

Importance of predation by white shrimp *Litopenaeus setiferus* on estuarine subtidal macrobenthos

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Abstract

Macrobenthic invertebrates are an important food source for higher trophic levels in freshwater and marine habitats, yet the importance of predation impacting regular seasonal changes in macrobenthos abundance remains unclear. Benthic invertebrates and transient marine species in temperate estuaries display inverse patterns of seasonal abundance, suggesting a link between predation and summer macrobenthos abundance minima. We conducted manipulative caging experiments to test the importance of predation by white shrimp (*Litopenaeus setiferus*) in regulating estuarine subtidal macrobenthos densities. We predicted greater declines in macrobenthos densities with increased shrimp densities due to predation rather than disturbance and macrobenthos emigration. Using these field and laboratory data, we estimate whether white shrimp predation can significantly contribute to the macrobenthos seasonal abundance minima observed in long-term monitoring data.

White shrimp predation was measured in the field using 7-d predator enclosure/exclusion experiments. Within the uppermost 0–2 cm of sediment, total macrobenthos densities decreased within shrimp enclosure cages using 12 or 36 shrimp m⁻². Laboratory experiments distinguished between the effects of shrimp predation versus shrimp disturbance and macrobenthos emigration. Shrimp predation significantly reduced macrobenthos densities, while effects of shrimp disturbance and macrobenthos emigration were not significant in these experiments. Despite the impacts from other ambient predators and other abiotic factors, white shrimp were clearly capable of driving subtidal macrobenthos from their annual maximum density in winter/spring to their summertime minimum density. © 2007 Elsevier B.V. All rights reserved.

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1. Introduction

Macrobenthic organisms are an important food source for higher trophic levels in most estuaries and nearshore marine environments (Whitfield, 1988; Pihl et al., 1992;

McTigue and Zimmerman, 1998; Stehlik and Meise, 2000; Albertoni et al., 2003). Shallow-water macrobenthic communities often show seasonal patterns of abundance, recruitment, and mortality (Boesch et al., 1976). Biweekly collections from subtidal creeks in the North Inlet Estuary, South Carolina, USA, between 1981 and 1992 demonstrated consistent winter peaks in abundance of macrobenthos followed by declines to minima in mid-summer (Fig. 1A) (Service and Feller, 1992; Feller et al., 2004);

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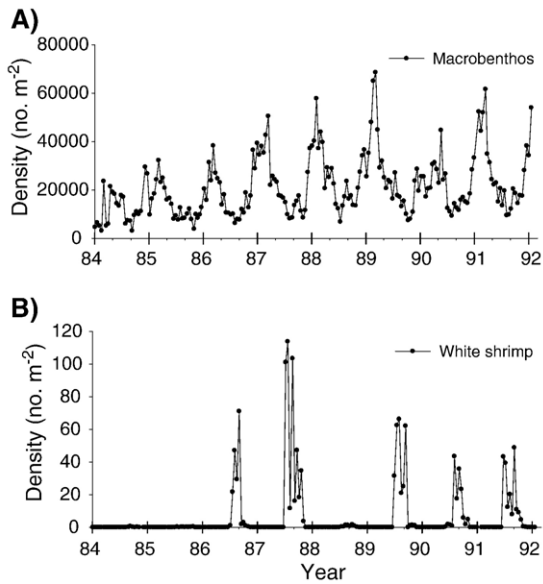


Fig. 1. Biweekly density (m^{-2}) of (A) macrobenthos and (B) white shrimp January 1984–March 1992. White shrimp abundances are from one standardized seine haul at low tide in Oyster Landing Creek, North Inlet, SC, and macrobenthos abundances are the average of 2 (1984) or 8 (1985–1992) replicate subtidal core samples of (5 cm dia, 5 cm depth) from Bread and Butter Creek, North Inlet, SC. Long dashes along the abscissa indicate January of each year.

meiofauna displayed similar seasonal cycles (Coull, 1985). Clear empirical demonstrations of the role of epibenthic predators in the seasonal abundance cycles of macrobenthic prey are relatively uncommon (Kneib, 1988; Gee, 1989).

Populations of transient epibenthic predators in the North Inlet Estuary, SC, also undergo seasonal abundance cycles, with abundance peaks in the summer months and few to no individuals remaining throughout the winter and early spring (Fig. 1B). Juvenile penaeid white shrimp, *Litopenaeus setiferus* (Pérez Farfante and Kensley, 1997) and juvenile spot, *Leiostomus xanthurus* (Lacépède, 1802) are among the most abundant. Previous caging experiments have reported significant declines in meiofaunal abundances in the presence of high densities of juvenile spot (Ellis and Coull, 1989); however, the results were inconsistent when spot were held at natural densities, and when spot were feeding on macrobenthos (Service et al., 1992). In contrast, penaeid shrimp are well-known as epibenthic predators on a wide variety of macrobenthic prey (Mayer, 1985; Hunter and Feller, 1987; Kneib and Knowlton, 1995; McTigue and Zimmerman, 1991, 1998; Pape-Lindstrom et al., 1997). Stephenson (1980) reported a negative correlation between the abundance of benthos and shrimp and suggested that abundant shrimp populations could deplete the benthos.

In this paper, we report the results of 7-d manipulative field- and laboratory-based predation experiments using white shrimp and their ambient subtidal macrobenthic prey assemblage. While we recognize that other epibenthic predators are present in the subtidal creeks during the summer months, no single predatory species has yet been demonstrated to play an important role in shaping macrobenthos seasonal abundance cycles. We chose to investigate the role of white shrimp predation due to their benthic foraging habits, their carnivory on benthic invertebrates, and their abundance in subtidal creeks during the summer months. We wanted to determine whether normal and/or elevated white shrimp predation (as a function of shrimp density) could reduce macrobenthos abundances in the field, and, whether these reductions were great enough to significantly contribute to the seasonal abundance minima. Short-term experiments were deemed most valuable for examining the direct effects of predation because these more immediate effects may be obscured in longer term manipulative experiments as the prey community responds to perturbation (Bender et al., 1984). The white shrimp densities used in the present study were within the upper range of summer low tide shrimp densities – despite being, by design, artificially restricted in time and space – and were selected to determine the maximum predation effect. Potential caging artifacts (Vimstein, 1978; Dayton and Oliver, 1980) were minimized by conducting short-term experiments, using cage controls and replicated, randomized sampling.

