

Effects of epibenthic predators in flow: transport and mortality of juveniles of the soft shell clam *Mya arenaria*

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ABSTRACT: During the early post-settlement period, dispersal and predation can drastically alter patterns of distribution and abundance of benthic invertebrates. These 2 processes may interact if predators cause disturbance and alter rates of transport of juvenile clams. In this study, experiments were conducted in an annular flume to examine the effect of 2 epibenthic predators, the seven-spine bay shrimp *Crangon septemspinosa* and juveniles of the green crab *Carcinus maenas*, on rates of erosion and mortality of juvenile soft shell clams *Mya arenaria*. Clams were exposed to 2 flow speeds ($u = 9 \text{ cm s}^{-1}$, shear velocity $u_* = 0.30 \text{ cm s}^{-1}$ and $u = 27 \text{ cm s}^{-1}$, $u_* = 0.97 \text{ cm s}^{-1}$) in the presence and absence of predators. Erosion of sediment and clams, and formation of ripples occurred at the high-flow velocity only in the presence of shrimp. This also occurred when shrimp disturbed the sediment prior to the experimental run, suggesting that shrimp activity changed bottom topography and the erosion threshold of the sediment. Juvenile green crabs caused less disturbance of the sediment and their activities did not result in transport of sediment or clams. Gut content analysis indicated that juvenile green crabs preyed on juvenile *M. arenaria*. Shrimp preyed on clams in 1 of 2 experiments, probably due to a difference in size of clams between experiments (shell length = 1.0 vs. 3.0 mm). This study demonstrates that, in addition to causing mortality, predators can indirectly affect their prey by causing transport of sediment and associated small benthic invertebrates.

KEY WORDS: Predators · Postlarval dispersal · Bivalves · Sediment transport

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INTRODUCTION

Recruitment variability can play an important role in the population and community dynamics of benthic marine invertebrates, potentially limiting the distribution and abundance of adults, and the intensity of biological interactions. Initial distributions and abundance of benthic marine invertebrates are influenced not only by larval supply and settlement patterns, but also by spatially-varying rates of early post-settlement mortality (reviewed by Ólafsson et al. 1994, Hunt & Scheibling 1997) and dispersal (reviewed by Günther 1992, Palmer et al. 1996). Postlarval dispersal of macrofaunal invertebrates is likely to be particularly important in soft-bottom habitats because juveniles often live close to the sediment surface where they are likely

to be eroded by currents and waves. We currently have a poor understanding of the role of postlarval dispersal in determining patterns of distribution and abundance of benthic macrofauna.

Many bivalves are known to disperse as postlarvae (Williams & Porter 1971, Sigurdsson et al. 1976, Baker & Mann 1997). Bivalves and the sediment they are living in may be resuspended and transported short distances in the water column or may travel along the bottom as bedload (Commito et al. 1995b, Turner et al. 1997). A variety of factors can influence the rate of postlarval transport of bivalves. For example, laboratory experiments have demonstrated that the vulnerability of juvenile *Mya arenaria* to transport increases with current velocity (Roegner et al. 1995) and decreases with increasing clam size (Mullineaux et al.

1999). Behaviour of bivalves also can be important in preventing or promoting resuspension and dispersal. Burrowing can allow bivalves to maintain position in the sediment and avoid passive erosion, at least at flow speeds less than the sediment's critical erosion velocity (Roegner et al. 1995). Some bivalves disperse actively as postlarvae by drifting in the water column, producing threads that increase their drag and promote resuspension (Sigurdsson et al. 1976, Cummings et al. 1993). The propensity of bivalves to drift varies among species (de Montaudouin 1997, Turner et al. 1997, Olivier & Retière 1998).

In the present study, the potential interaction between postlarval transport and the presence of predators was examined. Predators have strong direct effects on the abundance of juvenile bivalves through consumption (e.g. Micheli 1997, Richards et al. 1999, Hunt & Mullineaux 2002), but predation may also have other impacts on prey species. Predators could cause mortality through disturbance or have non-lethal effects by modifying prey behaviour, resulting in reduced growth (Nakaoka 2000) or increased emigration rates (amphipods and polychaetes, Ambrose 1984). Predator foraging also has the potential to increase erosion of sediment and the juvenile bivalves living within it. Disturbance by fish has been demonstrated to increase rates of drift of meiofauna (Palmer 1988). The effect of predator disturbance on transport of postlarval bivalves has not yet been directly investigated. However, Commito et al. (1995a) examined dispersal of juvenile *Gemma gemma* into pits created by foraging horseshoe crabs. The dispersal rate of *G. gemma* into these pits and into bottom traps was greater in summer, which was attributed to increased sediment disturbance by horseshoe crabs at this time of year.

The soft shell clam *Mya arenaria* was chosen as a 'model' organism in these experiments. *M. arenaria* is abundant in estuaries and sheltered bays in many parts of North America and Europe. Juvenile *M. arenaria*, <5 mm in length, are found in the top 1 cm of sediment (Zwarts & Wanink 1989) and are vulnerable to transport by storms and tidal currents (Emerson & Grant 1991, Hunt & Mullineaux 2002) and to predation (Kelso 1979, Blundon & Kennedy 1982, Commito 1982, Hunt & Mullineaux 2002). Subsurface physical disturbance caused by movement of the highly abundant mud snail *Ilyanassa obsoleta* has been shown to increase rates of erosion of juvenile *M. arenaria* in flume and field studies (Dunn et al. 1999).

