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Complex trophic and nontrophic interactions between meiobenthic copepods and marine snow

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Abstract

Trophic and nontrophic interactions between sediment-associated metazoans and marine snow (organic aggregates ca. 0.5 mm in diameter) in the water column represent an unexplored potential link between benthic and pelagic environments. To investigate the possibility that such a link exists, we examined the effects of meiobenthic harpacticoid copepod assemblages on the formation and development of laboratory-generated marine snow. Known densities of a mixed-species copepod assemblage collected from *Spartina alterniflora* Loisel stems were added to rotating cylinders filled with 63 μm filtered natural seawater collected from a tidal creek on Sapelo Island, GA, USA. Copepod effects on aggregate numbers, aggregate volume and nonaggregate and aggregate total particulate matter (TPM), total particulate carbon (TPC), and bacterial densities were determined after 18 h. Aggregate numbers declined and aggregate volume increased significantly in the presence of as few as 4 copepods l^{-1}. The presence of copepods produced larger, less-dense aggregates in contrast to expected animal grazing effects on marine snow. Changes in TPM were inconsistent and ranged from no difference in nonaggregate amounts between treatments to an ca. 50% decrease in aggregate amounts with increased copepod density. Treatment level differences in both nonaggregate or aggregate TPC could not be attributed to a copepod effect. Copepod activities produced either a decrease in the concentration of bacteria on aggregates or a decrease in both nonaggregate and aggregate bacterial densities. Although results do not allow us to conclude which mechanisms generate the observed copepod effects on marine snow, experiments indicate that benthic copepods in the water column can affect significantly the physical and biological dynamics of marine snow aggregates in shallow coastal systems.

Keywords: Marine snow; Harpacticoid copepods; Bacteria; Particulate matter; Aggregate dynamics; Benthic–pelagic interactions

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1. Introduction

Marine snow (organic aggregates ca. 0.5 mm in diameter), is abundant in the water column and comprises a significant fraction of the suspended matter in coastal environments (Alldredge and Silver, 1988). Although physical factors are critical to aggregate formation (McCave, 1984; O'Melia and Tiller, 1993), aggregate degradation and break-up probably are mediated by biological activities (Biddanda and Pomeroy, 1988; Alldredge et al., 1990; Smith et al., 1992). Aggregate microbial assemblages typically undergo rapid successional changes that may influence marine snow integrity (Davoll and Silver, 1986; Biddanda and Pomeroy, 1988; Gotschalk and Alldredge, 1989; Müller-Niklas et al., 1994). Increased densities of microflagellates and ciliates can occur within a few days of snow formation and cause a decline in the rapidly growing bacterial populations on aggregates (Pomeroy and Deibel, 1980; Pomeroy et al., 1984; Davoll and Silver, 1986; Gotschalk and Alldredge, 1989). In addition to microbial effects on aggregate dynamics, pelagic and benthic metazoans also are associated with marine snow and may affect aggregate break-up.

Pelagic metazoans appear to have an ambiguous role in marine snow dynamics. Although zooplankton are found on aggregates (Alldredge, 1976; Ohtsuka and Kubo, 1991; Steinberg et al., 1994), the association between zooplankton and snow may be weak (Shanks and Edmondson, 1990). A few studies indicate that zooplankton are capable of feeding on aggregate surfaces when found on snow (Alldredge, 1972, 1976; Ohtsuka and Kubo, 1991). Snow material can dominate the diets of some micronekton (Lampitt et al., 1993), but the ability of zooplankton to feed on snow may not be universal (Bochdansky and Herndl, 1992). Exudates released by diatoms forming aggregates actually may inhibit zooplankton grazing on marine snow (Malej and Harris, 1993).