Based on long-term monitoring data in the North Inlet Estuary, SC, we developed these experiments to test the importance of white shrimp predation in regulating the abundance of macrobenthic prey in subtidal creeks during the summer. We predicted: (1) greater declines in subtidal macrobenthos densities would be observed with increased white shrimp densities, (2) subtidal macrobenthos densities would decline to a greater extent as a result of white shrimp predation compared to the impacts of white shrimp disturbance and macrobenthos emigration, and (3) the magnitude of shrimp reductions of macrobenthos abundance would be great enough to possibly account for the seasonal macrobenthos abundance minima observed in the long-term monitoring data.

2. Materials and methods

2.1. Study site

The field portion of this study was conducted in the summer of 2003 in Crabhaul Creek (33° 20' N, 79° 10' W), located in the North Inlet Estuary near Georgetown,

SC, USA. The warm temperate North Inlet Estuary (3300 ha) is high-salinity, well-mixed, and has semidiurnal tides with mean range 1.4 m. Crabhaul Creek is adjacent to the forested uplands and depressed salinities can occur after major rainfalls. Several major habitat types are present, including 71% marsh and intertidal creeks, 13% fringing oyster reefs and mudflats, and 16% subtidal channels (Potthoff and Allen, 2003).

Juvenile white shrimp were collected for use in all experiments using 1 cm mesh seine and cast nets at low tide in subtidal creeks near the study sites. Shrimp were transferred to continuously-circulating seawater tanks in a screened outdoor laboratory and held under ambient conditions for not longer than 4 d before use in the experiments. Shrimp were fed twice daily using commercially-produced sinking feed pellets (Hartz Corp., Seacaucus, NJ).

2.2. Creek Cage experiments

Two 7-d manipulative caging experiments were conducted in the summer of 2003. This duration was chosen to reduce potential cage artifacts such as sedimentation and algal growth, while allowing adequate time for detection of changes in infaunal densities (Virmstein, 1978). Prior to initiation of the experiments, we used variance estimates from similar-size replicate core samples from the Baruch Institute long-term database (1984–1992) to calculate the number of core samples needed in our experiment to detect changes in macrobenthos abundance with adequate statistical power. Maximum flow velocities were determined using a Marsh McBirney Model 201D Portable (electromagnetic) water current meter deployed by boat into the center of the creek on either side of slack high and slack low tide. We also determined the sediment organic content and grain size from 0 to 2 cm depth by collecting cores along a series of three transects across the subtidal portion of each creek where the experimental cages were emplaced.

Long-term sampling of the nekton community is conducted biweekly on midday low tides in the Oyster

Landing Basin, North Inlet, SC, using one pass of a 6 mm mesh bag seine in an intertidal creek pool (Allen et al., 2004). The pool is approximately 308 m² with a bottom substrate of mud and scattered oyster shell. Between 1984 and 1988, seasonal collection efficiencies were obtained by conducting 12 to 14 additional seine hauls; white shrimp were collected from the entire pool with 25% efficiency. We thus multiplied the number of white shrimp collected per seine haul by 4 prior to converting to numbers of shrimp per m² to provide a rough estimate of subtidal shrimp density. The white shrimp densities used in the present study were within the range of summer low tide shrimp densities for the intertidal creek pool (mean 15.2 ind m⁻²) (Fig. 1B). Using drop traps, Zimmerman and Minello (1984) reported mean summer densities of white shrimp on nonvegetated bottom in a Texas salt marsh of 12 ind m⁻². In August, Wenner and Beatty (1993) collected juvenile white shrimp at night from intertidal Church Creek, SC on ebb and flood tides with the greatest mean density of 11.1 ind m⁻³.

Five replicates of the following 5 experimental treatments were used: (1) uncaged open plot (OP); (2) partial cage (HC); (3) predator exclusion cage (CC); (4) normal shrimp density cage (1×: 12 shrimp m⁻²); and (5) elevated shrimp density cage (3×: 36 shrimp m⁻²). Cage frames were constructed with 1.3 cm diameter PVC and covered with 0.6 cm mesh galvanized steel hardware cloth. Cages were 1×1×0.5 m (L×W×H) with similarly constructed lids; 8 aluminum bolts and wing nuts (2 each side) connected the lid to the frame. Partial cages had 50% mesh walls on four sides and 50% mesh lid to mimic some of the physical effects of the cage structure (Fig. 2).

Two Creek Cage experiments were conducted in Crabhaul Creek, North Inlet, SC from July 12–19 (Expt I) and July 24–31, 2003 (Expt II). On Day 1 of each experiment, each treatment cage was assigned randomly to a grid position in the subtidal portion of the creek. Cages were placed at least 2 m apart, with the PVC legs pressed by hand 15 cm into the sediment. A 10×10 grid was established inside each cage (grid

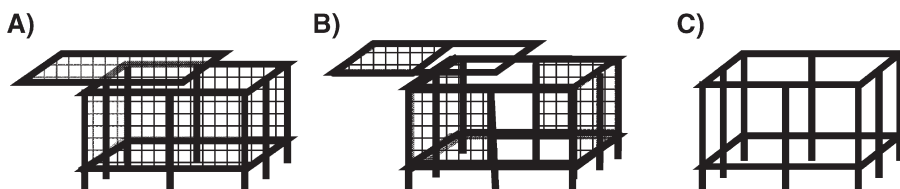


Fig. 2. Three cage types used in Creek Cage experiments: (A) full cage and lid used for shrimp inclusion and exclusion treatments, (B) partial cage and lid, (C) open plot. Dimensions for all cage types are 1×1×0.5 m (L×W×H) with 0.6 cm mesh.

locations directly adjacent to the cage edge were excluded from sampling). To quantify the initial macrobenthos densities prior to the experimental manipulations, 6 cores (25.95 cm² surface area=5.75 cm inside dia×20 cm length) were taken by hand to collect the upper 2 cm from randomly assigned locations within each cage. Defaunated sediment was placed into the resulting pits in the creek bottom. The core samples were kept in coolers in the field until the end of sampling (~2–3 h), and then taken to the laboratory where they were preserved in 10% buffered seawater formalin with Rose Bengal stain added, stirred gently and equilibrated for a minimum of 48 h before processing. Most samples were held 6–18 mo prior to processing.