In this study, a series of experiments were conducted in a laboratory flume

to examine the effects of 2 common estuarine predators, the seven-spine bay shrimp *Crangon septemspinosus* and juveniles of the green crab *Carcinus maenas* on erosion and mortality of juvenile *Mya arenaria*. I addressed the following questions: (1) What are the impacts of predators on transport and mortality of juvenile *M. arenaria*? (2) Do the effects of predators vary with flow speed and predator species? (3) What is the mechanism of any predator effect on clam erosion, i.e. does transport result from direct resuspension of clams?

MATERIALS AND METHODS

***Mya arenaria*.** Experiments were conducted in May (first *Crangon septemspinosus* experiment), July (*Carcinus maenas* experiment) and November (second *C. septemspinosus* experiment) 2001. The source and size of juvenile *Mya arenaria* varied among experiments because of constraints in availability of clams from hatcheries and of the flume facilities. Each hatchery spawned only 1 batch of *M. arenaria* per year; juveniles for the 3 experiments were obtained from Marshall Point Sea Farm in Port Clyde, Maine, Spinney Creek Shellfish in Eliot, Maine and Middle Peninsula Aquaculture in Foster, Virginia, respectively. Clams used in the experiments were 1.0 to 3.0 mm in shell length (SL) (Table 1).

Clams were held on 180 µm mesh in plastic containers filled with 1 µm filtered seawater in a controlled environment room (20°C). The containers were aerated and the seawater was changed every third day. Clams were fed daily with *Isochrysis* spp. and *Tetraselmis suecica*. These algae were obtained from the Provasoli-Guillard National Center for Culture of Marine Phytoplankton (CCMP) at Bigelow Laboratories, Maine and cultured in sterilized seawater enriched with Kent ProCulture F/2 algal culture medium.

Table 1. Treatments, clam size, predator size and density, and length of runs for flume experiments examining the effects of the presence of predators (*Crangon septemspinosus* and *Carcinus maenas*) and flow velocity (u at 10 cm above bottom 9 and 27 cm s^{-1}) on the proportion of juvenile *Mya arenaria* retrieved from patches

Experiment	Treatment	Clam size (mm ± 1SD)	Predator size (mm)	Predator density (ind. m ⁻²)	Length of run (h)
1st <i>Crangon</i> experiment	Low speed/ <i>Crangon</i>	3.0 ± 0.5	27–50	5.1	4
	High speed/ <i>Crangon</i>				
	High speed/no <i>Crangon</i>				
<i>Carcinus</i> experiment	Low speed/ <i>Carcinus</i>	2.4 ± 0.3	21–34	0.9	1
	High speed/ <i>Carcinus</i>				
	High speed/no <i>Carcinus</i>				
2nd <i>Crangon</i> experiment	High speed/ <i>Crangon</i> High speed/Pit treatment	1.0 ± 0.14	30–56	5.1	4

Predators. The effect of flow speed and predator presence was examined in 3 experiments, 2 using the seven-spine bay shrimp *Crangon septemspinosus* (in May and November) and 1 using juveniles of the green crab *Carcinus maenas* (in July). These predators were selected because they are common in estuaries on the NE coast of North America and are predators of juvenile bivalves (e.g. *C. maenas* feeding on *Cerastoderma edule*, *Macoma balthica* and *Mya arenaria*: Jensen & Jensen 1985, van der Veer et al. 1998, Richards et al. 1999; *C. septemspinosus* feeding on *Spisula solidissima*: Viscido 1994). Juvenile *C. maenas* rapidly consume small (1 to 2 mm) juvenile *M. arenaria* in the laboratory (unpubl. data) and may be important predators of juveniles of this species in New England (Hunt & Mullineaux 2002). Although *C. septemspinosus* has not yet been documented to feed on *M. arenaria* in the field, it exhibits only minor morphological differences from the European *C. crangon* (reviewed by Haefner 1979), which is an important predator of *M. arenaria* (Pihl & Rosenberg 1984, van der Veer et al. 1998). *C. septemspinosus*, juvenile *C. maenas* and *M. arenaria* co-occur on intertidal flats and in the shallow subtidal in many areas, including the collection sites for this study.

Crangon septemspinosus were collected by seining in the Navesink River and Sandy Hook Bay, New Jersey. Because a large number of individuals were required, the full range of sizes of shrimp caught was used in the experiments (Table 1). Individuals of both sexes, including egg-bearing females, were used. *Carcinus maenas* were collected in late June with a minnow net in Barnstable Harbor, Massachusetts. The crabs used in this experiment were juveniles, 21 to 34 mm in carapace width (Table 1). Both shrimp and crabs were maintained in tanks in a recirculating seawater system until they were used in the experiments. Each individual was only used in 1 experimental run. *C. septemspinosus* were fed frozen brine shrimp once a day, after the shrimp for that day's run were removed from the tank. *C. maenas* were fed frozen whitefish and were starved for 48 h before use in the experiment. Shrimp and green crabs were fed at different intervals before the experiments because they appeared to differ in their feeding behavior. Shrimp fed less frequently than every 24 h exhibited high levels of cannibalism while green crabs fed less than 48 h prior to experiments did not consume clams in the flume.