Benthic metazoans (e.g., nematodes and harpacticoid copepods) commonly are associated with marine snow in the water column (Herndl and Peduzzi, 1988; Shanks and Edmondson, 1990) and may have significant trophic and/or nontrophic effects on aggregate dynamics. In sediments, nematodes and copepods are polyphagous and feed on a range of organisms including protists, bacteria and microalgae (e.g., Hicks and Coull, 1983; Heip et al., 1985). Trophic interactions among nematodes, copepods, and microbes are known to affect sediment-associated microbial assemblages (see Walters and Moriarty, 1993). Benthic metazoans also are able to forage on aggregate assemblages while in the water column (Rieper-Kirchner et al., 1991; Bochdansky and Herndl, 1992). In some instances benthic copepods actually may prefer planktonic food sources (Decho, 1986, 1988). However, the overall effects of benthic metazoans on aggregate microbial assemblages and marine snow dynamics remain undocumented.

In this paper, we experimentally investigate the effects of one group of benthic metazoans, harpacticoid copepods, from an intertidal saltmarsh habitat on the development of marine snow and the dynamics of aggregate bacterial assemblages in shallow coastal environments. Specifically we manipulate copepod densities to examine potential trophic and nontrophic effects on nonaggregate and aggregate bacterial assemblages and the physical characteristics of marine snow.

2. Materials and methods

Experiments were conducted in July and October 1992 to encompass the range of natural conditions experienced in Southeastern saltmarsh environments. Marine snow was generated within rotating cylinders (1.2 l total volume) in the laboratory following the methods of Shanks and Edmondson (1989). Although cylinders do not mimic natural hydrodynamic regimes (Jackson, 1994), cylinder-formed aggregates are similar to field aggregates in density, size and composition (Shanks and Edmondson, 1989). Seawater for experiments was collected from South End Creek on Sapelo Island, GA, USA (81°17′ W, 31°24′ N) during the latter stages of an incoming tide. Average water temperature, salinity and pH at the collection site varied from 29.5 to 23.8°C, 23.2 to 25.9 ppt and 7.7 to 7.8, respectively, between the July and October experimental dates.

2.1. Seawater pretreatment

Seawater collected for experiments first was filtered through a 63 μm mesh to remove any zooplankton or benthic metozoa that would complicate the establishment of density treatments. Preliminary experiments indicated that filtration did not affect any of the aggregate characteristics measured. Aggregate concentration, number l^{-1}, ($F = 2.25$; df = 1,8; $P \geq 0.05$), length ($F = 2.80$; df = 1,8; $P \geq 0.05$), width ($F = 3.58$; df = 1,8; $P \geq 0.05$), total particulate matter amounts ($F = 0.05$; df = 1,8; $P \geq 0.05$), or bacterial densities ($F = 3.08$; df = 1,8; $P \geq 0.05$) were not significantly different between filtered and unfiltered seawater.

2.2. Copepod addition experiments

To begin each experiment filtered seawater was placed into cylinders with varying treatment densities of meiobenthic copepods. The harpacticoid copepods added to cylinders consisted of a mixed-species assemblage of adult individuals extracted from *Spartina alterniflora* Loisel stems collected along the banks of South End Creek the day before each experiment. Use of a mixed-species assemblage was designed to mimic natural field conditions in which a variety of harpacticoid species are found in the water column (Palmer and Gust, 1985). The selection of stem-associated copepods for experiments was based on observations that indicated harpacticoids on stems disperse through the water column and frequently may be found in the pelagic environment (Walters, pers. obs.). Live stems were excised at the sediment surface in the field and placed in a 22.7 l bucket with an ca. 7.5% solution of the general anaesthetic $MgCl_2$. After 20 min stems were removed and the remaining slurry passed through 1000 and 63 μm mesh sieves to remove debris and to retain copepods respectively. In the laboratory different densities of the mixed copepod species assemblage corresponding to the different treatment levels were placed into vials with filtered seawater and stored overnight. After examination to verify that no mortality occurred, copepods were added to cylinders the next day. In July three copepod density treatment levels (0×, 1×,

10×) were established that were equivalent to 0, 4 and 40 copepods l^{-1}. Four treatment levels (0×, 1×, 5×, 10×) equivalent to 0, 4, 20 and 40 copepods l^{-1} were established in October. The range of treatment levels included naturally occurring water column densities of copepods in salt marsh (Palmer and Gust, 1985) and near shore habitats (Shanks and Edmondson, 1990).