A random subsample of 25 shrimp (of the 250 used in each experiment) was measured for total length (TL=tip of rostrum to end of uropods) such that shrimp within a similar size range (45 to 77 mm) were used in both experiments. Shrimp were then placed within the shrimp treatment cages using a dip net at densities of either 12 shrimp m⁻² (1×) or 36 shrimp m⁻² (3×), and cage lids were affixed with stainless steel bolts. Cages were monitored daily at low tide to check for scouring under the cage walls or trapped vegetation.

Seven days after initiation of each trial, cage lids were removed and 6 cores were again taken from randomly assigned locations within the grid of each cage (chosen to prevent re-sampling the same area sampled on day 1). Core samples were fixed in the same manner as on day 1. After at least 48 h of fixation, each sample was gently sieved through a 500 µm screen. All organisms retained on the screen were sorted and identified to family level using a stereo microscope at 25–50× magnification.

Concurrent with the caging experiments, water temperature (°C) was measured at 10 min intervals using an Onset StowAway Tidbit Temperature Logger (accuracy±0.4 °C at 21.1 °C) attached halfway up the side of one cage near the center of the cage array. Surface salinity (psu) was measured daily at slack low tide using an optical, temperature compensated refractometer (accuracy 1 psu).

Water flows within the different cage types were qualitatively measured using alabaster and Plaster-of-Paris “clod cards” (Doty, 1971). Water flow causes the cards to slowly dissolve, with faster flows resulting in faster dissolution of the cards. In July 2004, dried, pre-weighed alabaster (calcium sulfate dihydrate) and Plaster-of-Paris (calcium sulfate semi-hydrate) clod cards were anchored on the sediment surface using metal stakes within each of the three cage structures (open, partial or full cage, 2 replicates each), within

subtidal Crabhaul Creek, SC. After 7 d, the cards were removed from the creek, dried for 6 d (60 °C) and reweighed.

2.3. Shrimp retention experiments

On day 7 of each Creek Cage experiment, we attempted to re-collect the shrimp from the cages using dip-nets before taking the cores; shrimp would often swim or jump out of the cages once the lids were removed or while cores were being taken, thus we were largely unsuccessful at recollection. Based on observations of relatively shallow shrimp burrowing (2 cm) in laboratory aquaria, we assumed that the shrimp were unable to burrow under the 15 cm buried cage walls and that any loss would be due to cannibalism within the cages. To verify that shrimp were surviving and successfully retained within the cages for 7 d we conducted supplementary “shrimp retention” experiments. Cages similar to those used in the Creek Cage experiments were fitted with a mesh bottom addition to make shrimp quantification within the cages possible at recovery. Shrimp were placed in two cages at the 1× treatment density (12 shrimp m⁻²), and in two cages at the 3× treatment density (36 shrimp m⁻²). After 7 d, the cages were extracted from the creek (with shrimp retained on the mesh bottom) for quantification and validation of shrimp retention and survival within the cages.

2.4. Predation, Disturbance and Emigration (PDE) experiments

Four 7-d laboratory experiments were conducted in the summer of 2004 to measure the effects of shrimp predation, disturbance and emigration (PDE) on the density of macrobenthos that may have occurred during the field experiments. While shrimp predation reduces macrobenthos abundances through consumption of organisms, predation-associated sediment disturbances may further reduce epibenthic or shallow macrobenthos abundances by forcing organisms deeper into the sediment (Bonsdorff and Pearson, 1997), or by suspending them in the water column followed by downstream advective transport (Palmer, 1988) or additional predation risk once exposed. Three large benthic cores (269 cm² surface area=18.5 cm inside dia×5 cm depth) were collected in the subtidal portion of Crabhaul Creek and placed into three similarly sized glass fingerbowls (18.5 cm inside dia×6.5 cm depth) for use in the PDE experiments. Four additional cores (26 cm² surface area=5.75 cm inside dia×5 cm depth)

were collected near the large cores to quantify the initial density of macrobenthic organisms; these smaller cores were immediately preserved in 10% buffered seawater formalin with Rose Bengal dye. The bowls containing the three large cores were brought into the laboratory and submerged in a filtered seawater holding tank and allowed to acclimate under ambient environmental conditions for 24 h. Extreme care was exercised so as not to disturb the sediment–water interface. After 24 h, numerous polychaete tubes were again visible at the sediment surface.

For the PDE experiments, 3 experimental treatments were used. To limit intraspecific interactions, shrimp densities were set at 1 shrimp tank⁻¹ so that the areal density was similar to the 36 shrimp m⁻² (3×) Creek Cage treatment. The first treatment (Treatment E, no shrimp tank⁻¹) was used to quantify the effect of emigration on macrobenthos density without the effects of shrimp disturbance and predation. The second (Treatment DE, 1 non-feeding shrimp tank⁻¹) was used to additionally quantify the effect of shrimp disturbance (+emigration) on macrobenthos density; the shrimp used in this treatment had the chelae removed from each chelate pereopod to prevent them from grasping prey. The third (Treatment PDE, 1 shrimp tank⁻¹) quantified the combined effect of shrimp predation (+disturbance+emigration) on macrobenthos density. Removing the shrimps' chelae did not affect survival; no mortalities were recorded for shrimp in either treatment.