The flume. The experiments were carried out in an annular flume at the Institute of Marine and Coastal Sciences at Rutgers University (<http://marine.rutgers.edu/flume/annular.html>). The annulus shape of the flume allowed the predators to walk and swim upstream or downstream without encountering barriers to their movement. The annular flumes at Rutgers are

modeled on one at Delft University of Technology in the Netherlands (Visser et al. 1992, Booij 1994). The diameter of the Delft flume is slightly smaller than that of the Rutgers flume, but the channel width is the same. The flume has an outside diameter of 400 cm (circumference 12.7 m) and a cross-channel width of 30 cm, with a bottom area of 3.5 m². The channel was filled to a depth of 20 cm. Flow is driven by rotation of the top plate and the simultaneous counter-rotation of the flume channel. The flume rotation speeds are controlled through a PC-based process control and data acquisition system Camile 2000 (Dow Chemical Corporation), enabling precise control and repeated setting to specified speed set points. The counter-rotation minimizes the cross-channel flow caused by water moving continuously in a circle, but does not eliminate it. A rotation ratio of 1.4:1 was chosen because it appears to minimize secondary flow (C. M. Fuller & G. L. Taghon unpubl. data). At the flow speeds used in this experiment (see below), the VW (cross-channel and vertical) velocity vectors are <15% of the horizontal (U) velocity, except in the outer half of the channel where they reach 12 to 28% at some heights (Hunt & C. M. Fuller unpubl. data). At these flow settings, horizontal velocities are uniform across the channel and then decrease by approximately 20% within 20 cm of the channel walls (but by 30% near the inner wall at the low-flow speed).

Flow velocities over a flat bed were measured with a 2-axis laser doppler velocimeter (LDV). Flow velocities were measured at 19 heights above the bottom (ranging from 1.5 to 14 cm) in the center of the channel to obtain a vertical profile of flow speeds. Flow was measured at a data rate of 60 to 100 Hz and 4000 data points were averaged for each height. Shear velocities, u_* , were estimated from the flow profiles. Assuming the profile is logarithmic, the 'law of the wall' equation:

$$u(z) = \frac{u_*}{\kappa} \ln\left(\frac{z}{z_0}\right)$$

where $u(z)$ is the observed current profile at depth z , z_0 is the bottom roughness parameter, and κ is von Karman's constant, predicts that u_* is proportional to the slope of the velocity profile in log-space (Vogel 1994). Since only 13 of the recorded points (up to 3.9 cm above the bottom) were within the log layer (as determined graphically), points above 3.9 cm were not used in the calculation of u_* . This resulted in a good linear fit to the log profile ($r^2 = 0.90$ to 0.99 , $p < 9.3 \times 10^{-7}$; $n = 6$ profiles per flow speed). In cases where ripples developed in the sediment (see 'Results'), shear velocities are likely to have changed somewhat over the course of a flume run. For example, S. G. Newby (unpubl. data), using the same sediment in this flume, found that the presence of shell hash and the development of

ripples resulted in an increase in u_* , particularly at ripple crests [mean ± 1 SD; increase in u_* from 0.74 ± 0.06 for flat sand bed to 1.59 ± 0.79 (average of crests and troughs of ripples) for shell hash].

Experimental setup: The flume was filled with 3 cm of sediment and 20 cm of 5 μm filtered seawater at the start of the experiments. The seawater was at room temperature, 18 to 20°C. The sediment was collected at a depth of 15 m from Rutgers University's underwater observatory (LEO) on the inner continental shelf off Tuckerton, New Jersey and sieved through a 1.5 mm mesh sieve to remove large macrofauna. The median grain size of the sediment was 210 ± 50 (mean \pm SD) μm . This sediment was used because it was within the range of grain sizes in which *Mya arenaria* (grain size 63 to 250 μm , Φ 4.0 to 2.0 e.g. Möller & Rosenberg 1983, Strasser et al. 1999), *Crangon septemspinosa* (fine to coarse sand: Wilcox & Jeffries 1974, Viscido et al. 1997) and *Carcinus maenas* (fine sediment to sheltered rocky shores) occur. There were no naturally occurring *M. arenaria* in this sediment prior to sieving, but juveniles placed on it burrowed rapidly and appeared to behave normally.