Cylinders containing the different copepod density treatments were allowed to rotate a total of 18 h that included 12 h of darkness. Aggregates typically formed within 1 h after the onset of rotation. At the end of the 18-h period, the contents of each cylinder were photographed, to determine aggregate numbers and size, and sampled while rotating. Photographs were taken by placing a black background behind each cylinder and 500 W floods on either side. An f-stop was selected that permitted sufficient depth of field to visualize all aggregates within the cylinder. Multiple samples of nonaggregate and aggregate seawater were extracted by syringe through a serum stopper in the side of the cylinder. Nonaggregate samples contained no visible (≥ 0.5 mm) aggregates. Aggregate samples contained varying numbers of visible snow particles, enumerated during the sampling, and surrounding seawater. One set of nonaggregate (30 ml) and aggregate (5 ml) samples were filtered through preashed Whatman GF/F filters and immediately frozen at −70°C. Total particulate matter (TPM) and total particulate carbon amounts (TPC) were determined from filter samples. Additional nonaggregate (10 ml) and aggregate samples (5 ml) were preserved in a 2% formaldehyde solution and refrigerated for later enumeration of bacterial densities.

2.3. Sample processing

Samples were processed within 6 months of collection. Aggregate numbers and linear dimensions were determined from 1:1 photographs of cylinders examined under a dissecting microscope at 6×. Aggregate numbers within cylinders were determined either by enumerating all or a randomly selected subsample of the visible aggregates in photographs. A randomly selected subset of aggregates also were measured to determine size. Lengths and widths of aggregates were measured with an ocular micrometer and volumes calculated based on formulas for a sphere, if length and width were equal, or right cylinder, if length exceeded width. Aggregate volume per liter was calculated by multiplying the mean number of aggregates per liter times the average aggregate volume. Material collected on GF/F filters was dried at 60°C for 24 h and weighed to determine TPM. Elemental analyses was performed for October samples on material retained on GF/F filters using a Perkin Elmer 2400 CHN analyzer. October aggregate TPM and TPC amounts were corrected by subtraction for nonaggregate TPM and TPC amounts unavoidably collected in the seawater when aggregates were sampled. Bacterial numbers were counted by epifluorescence microscopy after staining with acridine orange (Hobbie et al., 1977). Ten haphazardly selected fields per sample (≥ 200 cells) were determined to be sufficient to estimate bacterial densities (see Kirchman, 1993). Aggregate bacterial densities were corrected by subtraction for nonaggregate bacteria also collected in July and October aggregate samples.

2.4. Statistical analyses

Results were analyzed by ANOVA and Ryan's Q multiple comparison tests (Day and Quinn, 1989) on appropriately transformed data or by a Kruskal–Wallis distribution-free test if data could not be transformed to satisfy ANOVA assumptions. A hierarchical log-linear model for complex surveys (Fay, 1985) was used to analyze data that were not statistically independent (e.g., nonaggregate and aggregate samples from the same cylinder) and generate a likelihood ratio χ^2 value. A nested design with counts from individual fields treated as subsamples was used to analyze bacterial densities. All tests were run on an IBM PS/2 using SAS 6.04 and the GLM or NPAR1WAY statistical routines (Joyner, 1985) or CPLX (Fay, 1985). Detectable effect sizes for individual tests were calculated based on observed field or 0 × treatment sample variability using Cohen (1988).

3. Results

Initial water column bacterial densities and TPM amounts varied between experiments (Fig. 1). Bacteria ($F = 42.29$; df = 1,8; $P \leq 0.0005$) and TPM ($F = 8.60$; df = 1,8; $P \leq 0.05$) were significantly greater at the start of July compared to October experiments. There were no visible aggregates in the water column at the outset of either experiment.

