFORD, M. H. HIEGEL, K. R. KAUMEYER, AND J. A. MIHURSKY. 1980. Influence of predation on infaunal abundance in upper Chesapeake Bay, USA. *Mar. Biol.* **57**: 221–235.
- HUNT, H. L., AND R. E. SCHEIBLING. 1997. Role of early post-settlement mortality in the recruitment of benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* **155**: 269–301.
- HURLBERG, L. W., AND J. S. OLIVER. 1980. Caging manipulations in marine soft-bottom communities: Importance of animal interactions or sedimentary habitat modifications. *Can. J. Fish. Aquat. Sci.* **37**: 1130–1139.
- JENSEN, K. T., AND J. N. JENSEN. 1985. The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *J. Exp. Mar. Biol. Ecol.* **89**: 157–174.
- JUANES, F. 1992. Why do decapod crustaceans prefer small-sized molluscan prey? *Mar. Ecol. Prog. Ser.* **87**: 239–249.
- KELSO, W. E. 1979. Predation on soft-shell clams, *Mya arenaria*, by the common mummichog, *Fundulus heteroclitus*. *Estuaries* **2**: 249–254.
- LOOSANOFF, V. L., H. C. DAVIS, AND P. E. CHANLEY. 1966. Dimensions and shapes of larvae of some marine bivalve molluscs. *Malacologia* **4**: 351–435.
- MARCOTTI, T., AND D. F. LEAVITT. 1997. The Barnstable Harbor shellfish recruitment enhancement project. Report to the Town of Barnstable, Massachusetts.
- MATTHIESSEN, G. C. 1960. Intertidal zonation in populations of *Mya arenaria*. *Limnol. Oceanogr.* **5**: 380–388.
- MILLER, M. C., I. N. MCCAVE, AND P. D. KOMAR. 1977. Threshold of sediment motion under unidirectional currents. *Sedimentology* **24**: 507–527.
- MULLINEAUX, L. S., R. DUNN, S. W. MILLS, H. L. HUNT, AND L. K. GULMANN. 1999. Biological influences on transport of postlarval soft-shell clams (*Mya arenaria*). Coastal Ocean Processes Symposium: A Tribute to William D. Grant; Woods Hole Oceanogr. Inst. Tech. Rep. **4**: 155–162.
- OLAFSSON, E. B., C. H. PETERSON, AND W. G. AMBROSE JR. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: The relative significance of pre- and post-settlement processes. *Oceanogr. Mar. Biol. Annu. Rev.* **32**: 65–109.
- OLIVIER, F., C. VALLET, J.-C. DAUVIN, AND C. RET. 1996. Drifting in post-larvae and juveniles in an *Abra alba* (Wood) community of the eastern part of the Bay of Seine (English Channel). *J. Exp. Mar. Biol. Ecol.* **199**: 89–109.
- PETERSON, C. H. 1977. Competitive organization of the soft-bottom macrobenthic communities of Southern California lagoons. *Mar. Biol.* **43**: 343–359.
- . 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons, p. 233–264. *In* Livingston R. J. [ed.], *Ecological processes in coastal and marine systems*. Plenum.
- , AND B. F. BEAL. 1989. Bivalve growth and higher order interactions: Importance of density, site, and time. *Ecology* **70**: 1390–1404.
- PIHL, L. 1985. Food selection and consumption of mobile epibenthic fauna in shallow marine areas. *Mar. Ecol. Prog. Ser.* **22**: 169–179.
- REISE, K. 1978. Experiments on epibenthic predation in the Wadden Sea. *Helgol. Meeresunters.* **31**: 55–101.
- . 1979. Moderate predation on meiofauna by the macrobenthos of the Wadden Sea. *Helgol. Meeresunters.* **32**: 453–465.
- RICHARDS, M. G., M. HUXHAM, AND A. BRYANT. 1999. Predation: A causal mechanism for variability in intertidal bivalve populations. *J. Exp. Mar. Biol. Ecol.* **241**: 159–177.
- ROEGNER, C., C. ANDRE, M. LINDEGARTH, J. E. ECKMAN, AND J. GRANT. 1995. Transport of recently settled soft-shell clams (*Mya arenaria* L.) in laboratory flume flow. *J. Exp. Mar. Biol. Ecol.* **187**: 13–26.
- ROEGNER, G. C. 1996. Hydrodynamic factors affecting the recruitment of bivalve molluscs in a tidally dominated estuary. Ph.D. thesis, Dalhousie University.
- SANDERS, H. L., E. M. GOUDSMIT, E. L. MILLS, AND G. E. HAMPSON. 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.* **7**: 63–79.
- SCHERER, B., AND K. REISE. 1981. Significant predation on micro- and macrobenthos by the crab *Carcinus maenas* L. in the Wadden Sea. *Kieler Meeresforsch. Sonderh.* **5**: 490–500.
- SIGURDSSON, J. B., C. W. TITMAN, AND P. A. DAVIES. 1976. The dispersal of young post-larval bivalve molluscs by byssus threads. *Nature* **262**: 386–387.

- SOULSBY, R. L. 1990. Tidal-current boundary layers, p. 523–566. In Le Méhauté B. and D. M. Hanes [ed.], *The sea*. Wiley.
- SUMMERSON, H. C., AND C. H. PETERSON. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Mar. Ecol. Prog. Ser.* **15**: 63–77.
- TAMAKI, A. 1987. Comparison of resistivity to transport by wave action in several polychaete species on an intertidal sand flat. *Mar. Ecol. Prog. Ser.* **37**: 181–189.
- TURNER, S. J., J. GRANT, R. D. PRIDMORE, J. E. HEWITT, M. R. WILKINSON, T. M. HUME, AND D. J. MORRISEY. 1997. Bedload and water-column transport and colonization processes by post-settlement benthic macrofauna: Does infaunal density matter? *J. Exp. Mar. Biol. Ecol.* **216**: 51–75.
- VIRNSTEIN, R. W. 1979. Predation on estuarine infauna: Response patterns of component species. *Estuaries* **2**: 69–86.
- WATZIN, M. C. 1983. The effects of meiofauna on settling macrofauna: Meiofauna may structure macrofaunal communities. *Oecologia* **59**: 163–166.
- . 1986. Larval settlement into marine soft-sediment systems: Interactions with the meiofauna. *J. Exp. Mar. Biol. Ecol.* **98**: 65–113.
- WERME, C. E. 1981. Resource partitioning in a salt marsh fish community. Ph.D. thesis, Boston University.
- WILTSE, W. I. 1980. Effects of *Polinices duplicatus* (Gastropoda: Naticidae) on infaunal community structure at Barnstable Harbor, Massachusetts, USA. *Mar. Biol.* **56**: 301–310.
- ZWARTS, L., AND J. WANINK. 1989. Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves. *Mar. Biol.* **100**: 227–240.

Received: 22 June 2000

Accepted: 24 September 2001

Amended: 23 October 2001