In each experimental run, 6 patches of juvenile *Mya arenaria* were set up in the flume. The density of clams in these patches ($12\,000 \text{ ind. m}^{-2}$) was high, but within the range of densities observed in the field (Hunt & Mullineaux 2002, Hunt et al. 2003). The patches were in the center of the flume channel and equidistant from one another, 2 m apart. Each patch was established by dropping 60 juvenile *M. arenaria* into a vertical cylinder (8 cm diameter) that had been placed gently on the sediment. The cylinder was then removed and the clams were allowed 20 min to burrow. In procedural controls without flow to assess the loss of juvenile clams during placement in the flume, an average of $97 \pm 5\%$ (mean ± 1 SD) of the juvenile *M. arenaria* were recovered. After the burial time, predators, if needed in the run, were gently placed into the water using an aquarium net at locations between patches around the flume. The top plate of the flume was lowered and the flow was gradually increased to the desired velocity. After the flow was stopped, the top plate was raised, and predators were removed and preserved in ethanol. The contents of the esophagus, cardiac and pyloric stomach, and gastric mill of the predators were examined later under a dissecting microscope to determine whether they contained juvenile clams. The patches of clams were sampled by taking cores of sediment wider (11 cm diameter) than the cylinder used to deposit the clams. An acrylic plate had been positioned under the sediment in the location of each patch to allow easy removal of the cores. The sediment was sieved on a 500 μm sieve to collect the clams, which were preserved in 75% ethanol until they could be stained with

Rose Bengal and enumerated. The sediment downstream of the patches was swept with a 1 mm mesh fish net to determine whether clams had dispersed downstream; it was not intended to systematically account for all of the clams in each run. Sweeping with the net suggested that clams did not disperse from 1 patch to another.

Treatments: The loss of juvenile *Mya arenaria* from the patches was examined in the presence of predators at low-flow, and in the presence and absence of predators at high-flow (Table 1). The 2 flow treatments were velocities (u at 10 cm above bottom) of 9.3 ± 0.1 (mean ± 1 SD) and $26.7 \pm 0.3 \text{ cm s}^{-1}$, which resulted in shear velocities (u_*) of 0.30 ± 0.04 and $0.97 \pm 0.04 \text{ cm s}^{-1}$, respectively. These speeds were in the low to mid range of those recorded (speeds of 0 to 45 cm s^{-1} during neap tides and 0 to 57 cm s^{-1} during spring tides; 22 cm above bottom) on tidal flats on Cape Cod (Hunt & Mullineaux 2002) where *M. arenaria* and *Carcinus maenas* were abundant, and *Crangon septemspinosa* were present. Based on previous flume experiments (Roegner et al. 1995, Dunn et al. 1999, Gulmann et al. 2001), transport of juvenile clams was not expected in the low-flow treatment and any losses from the patches in these runs would result from predator-induced mortality. No low-flow/no predator treatment was used due to time constraints and because a preliminary experiment determined that no transport or mortality of clams would occur under these conditions. In this preliminary experiment, carried out in a different flume (racetrack shaped), $96 \pm 2\%$ (mean ± 1 SD) of 2.2 mm juvenile *M. arenaria* were retrieved from their original location after 5 h of exposure to $u_* = 0.23 \text{ cm s}^{-1}$ ($u = 4 \text{ cm s}^{-1}$) flow in the absence of predators. In the present study, experiments were carried out with *C. septemspinosa* and juvenile *Carcinus maenas* as the predators. The densities of the predators used were 5.1 ind. m^{-2} for *C. septemspinosa* (18 ind. per run) and 0.9 ind. m^{-2} for juvenile *C. maenas* (3 ind. per run). The density of *C. septemspinosa* used is typical for estuarine and coastal habitats in New Jersey (Viscido et al. 1997, J. Pessutti pers. comm.). The density used for *C. maenus* was lower than that at which it can occur in the field (Hunt & Mullineaux 2002) and the experimental runs were shorter (1 h vs 4 h; Table 1) for the *C. maenas* experiment than for the *C. septemspinosa* experiments because juvenile crabs could consume virtually all of the clams in 4 h. The results of preliminary runs in which patches of *M. arenaria* were exposed to a density of juvenile *C. maenas* of 1.2 ind. m^{-2} (4 ind. per run) for 4 h are described in the 'Results' section to illustrate this; all other aspects of these runs were the same as the other green crab runs. Four replicate runs were carried out for each treatment combination in each experiment. All of the runs were carried

out with the glass sides of the flume covered with black plastic since both of these predators are more active in darkness (*C. maenas*: Ropes 1968, Burrows et al. 1994; *Crangon*: Wilcox & Jeffries 1974).

The effect of the high-flow *Crangon septemspinosa* treatment in the first experiment on sediment and clam transport could have resulted either from resuspension of sediment and clams by shrimp in flow or from the effects of the shrimp on bottom topography. A second experiment was conducted with *C. septemspinosa* to compare the effect of sediment disturbance by shrimp on the transport of clams and sediment in the presence and absence of the shrimp. Two treatments were used in this experiment, both conducted at the high-flow velocity. One treatment was the presence of *C. septemspinosa*, as described for the previous experiment. The second treatment was prior disturbance of the sediment surface by *C. septemspinosa*, termed *C. septemspinosa* 'pits'. In these runs, shrimp were placed in the flume for 4 h in the absence of water flow and clams. They disturbed the sediment by foraging and burying themselves in it, creating pits the size of their body (4 to 6 cm long, 1 cm deep). The shrimp were then removed, clams were placed in the flume and the runs were conducted in the same way as in the previous experiments.