The four PDE experiments were conducted from late July to late September, 2004. On day 1 of each trial, one bowl containing a large sediment core was placed into each experimental tank (55×38 cm). Vexar 0.6 cm mesh (Memphis Net and Twine, Memphis, TN) was placed around each bowl to create similar water flow patterns as would occur inside cages used in the Creek Cage experiments. Filtered (10 μm) seawater was slowly introduced to one end of each tank; once the water level was several centimeters above the lip of the sediment bowl, flow was increased to approximately 1 cm s⁻¹. A standpipe with holes along the vertical axis was placed over the drain on the opposite end of the tank to maintain constant water level and allow drainage from different depths. A cod end with 263 μm mesh was attached to the downstream end of the drainpipe and was immersed in seawater so that any macrobenthic organisms emigrating out of the sediment bowl and into the surrounding water would be collected. After the three tanks were filled, juvenile shrimp were added to the appropriate treatments. All three treatments occurred simulta-

neously with the same ambient sediment for each of the four PDE experiments.

Salinity, temperature and dissolved oxygen were measured daily using a Hydrolab H20 Multiparameter Water Quality Data Transmitter. Seven days after initiation of the trial, the remaining sediment and organisms were collected and preserved in 10% seawater buffered formalin with Rose Bengal stain and allowed to equilibrate for at least 48 h before sieving through a 500 μm mesh. Organisms were also collected from the cod end of each tank and preserved in the same way. All retained organisms were sorted and identified to family level using a stereo microscope.

3. Statistical analyses

Statistical analyses were performed on the macrobenthos density data extrapolated to 1 m². For the Creek Cage experiments, macrobenthos densities were tested for the assumptions of normality and homogeneity of variances using the Kolmogorov–Smirnov test and the Variance Ratio test. Despite attempts at data transformation using both the log₁₀(n+1) and √(n+1) transformations, data did not meet the assumptions of analysis of variance, thus nonparametric Mann–Whitney Rank Sum tests were used in lieu of *t*-tests in our statistical analyses. All statistical tests were performed at the α=0.05 level.

For each Creek Cage experiment, total macrobenthos density on day 1 was compared to day 7 density for each experimental treatment. Macrobenthos densities from the 5 replicate cages of each experimental treatment were compared both for individual replicates and for the pooled data (all 5 replicates of each treatment) to detect significant changes. Densities of the major macrobenthic taxa, defined as those that constituted ≥10% of the total macrobenthos collected, were compared separately for each trial within treatments from day 1 to day 7. There was insufficient statistical power to detect a difference between the different treatments (e.g., 3× versus 1×).

The PDE experiments were run over a period of 6 weeks, and thus the densities of total macrobenthos and major macrobenthic taxa on day 1 and day 7 were first examined individually for each of the 4 experiments. To make comparisons across treatments (since each tank did not have the same initial density of macrobenthos), macrobenthos densities from each experiment were converted to percentages and then pooled with the mean initial macrobenthos density assigned as 100%. The mean percentage of initial macrobenthos remaining in each treatment was then calculated.

4. Results

Results of the supplementary shrimp retention experiments confirmed that most shrimp were retained within the cages for 7 d. When placed at the 1× density (12 shrimp m⁻²), the mean number of shrimp remaining after 7 d was 9.5 shrimp m⁻², and at the 3× density (36 shrimp m⁻²), the mean number of shrimp remaining was 32 shrimp m⁻². Although some shrimp were lost, roughly three times as many shrimp remained in the 3× treatment as in the 1× treatment.

The maximum measured flow velocity at Crabhaul Creek, SC, was 0.09 m s⁻¹. Using the clod card dissolution method, both the alabaster and Plaster of Paris clod cards dissolved least in the full cages, indicating the lowest water velocities, followed in order of increasing dissolution by the partial and open plots, indicating higher flow conditions. Surface sediment organic contents (% by dry weight) in Crabhaul Creek, SC ranged from 0.53 to 2.79%, with mean (±SE) 0.92±0.20%; sediment grain sizes ranged from clay to very coarse sand, with a mean (±SD) of 302.7±206.1 μm (medium sand). The highest densities of macrobenthos were always present in the top 2 cm of sediment (Table 1).

4.1. Creek Cage experiments

The two 7-d Creek Cage experiments were initiated on July 12, 2003 and July 24, 2003. Mean (±SE) shrimp total length (TL=tip of rostrum to end of uropods) for these experiments was 61.4±1.5 mm and 56.6±1.6 mm respectively. Water temperature and salinity (psu) ranged from 22.0 to 32.3 °C and 16.5–36.0 in Expt I, and 23.2–33.7 °C and 5.6–35.5 in Expt II.

In both experiments, the most statistically significant changes in total macrobenthos density were observed in the normal (1×) and elevated (3×) shrimp treatments (Table 2). In Expt I, average total macrobenthos density decreased by 36% over 7 days in the 1× treatment (7240 to 4781 ind m⁻²), and by 63% in the 3× treatment (7474

Table 1

Mean vertical distribution of total macrobenthic organisms, polychaetes only, and macrobenthic organisms excluding polychaetes (% of the total in core) in cross-creek transects in Crabhaul Creek, North Inlet, SC on June 28, 2004 (N=24 cores)

Sediment depth stratum (cm)	Total macrobenthos	Total polychaetes	Total non-polychaetes
0–2	65	75	60
2–5	14	11	14
5–10	9	6	12
10–15	12	8	14

Table 2

P-value results from the Mann–Whitney Rank Sum Test for differences in abundance of total macrobenthos in each treatment (CC: control cage, HC: partial cage, OP: open plot, 1×: 12 shrimp m⁻², 3×: 36 shrimp m⁻²) between day 1 and day 7 in Expt I (July 12, 2003) and Expt II (July 24, 2003)

Treatment	Expt I	Expt II
CC	0.015*	0.004*
HC	0.078	0.01*
OP	0.004*	0.160
1×	0.003*	0.002*
3×	<0.001*	<0.001*

Significant p-values indicated with an asterisk.

to 2757 ind m⁻²) (Fig. 3A). Initial macrobenthos densities in Expt II were slightly lower than for the start of Expt I (Fig. 3B). In the 1× treatment, average total macrobenthos density declined by 44% from 6009 to 3336 ind m⁻², and by 58% in the 3× treatment, from 5197 to 2168 ind m⁻².