For each experiment, the proportion of clams retrieved from the patches was compared among treatments and among runs (within treatments) using nested ANOVA. Prior to analysis, data were arcsine \sqrt{x} -transformed to normalize them (as assessed by graphical examination of residuals) and to reduce heterogeneity of variances (as assessed by Cochran's test).

RESULTS

Crangon septemspinosa had a significant effect on the proportion of juvenile *Mya arenaria* (SL 3.0 ± 0.5 mm) retrieved from the patches in the first experiment (Fig. 1). The proportion of clams retrieved differed significantly among the treatments (Table 2) and was significantly lower in the high-flow treatment with shrimp present than in the high-flow no shrimp or low-flow with shrimp treatments (Tukey's posthoc test, $p < 0.05$). Ripples (typically 2 to 4 cm in height, 5 to 8 cm between crests) developed only in the presence of shrimp at the high-flow speed. In the high-flow treatment with shrimp present, 3 to 62 clams per run were recovered by sweeping a net through the sediment up to 50 cm

downstream of the patches. Pooling across treatments and runs, almost all (96%) of the clams placed in the flume were recovered, indicating little mortality of clams during the experiment. Gut content analysis of the shrimp in 4 of the runs, 2 at the high and 2 at the low velocity, indicated that very few of the shrimp consumed clams. Of the 68 shrimp dissected, 2 of the largest individuals (42 and 52 mm in length), both from low-flow runs, contained 1 juvenile *M. arenaria* each. These results suggest that the loss of individuals from patches in the high-flow shrimp treatment was due to transport and not to consumption of clams.

In contrast to the effects of the shrimp in the first experiment, juvenile green crabs consumed juvenile *Mya arenaria* (SL of clams in this experiment 2.4 ± 0.3 mm) but did not appear to increase their transport rate. The proportion of clams retrieved varied considerably

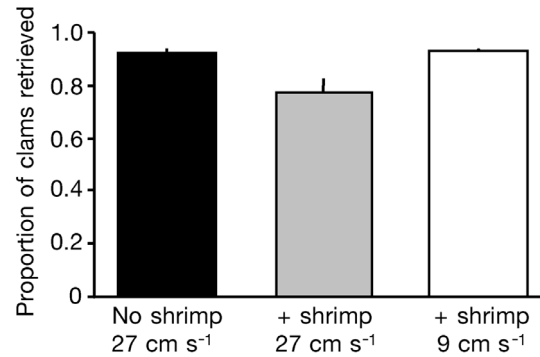


Fig. 1. Mean (± 1 SE) proportion of juvenile *Mya arenaria* (SL 3.0 ± 0.5 mm; mean ± 1 SD) retrieved from patches in 3 treatments: high-flow ($u = 27$ cm s⁻¹; $u_* = 0.97$ cm s⁻¹) in the absence of the seven-spine bay shrimp *Crangon septemspinosa*, high-flow with shrimp and low-flow ($u = 9$ cm s⁻¹; $u_* = 0.30$ cm s⁻¹) with shrimp. $n = 4$ runs for each treatment

Table 2. Nested ANOVA examining the effects of predator/velocity treatment and flume run (nested within treatment) on the proportion of juvenile *Mya arenaria* (arcsine \sqrt{x} -transformed) retrieved from the patches of clams set up in an annular flume. Two experiments were conducted with *Crangon septemspinosa* as the predator and one with juvenile *Carcinus maenas*. ** $p < 0.001$, *** $p < 0.01$

Experiment	Source	df	MS	F	p
1st <i>Crangon</i>	Treatment	2	0.418	10.455	0.004**
	Run (Treatment)	9	0.040	1.585	0.141
	Error	59	0.025		
<i>Carcinus</i>	Treatment	2	0.508	1.123	0.367
	Run (Treatment)	9	0.452	7.168	<0.001***
	Error	59	0.063		
2nd <i>Crangon</i> (pit treatment)	Treatment	1	7.437	70.83	<0.001***
	Run (Treatment)	6	0.105	1.82	0.12
	Error	40	0.06		

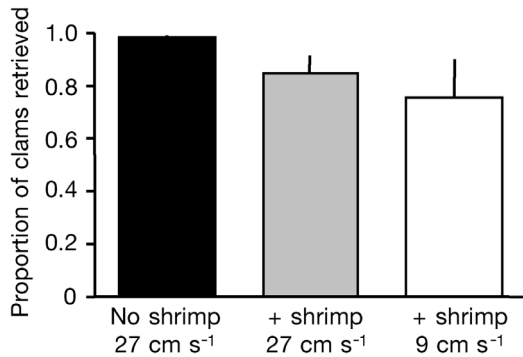


Fig. 2. Mean (± 1 SE) proportion of juvenile *Mya arenaria* (SL 2.4 ± 0.3 mm; mean ± 1 SD) retrieved from patches in 3 treatments: high-flow ($u = 27$ cm s^{-1} ; $u_* = 0.97$ cm s^{-1}) in the absence of juveniles (21 to 34 mm) of the green crab *Carcinus maenas*, high-flow with crabs, and low-flow ($u = 9$ cm s^{-1} ; $u_* = 0.30$ cm s^{-1}) with crabs. $n = 4$ runs for each treatment

among patches and runs. The proportion of juvenile *M. arenaria* retrieved varied significantly among runs but did not vary significantly among treatments (Table 2 & Fig. 2). Sediment ripples did not form in the presence of juvenile green crabs at either velocity. The main sedi-

Table 3. Gut content analysis of juvenile green crabs *Carcinus maenas* to determine whether crabs preyed on juvenile (2.4 ± 0.3 mm; mean ± 1 SD) *Mya arenaria* at high ($u = 27$ cm s^{-1}) and low ($u = 9$ cm s^{-1}) velocities. $n = 4$ runs for each treatment. Number of *M. arenaria* in the stomach was determined from the number of clam umbos; shells were crushed

Velocity	Run	Crab size (mm)	Number of <i>Mya arenaria</i>
High ($u = 27$ cm s^{-1})	1	30	0
		29	0
		23	10
	2	31	50
		36	1
		22	15
	3	29	0
		30	0
		28	0
	4	21	0
		28	0
		38	0
Low ($u = 9$ cm s^{-1})	1	28	45
		28	0
		26	28
	2	30	0
		23	0
		30	16
	3	30	3
		24	0
		31	0
	4	27	0
		34	0
		31	0

ment disturbances observed were small depressions from the tips of the crabs' walking legs, although crabs did occasionally burrow into the sand. Only 2 to 9 clams per run were collected downstream of the patches by sweeping through the sediment with a net. Examination of the gut contents of the crabs indicated that the crabs consumed clams, in some cases in great numbers (up to 50 clams in an individual crab in a 1 h run) (Table 3). However, no clams were consumed in 2 of the high-flow runs and 1 low-flow run (Table 3). There was a significant negative relationship between the proportion of clams retrieved in a run and the number of clam umbos recovered from the stomachs of the crabs ($F_{1,6} = 22.4$, $p = 0.003$, $r^2 = 0.789$). Preliminary runs provided additional evidence of high rates of predation by green crabs on juvenile *M. arenaria*. The percentage of *M. arenaria* retrieved in the patches in these runs, which were longer (4 vs 1 h) and had a higher crab density (1.2 vs 0.9 ind m^{-2}), was only 6.7% in a high-flow run, and 16.1 and 12.2% in 2 low-flow runs.

Disturbance of the bottom by *Crangon septemspinosa* resulted in pits the size of the shrimp, formed by the shrimp foraging along the bottom of the flume and burrowing into the sand to hide (Fig 3a). In the second experiment with *C. septemspinosa*, ripples

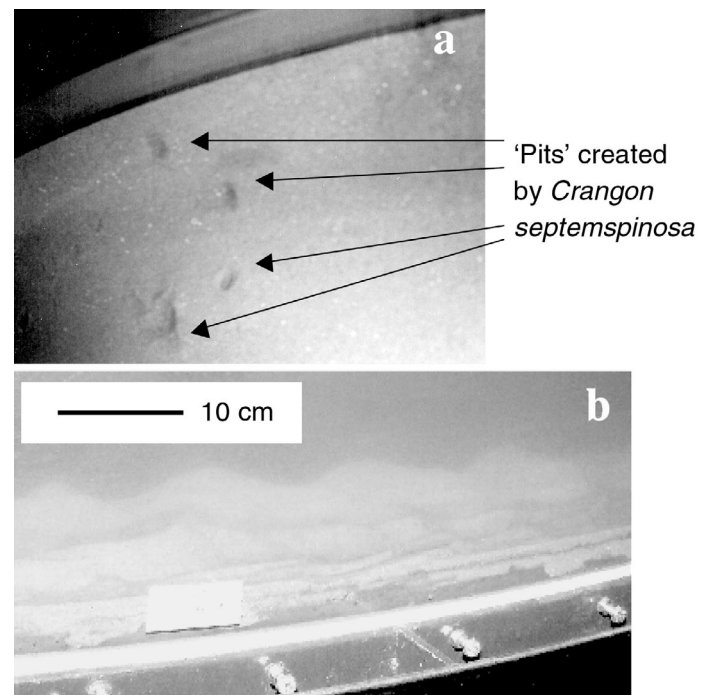


Fig. 3. (a) Top view of sediment disturbance created by the seven-spine bay shrimp *Crangon septemspinosa* in still water. 'Pits' are ~4 to 6 cm long, 1 cm deep. (b) Side view of flume and ripples that developed in the presence of *Crangon* disturbance (pit treatment) at the high-flow velocity ($u = 27$ cm s^{-1} ; $u_* = 0.97$ cm s^{-1}). Ripples are 2 to 4 cm in height and 5 to 8 cm between crests