Total macrobenthos densities declined to a greater extent in the high-density shrimp cages than in the cage treatments without shrimp. However, we also observed significant changes in macrobenthos density within the non-shrimp cages (Table 2), suggesting that other factors may have influenced macrobenthos densities in the absence of shrimp. In Expt I, total macrobenthos

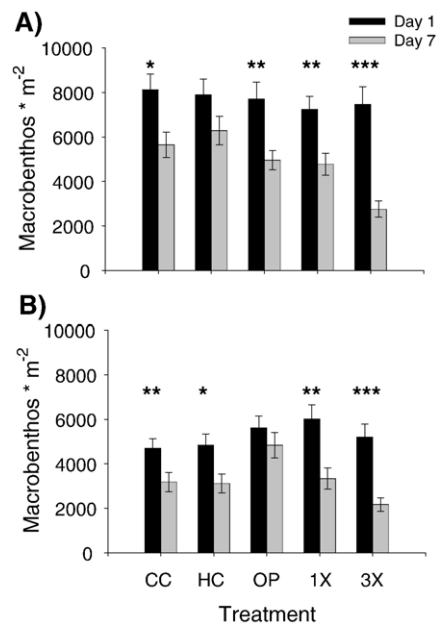


Fig. 3. Mean (±1 s.e.) density of total macrobenthos in the Creek Cage experiments on day 1 and day 7 for (A) Expt I, July 12, 2003, and (B) Expt II, July 24, 2003. Treatments: Control Cage — CC, Partial Cage — HC, Open Plot — OP, 12 shrimp m⁻² — 1×, 36 shrimp m⁻² — 3×. Mann–Whitney Rank Sum nonparametric *t*-tests: **p*<0.05, ***p*<0.01, ****p*<0.001.

Table 3

P-value results from the Mann–Whitney Rank Sum Test for differences in abundance of major taxa ($\geq 10\%$ of total macrobenthos) in each treatment (CC: control cage, HC: partial cage, OP: open plot, 1 \times : 12 shrimp m^{-2} , 3 \times : 36 shrimp m^{-2}) between day 1 and day 7 in (A) Expt I (July 12, 2003) and (B) Expt II (July 24, 2003)

A. Experiment I					
	Capitellidae	Cirratulidae	Spionidae	Syllidae	Oligochaete
CC	0.197	0.073	0.008*	0.279	0.477
HC	0.153	0.801	0.046*	0.041*	0.108
OP	0.002*	0.094	0.011*	0.069	0.740
1 \times	0.155	0.147	0.059	0.472	0.038*
3 \times	<0.001*	<0.001*	0.007*	0.016*	0.442

B. Experiment II				
	Capitellidae	Cirratulidae	Spionidae	Oligochaete
CC	0.097	0.004*	0.564	0.003*
HC	0.047*	0.005*	0.525	0.016*
OP	0.302	0.029*	0.681	0.965
1 \times	0.036*	0.006*	0.566	0.006*
3 \times	<0.001*	0.006*	0.174	<0.001*

Significant *p*-values indicated with an asterisk.

density significantly declined by 31% in the exclusion (CC) treatment (from 8133 to 5646 $ind\ m^{-2}$), and by 36% in the open plot (OP) treatment, from 7712 to

4955 $ind\ m^{-2}$ (Fig. 3A). No significant change in macrobenthos density occurred in the partial cage (HC) treatment. A similar pattern was observed in Expt II (Fig. 3B); total macrobenthos density declined by 32% in the CC treatment (from 4709 to 3182 $ind\ m^{-2}$), and by 36% in the HC treatment, from 4845 to 3117 $ind\ m^{-2}$. No significant change in macrobenthos density occurred in the OP treatment.

The most abundant macrobenthic organisms in Expt I were spionid polychaetes, followed in order of decreasing density by oligochaetes, capitellid, cirratulid and syllid polychaetes. In Expt II, spionid polychaetes and oligochaetes were followed by cirratulid and capitellid polychaetes; syllid polychaetes no longer represented $\geq 10\%$ of the total macrobenthos density.

In both Creek Cage experiments, the most significant declines in the densities of the majority of major taxa were observed in the elevated (3 \times) shrimp treatment (Table 3A,B). In Expt I, oligochaete densities declined significantly in the normal (1 \times) shrimp treatment; within the non-shrimp treatments (CC, HC and OP) there were few significant changes in the densities of the major taxa. In Expt II, significant declines in most of the major taxa were demonstrated in the shrimp (1 \times) and partial cage (HC) treatments; cirratulid and oligochaete densities

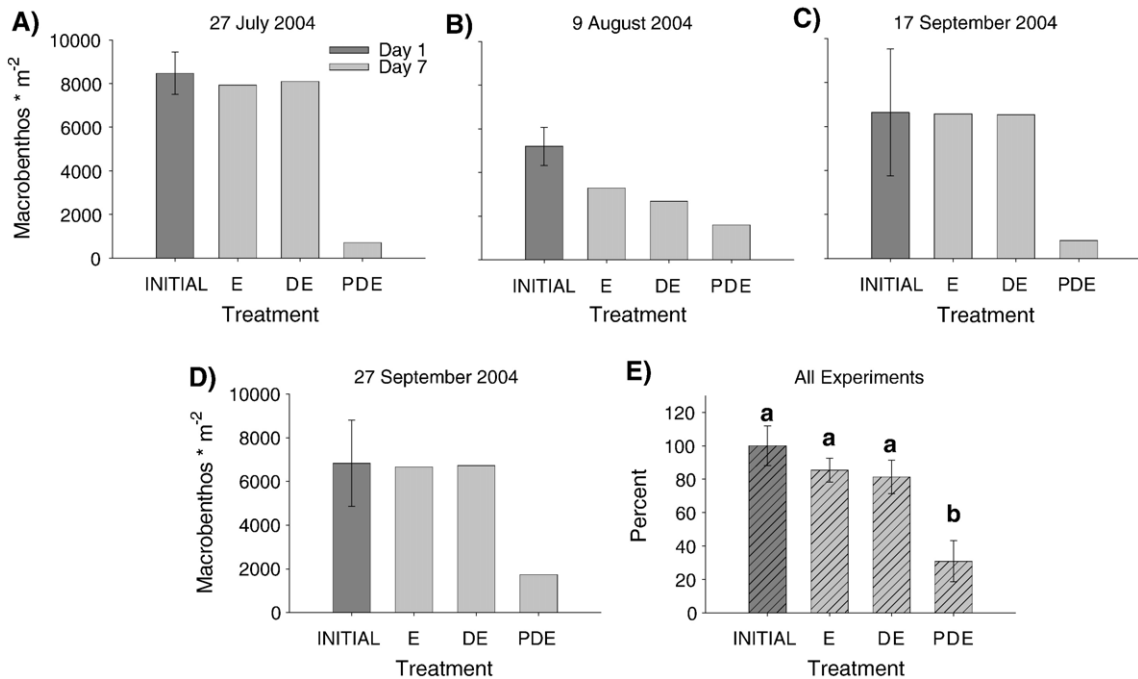


Fig. 4. A–D: Mean (± 1 s.e.) density of total macrobenthos in the PDE experiments on day 1 (Initial, $n=4$ cores) and day 7 using 3 different treatments per experiment: Emigration only (Treatment E, $n=1$ per experiment), Disturbance+Emigration (Treatment DE, $n=1$ per experiment), and Predation+Disturbance+Emigration (Treatment PDE, $n=1$ per experiment). E: Mean (± 1 s.e.) percent macrobenthos (pooled from all 4 experiments) on day 1 and mean (± 1 s.e.) percent macrobenthos remaining (pooled from all 4 experiments) on day 7; Mann–Whitney Rank Sum nonparametric *t*-tests, different lower-case letters indicate statistically significant differences at $p<0.05$.

changed significantly over 7 d regardless of experimental treatment.

4.2. Predation, Disturbance and Emigration (PDE) experiments

The first of four 7-d PDE (predation, disturbance, emigration) experiments was initiated on July 27, 2004; shrimp TL for all 4 experiments ranged from 72 to 83 mm with mean size (\pm SE) 76.5 ± 1.1 . Water temperature ranged from 23.0 to 27.7 °C, salinity (psu) from 26.6 to 33.7, and dissolved oxygen from 3.8 to 5.3 mg L⁻¹.

In the individual PDE experiments, there was a consistent pattern of drastic declines in macrobenthos densities in Treatment PDE (1 shrimp tank⁻¹), and only slight changes in Treatments DE (1 non-feeding shrimp tank⁻¹) and E (0 shrimp tank⁻¹) as compared to the initial density of macrobenthos 7 d earlier (Fig. 4A–D). After pooling the results from all four PDE experiments to conduct statistical analyses, the percent macrobenthos remaining in Treatment PDE (1 shrimp tank⁻¹) was significantly lower ($p=0.004$) than the initial value after 7 d (Fig. 4E). The percent macrobenthos remaining in Treatment PDE was also significantly lower than Treatment E (0 shrimp tank⁻¹) ($p=0.032$) and Treat-

ment DE (1 non-feeding shrimp tank⁻¹) ($p=0.032$). The percentages of macrobenthos remaining in Treatment E and Treatment DE were not significantly different from one another or from the pooled initial values. The macrobenthic organisms retained in the cod ends accounted for the reductions in Treatment E and Treatment DE. In Treatment PDE, additional losses of macrobenthos were attributed to predation by white shrimp.

The most abundant macrobenthic taxa in the PDE experiments were similar to those in the Creek Cage experiments. Capitellid and spionid polychaetes, oligochaetes and syllid polychaetes were the most numerous major taxa. Similar to the results for total macrobenthos, the greatest declines in the densities of individual major macrobenthic taxa were observed in Treatment PDE, with only minor changes in Treatments DE and E (Fig. 5A–D); this result was maintained even after pooling the results from all 4 PDE experiments (Fig. 5E). The percentage of major taxa organisms remaining in the pooled Treatment PDE (1 shrimp tank⁻¹) was significantly lower than the initial value after 7 d for spionids ($p=0.012$), capitellids ($p=0.026$), and oligochaetes ($p=0.042$), but not syllids. The percentage of these major taxa remaining in Treatment PDE was also significantly lower than in Treatment E and Treatment DE. For all of the major