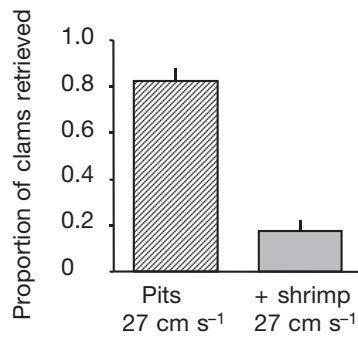


Fig. 4. Mean (± 1 SE) proportion of juvenile *Mya arenaria* (SL 1.0 ± 0.14 mm; mean ± 1 SD) retrieved from patches in 2 treatments: high-flow ($u = 27 \text{ cm s}^{-1}$; $u_* = 0.97 \text{ cm s}^{-1}$) with sediment disturbance (pits) created by the seven-spine bay shrimp *Crangon septemspinosa* prior to each run and high-flow with shrimp present. $n = 4$ runs for each treatment

formed in the sediment in both the high-flow treatment with 'pits' (Fig. 3b) and that with shrimp present. However, the proportion of juvenile *Mya arenaria* (SL 1.0 ± 0.14 mm) retrieved differed significantly between the 2 treatments (Table 2) and was considerably higher in the 'pit' disturbance treatment than in the high-flow treatment with *C. septemspinosa* present (Fig. 4). There was no significant variability among runs in the proportion of clams retrieved (Table 2). The difference between the treatments likely resulted from predation. Examination of gut contents of 30 shrimp (from 3 of the high-flow runs with shrimp) revealed evidence of predation on clams. Eleven of the shrimp contained finely crushed shell fragments, but it was not possible to determine how many clams were represented. Also, given the 4 h length of these runs, some clams may have passed out of the stomach before the shrimp were preserved.

DISCUSSION

Experiments with the seven-spine bay shrimp *Crangon septemspinosa* demonstrated that this epibenthic predator can increase the rate of transport of juvenile *Mya arenaria*. Transport of clams most likely occurred passively as the sediment was transported and ripples formed. I did not observe any significant transport of sediment or clams in the presence of juvenile green crabs *Carcinus maenas*. This lack of sediment ripples was not due to the shorter time interval for the crab flume runs since no evidence of ripple development was seen in preliminary 4 h runs with juvenile crabs. The crabs caused less sediment disturbance than the shrimp, resulting only in mm-scale depressions in the sand. Predator-induced transport of invertebrates has

previously been observed for meiofauna. Palmer (1988) found that drift of meiofauna was increased by fish foraging. In her study, the flow speed (12 cm s^{-1}) was not high enough to induce sediment transport and bedload transport of associated organisms. Meiofaunal drift may have resulted from resuspension by predators or from prey behaviour. The activities of predators also likely affect the transport of bivalves. Commito et al. (1995a) found that horseshoe crabs created pits with reduced densities of the gem clam *Gemma gemma* and that juveniles and adults of this small bivalve rapidly dispersed into these patches. Transport of juvenile *M. arenaria* induced by biological disturbance has been examined in 1 study, which did not involve predators (Dunn et al. 1999). In a laboratory experiment, they found that erosion of juvenile *M. arenaria* occurred in the presence of the mud snail *Ilyanassa obsoleta* at shear velocities that did not suspend undisturbed clams. Mud snails move below the sediment surface rather than being epibenthic, which likely mixes sediment and clams to the surface, and increases bottom roughness because their shells protrude above the sediment. Mud snails also occur at much higher densities (1000 ind. m^{-2} , Dunn et al. 1999) than most predators (e.g. *C. septemspinosa*, 5 ind. m^{-2}). For these reasons, they might be expected to have a greater disturbance effect than most epibenthic predators.

Organisms can stabilize or destabilize the bed and influence sediment transport in a variety of ways (reviewed by Widdows & Brinsley 2002). In this study, the formation of sediment ripples in the presence of *Crangon septemspinosa* may have occurred because of the effect of the shrimp on bottom topography and the consequent enhanced sediment erosion. Sediment transport occurred both when shrimp were present and when the shrimp were removed prior to the start of the run ('pit' treatment). The lower proportion of clams retrieved in the treatment with shrimp present than in the 'pit' treatment probably resulted from predation on the small clams by shrimp. The proportion of juvenile clams retrieved in the pit treatment (Fig. 4) was very close (82 vs 78%) to that in the high-flow treatment with shrimp in the first experiment (Fig. 1), when little predation occurred. Bioturbation and its associated topographic highs are known to result in sediment transport and modification of the bed at relatively low-flow speeds (Wheatcroft 1994). In a laboratory experiment, Fries et al. (1999) observed sediment motion and transport in the presence of mounds (1 to 2 cm tall, 3 to 4 cm diameter) constructed by the polychaete *Cistenides gouldii* at speeds below the critical stress for initiation of sediment motion. They found that sediment transport was induced by the presence of biogenic mounds and not by particle ejection from the worm tubes. Boundary layer separation and reattach-

ment also occurs at depressions in the bed (Leeder 1982). Depressions are well known to trap particles because of the reduced flow within the cavity (reviewed by Snelgrove et al. 1993). As the flow reattaches at the downstream edge of the depression, turbulent stresses are increased and have the potential to result in sediment transport (Leeder 1982). As far as I am aware, this is the first study to demonstrate transport of sediment and associated organisms due to biogenic depressions.