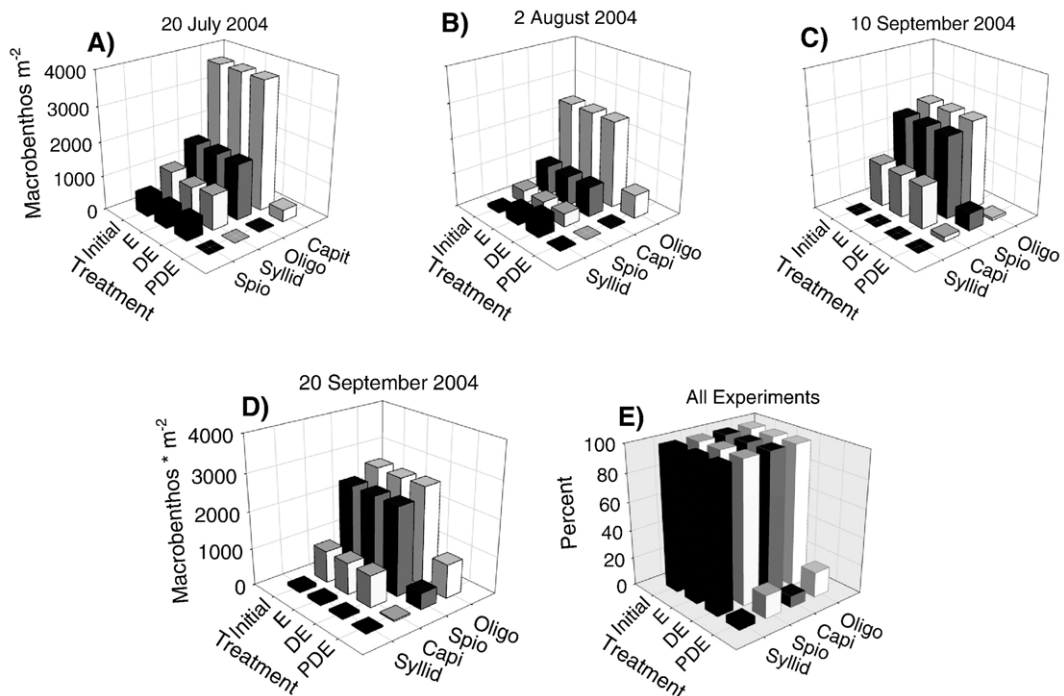


Fig. 5. A–D: Density of major macrobenthic taxa in the 4 PDE experiments on day 1 (initial) and 3 treatments on day 7 (Emigration: E, Disturbance+Emigration: DE, Predation+Disturbance+Emigration: PDE). Major taxa are arranged in order of density. E: Percent major macrobenthic taxa (pooled from all experiments) on day 1 and percent major macrobenthic taxa remaining (pooled from all experiments) on day 7 (Treatments: Emigration: E, Disturbance+Emigration: DE, Predation+Disturbance+Emigration: PDE). Note that taxon sequence varies for graphical clarity.

macrobenthic taxa, the percent macrobenthos remaining in Treatment DE and Treatment E were not significantly different from one another or from the initial value.

4.3. Comparison with long-term data

Our results indicate that, over 7 d, macrobenthos densities could be reduced up to $673 \text{ ind m}^{-2} \text{ d}^{-1}$ when shrimp were most abundant (36 shrimp m^{-2}), and $381 \text{ ind m}^{-2} \text{ d}^{-1}$ with 12 shrimp m^{-2} . We can compare these daily loss rates to linear regressions of seasonal density reductions of total macrobenthos in the long-term data during low and high density shrimp years from 1984 to 1991 (Street, 1997). In years when white shrimp were abundant (1986, 1987, 1989), the daily loss rates of total macrobenthos were higher (-185 ind d^{-1} , -209 ind d^{-1} , and -199 ind d^{-1}) than in summers when shrimp were scarce (1984, 1985, 1988; daily loss rates -122 ind d^{-1} , -86 ind d^{-1} , and -132 ind d^{-1} , respectively).

5. Discussion

In support of our first prediction, the results from the Creek Cage experiments demonstrated significant reductions in total macrobenthos densities in the shrimp inclusion treatments ($1\times$ and $3\times$), with the greatest reductions in the high density ($3\times$) shrimp treatment. White shrimp are voracious opportunistic epibenthic foragers (Williams, 1955; Young, 1959; Darnell, 1961), and have similarly reduced the numbers of peracarid crustaceans (Zimmerman et al., 2000) and annelid worms (Service et al., 1992; Zimmerman et al., 2000) in marsh sediments in laboratory experiments. Hunter and Feller (1987) reported frequent occurrences of gammarid amphipods and polychaete worms in *L. setiferus* gut contents from May to November using immunological assays. Animal parts were identified by Mayer (1985) in the gut contents of 98% of juvenile white shrimp collected in salt marsh intertidal creeks.

In separate experiments to be reported later, juvenile white shrimp within the size range used in these experiments were observed to feed within/disturb the top 2 cm of sediment (Beseres, unpublished data); thus their impact may disproportionately affect shallow-burrowing species. Because we also observed the highest densities of macrobenthos in core samples of the top 0–2 cm of sediment, these abundant shallow-burrowing species have an increased risk of mortality from shrimp predation. Virnstein (1979) reported reductions in the abundances of species that live exposed at or very close to the sediment surface due

to crab and fish predation. Using exclusion cages to examine changes in infaunal abundance, Posey et al. (2002) reported the strongest predation effects on taxa living near the sediment surface compared to deeper burrowing taxa.

In support of our second prediction, the results from the PDE experiments demonstrated that the reductions in total macrobenthos were primarily due to direct effects of shrimp predation rather than to substrate disturbance. Although gut content analyses were not performed, this pattern was consistent across all four PDE experiments, and for all major macrobenthic taxa, suggesting that shrimp predation was also the dominant force reducing macrobenthos densities within the shrimp inclusion cages in the Creek Cage experiments. However, because the laboratory experiments utilized only one shrimp tank⁻¹, they may underestimate the effects of multiple predator interactions in the field (Thrush, 1999). In Kneib's (1985) laboratory experiments using another decapod crustacean predator, *Palaemonetes pugio*, predation significantly reduced the densities of nematodes, an anemone, an ostracod and a sabellid polychaete, while disturbance only accounted for reductions in the densities of a gastropod. Our results support these findings, and suggest that predation was a much more important process in reducing total macrobenthic invertebrate densities. In contrast, Palmer (1988) reported significantly higher mortality of meiofauna when simulating disturbance by spot, *Leiostomus xanthurus*, than that due to predation by this juvenile fish.

The importance of motile predators in controlling patterns of benthic invertebrate distribution and abundance has been the subject of many investigations in intertidal and subtidal soft-sediment habitats (e.g., Woodin, 1974; Young et al., 1976; Reise, 1977, 1978; Peterson, 1979; Beukema et al., 1998 and others). While our results largely support previous studies by demonstrating that shrimp predation can significantly reduce macrobenthic densities in field and laboratory experiments, we had the unique opportunity to relate these experimental data back to the long-term data record from which our hypotheses and experiments were generated. We calculated significantly higher daily loss rates of macrobenthos in our Creek Cage experiments than were observed in the long-term data. While our calculated daily loss rates are likely overestimates due to the confinement of motile shrimp and exclusion of higher predators, significantly greater losses of macrobenthos with greater abundances of shrimp were observed in both the long-term data and in the Creek Cage experiments.

Because white shrimp are highly motile, and their presence in any section of the creek is likely temporary, it is difficult to extrapolate from these experiments to larger spatial or temporal scales. However, based upon identical caging experiments we conducted in a subtidal creek in Sapelo Island, Georgia, USA, the hypothesized impacts demonstrated by white shrimp on macrobenthos can be expected to vary considerably both spatially and temporally (Beseres, 2006). In those experiments, conducted later in the year (August–September), initial macrobenthos densities were almost an order of magnitude lower than those measured in North Inlet. This is consistent with observations reported by Strasser (2002) of significant predation by *Carcinus maenas* and *Crangon crangon* on bivalves in the Wadden Sea in June/July and August, with very few prey remaining by October. We did not observe any significant changes in macrobenthos densities in any of the five cage treatments, suggesting that there may be a low-density prey threshold or refuge (Eggleston et al., 1992) below which shrimp predation is no longer as important a process (Beseres, 2006). In support of this, macrobenthos densities actually increased within some of those shrimp inclusion cages; this may have resulted from reduced encounters with prey at these lower prey densities (Real, 1979), from reduced foraging activity (Taylor, 1984), or from predators switching to another food source when prey are scarce (Murdoch, 1969; Taylor and Collie, 2003). Alternatively, the relative intensity of predator-prey interactions such as those between white shrimp and macrobenthos may differ significantly between study areas (Rafaelli et al., 1989).

Although we would not conclude that white shrimp alone are responsible for the annual summer minima of macrobenthos densities in North Inlet, this study does demonstrate that white shrimp are major consumers of macrobenthos and can be expected to have a regulatory effect on macrobenthos densities, especially during summers when white shrimp are abundant. Strasser (2002) reported that reduced densities of epibenthic predators on tidal flats in the Wadden Sea following a severe winter resulted in significantly higher recruitment of bivalves compared to moderate and mild winters. Previous studies have identified other important factors that may have contributed to changes in macrobenthos abundances seen during the Creek Cage experiments, particularly in the treatments not containing shrimp. Very small benthic and infaunal predators may not have been effectively excluded by the mesh (e.g., Reise, 1977, 1978; Holland et al., 1980; Ambrose, 1984; Frid and James, 1988; Beukema et al., 2000), leading to a decrease in the macrobenthic prey of predatory infauna, even when epibenthic predators are absent (Commuto, 1982; Ambrose,

1984, 1991). Posey and Hines (1991) have carefully described strong indirect effects of epibenthic and nektonic predators upon benthic infaunal densities and community composition. We did not examine the effects of other resident and transient marine predators in combination with white shrimp, and this is an area for future research. Expanding these experiments to include additional predators may explain the reductions in benthic abundances in the non-shrimp cages. Additionally, we examined changes in macrobenthos densities at a gross taxonomic level — further analyses by species composition and/or guild is warranted and may yield a more complete representation of changes in community structure. Rafaelli et al. (1989) demonstrated that although the overall density of *Corophium sp.* was not affected by *Carcinus maenas* or *Crangon crangon* predation, significant changes in the population structure occurred. Abiotic factors may have also been important; while the PDE experiments indicated that sediment disturbance by a single white shrimp was not an important factor influencing benthos abundances, Hulberg and Oliver (1980) and Woodin (1978) described reductions in infaunal abundance due to sediment modifications and disturbance in other soft-bottom habitats.

Other than predation, the repeatedly observed summer minima in benthos abundances may also be influenced by bottom-up (food supply) factors. Seitz and Lipcius (2001) found that nutrient additions and predation both influenced bivalve abundance, with nutrients important at both small and large spatial scales and predation important only at small spatial scales. However, Posey et al. (2002) reported relatively little response of benthos to 4-wk nutrient additions in caging experiments in intertidal creeks, despite an increase in benthic primary production and porewater nutrients. Benthos living closer to the sediment surface may represent the largest proportion of the total macrobenthos decline during the summer months, whereas deep-burrowers may not be as affected by surface processes. Additionally, processes operating over the longer term such as periodic recruitment events or gradual warming throughout the summer would not have been captured in our short-term experiments. However, our sampling regime did depict some of the progressing seasonal reductions in macrobenthos abundance; densities of macrobenthos collected on day 1 of Expt I were notably higher than on day 1 of Expt II although the major macrobenthic taxa were generally the same.

Although the use of cages in soft-sediment habitats is cause for concern due to the potential for cage-induced habitat modifications (Arntz, 1977; Virnstein, 1978; Hulberg and Oliver, 1980), manipulative caging

experiments remain a valuable tool for studying the effects of predation by motile predators. Potential problems may be minimized or alleviated through careful planning and cautious interpretation (Vimstein, 1978). Within the Creek Cage experiments, the spatial layout of the treatments was randomized, treatments were replicated, and partial cages were used as cage artifact controls for any physical effects caused by the cage structures. Any potential impacts of macrobenthos recruitment were minimized by using short-term (7-d as compared to several months) experiments, reducing the chance that newly-settled larvae would grow to sufficient size as to be sampled by 500 μm mesh. Lastly, the Creek Cage and PDE experiments were independently compared *a posteriori* based on similar experimental treatments; hence both were unbiased estimators of the same processes in action. Although we expected to observe similar results in the HC (partial cage) and OP (open plot) treatments, the results instead indicated that macrobenthos densities were affected to different magnitudes, although to a lesser degree than in the shrimp inclusion treatments. Ambient predators may have foraged inside the HC and OP cages with different frequencies and intensities. The PDE experiments were designed using information gained from these unexpected field results and demonstrated that white shrimp predation had greater effects on macrobenthos densities than sediment disturbance.

While it is likely that other unmeasured factors contribute to the seasonal abundance minima of macrobenthos, this study demonstrates that white shrimp are major consumers of macrobenthos. Because declines in macrobenthos abundances from white shrimp predation exceeded declines measured both in the other field cage treatments and in the PDE experiments, this suggests that predation has primacy as a determinant in the seasonal cycle. Since white shrimp are motile, and their densities fluctuate widely inter- and intra-annually, their impact can also be expected to vary both spatially and temporally. However, shrimp predation can significantly reduce macrobenthos densities in subtidal soft-bottom sediments during the summer months.

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