As expected, the predators in these experiments also had effects through consumption of juvenile clams. There was no evidence of predation of shrimp on juvenile clams in the first experiment, but shrimp preyed on the smaller (SL 1 mm) clams used in the second shrimp experiment. The consumption rate of clams in the second shrimp experiment could not be determined because the clams were finely crushed and their umbos could not be distinguished. However, the proportion of clams retrieved in these experimental runs was very low (Fig. 4). This low recovery rate could result, in part, from greater rates of transport of 1 mm than 3 mm *Mya arenaria*. However, clams of either size were unlikely to be able to avoid transport if a ripple migrated through a patch. In both experiments, patches generally had high or low recovery rates; in those locations in which ripples had developed, almost all individuals had disappeared from the original patch. Therefore, differences in rates of recovery between experiments are likely to be due to predation. Although *Crangon septemspinosa* are capable of preying on larger prey, such as winter flounder <20 mm in length (Taylor 2003), 24 h still water experiments carried out at the time of the flume experiments (1 *C. septemspinosa* and 20 *M. arenaria* per bowl) indicated that the *C. septemspinosa* did not consume 3 mm *M. arenaria* but did feed on 1 mm *M. arenaria* ($45 \pm 39\%$ consumed in 1 d) (unpubl. obs.). Size-selective predation is common in crustaceans feeding on juvenile bivalves. For example, Pihl & Rosenberg (1984) examined the stomach contents of field-collected brown shrimp *C. crangon* and found that there was a positive relationship between body size of the shrimp (length 2 to 11 mm) and that of the juvenile *M. arenaria* in their stomachs. The maximum shell length of *M. arenaria* in their stomachs was 2 mm; the shrimp were juveniles, considerably smaller than the *C. septemspinosa* used in my experiments.

Juvenile green crabs also preyed on juvenile *Mya arenaria*. The experiment indicated that predation on clams could be intense, although feeding rates were extremely variable among runs, and among crabs (Table 3). No predation occurred in some of the later runs of the experiment, which was carried out over 2 to 3 wk. The crabs grew in captivity and individuals that

were close to molting may have avoided eating. Because of the need to prevent transport of clams from 1 patch to another, the patches were more isolated than natural clam patches. However, green crabs appeared to have no difficulty locating clam patches. In most runs where clams were consumed (Table 3), clams disappeared from more than 1 patch (in some cases from all 6). Juvenile green crabs are known to be important predators of juvenile bivalves in a variety of systems (e.g. Jensen & Jensen 1985, Richards et al. 1999). Hunt & Mullineaux (2002) suggested that juvenile green crabs were responsible for much of the effect of predator exclusion on the abundance of juvenile *M. arenaria* in an experiment carried out on tidal flats in Massachusetts.

The experiments in this study were carried out at realistic flow velocities, allowing me to assess the effects of predators on juvenile *Mya arenaria* in flow. Both crabs and shrimp were able to locate prey at the moderate flow speeds ($u = 9$ and 27 cm s^{-1}) used in this experiment. In the green crab experiment, I found no evidence of an effect of flow speed on predation rate, although there was a great deal of variability in feeding rates within and between runs. Flow patterns within the annular flume may have differed somewhat from those in nature, potentially affecting the ability of crabs and shrimp to find prey. Crustaceans use chemosensory cues to locate prey and the transport of such cues can vary with water flow (e.g. Weissburg & Zimmer-Faust 1993). Detection of an odor source (Weissburg & Zimmer-Faust 1993), and predation is generally maximal at low-flow speeds (Leonard et al. 1998). However, research on blue crabs *Callinectes sapidus* in tidal creeks found that increased flow (0.5 to 34 cm s^{-1}) did not impair the ability of crabs to reach an odor source (Finelli et al. 2000). At high-flow speeds, blue crabs walked more directly into the flow with straighter paths. The effect of increasing flow will probably differ depending on the range of flow speeds experienced. Extremely high-flow speeds (e.g. *Carcinus maenas* and *Cancer irroratus* at high-flow site with current speeds up to 120 cm s^{-1} , Leonard et al. 1998) are likely to reduce predation by any species. I could not assess the efficiency or the behaviour of the predators in my experiments because of the black plastic covering the flume sides to provide darkness.

This study demonstrates that *Crangon septemspinosa* can cause increased rates of sediment transport and dispersal of postlarval clams in flow. Although transport occurred over small spatial scales (cm in 4 h), such dispersal may have profound impacts on population dynamics if disturbance and movement occur frequently. Transport of juvenile clams appears to depend on the behaviour of the predator and the extent of their disturbance of the sediment. Sediment transport and

the formation of ripples were observed in the presence of the seven-spine bay shrimp *C. septemspinosus* but not of juvenile green crabs *Carcinus maenas*, which are a similar size. This study increases our understanding of the effects of epibenthic predators on juvenile bivalves, and demonstrates the need to consider both direct and indirect effects in understanding predation in flow. Foraging pits are common in sedimentary habitats (reviewed by Hall et al. 1992) and it is likely that other predators also influence the transport of sediment and juvenile macrofauna.

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