Numbers and sizes of aggregates formed over 18 h of rotation varied appreciably among copepod treatment levels. The trend was for fewer aggregates and greater aggregate volume per liter in treatments with copepods (Fig. 2 and Fig. 3). Aggregate numbers were not significantly lower in copepod treatments in July ($F = 3.35$; df = 2,9; $P \leq 0.05$) even though a difference of $\leq 50\%$ could be detected with 80% power at the 0.05 level of significance (Fig. 2a). October aggregate numbers (Fig. 3a) were

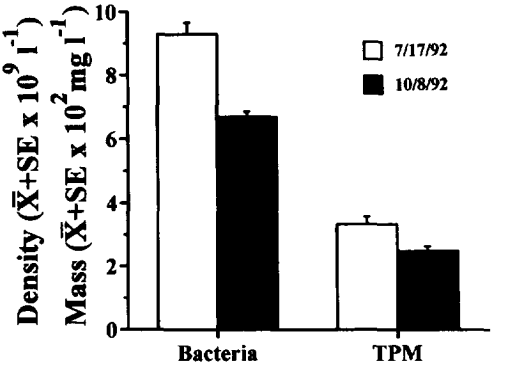

Fig. 1. Initial mean ($n = 5$) bacterial densities and total particulate matter in the water column after 63 μm sieving for July and October experiments.

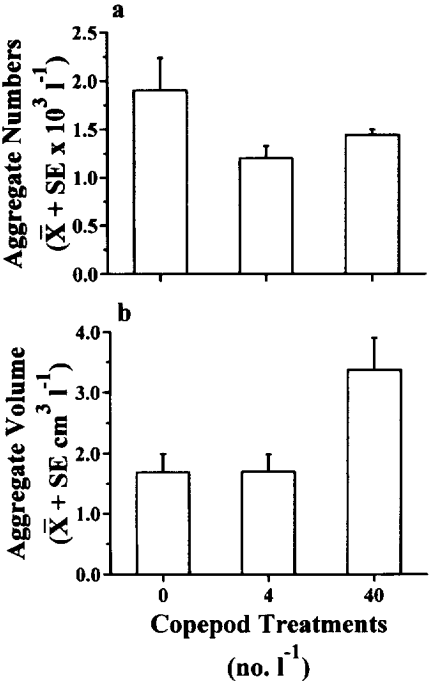

Fig. 2. The mean ($n = 4$) density (a) and volume (b) of aggregates formed in cylinders after 18 h of rotation in the July experiment.

significantly lower in copepod treatments ($F = 5.11$; df = 2,7; $P \leq 0.05$). Aggregate volume per liter, (Fig. 2b and Fig. 3b) was significantly greater in treatments with 20 or more copepods per liter both in July ($F = 6.27$; df = 2,9; $P \leq 0.05$) and October ($F = 5.60$; df = 2,7; $P \leq 0.05$). Aggregate volume per liter increased in spite of a decrease in aggregate numbers and reflected a 2.2–2.6-fold increase in the size of individual aggregates between 0 × and copepod additions.

Total particulate matter in aggregate samples varied among treatments in July (Fig. 4). Aggregate dry weights per unit volume (Fig. 4a) decreased significantly with the addition of copepods ($F = 14.23$; df = 2,9; $P \leq 0.002$). Copepods produced a significant 50% reduction in TPM cm^{-3} of aggregate between each treatment level (Ryan's Q, $P \leq 0.05$). The amount of aggregate TPM per liter (Fig. 4b) also declined between treatments ($F = 10.89$; df = 2,9; $P \leq 0.005$). Copepods significantly reduced the TPM per liter by over 50% (Ryan's Q, $P \leq 0.05$).

October TPM and TPC varied between nonaggregate and aggregate samples and copepod treatment levels (Fig. 5). Nonaggregate TPM ($F = 1.95$; df = 3,10; $P \geq 0.05$) and TPC (Kruskal–Wallis $\chi^2 = 7.23$; df = 3; $P \geq 0.05$) were not significantly different between copepod treatments (Fig. 5). Based on the variance in initial field TPM and TPC amounts, 18 and 7% differences were detectable with 80% power at the 0.05 level of significance, respectively. Unfortunately, unequal sample sizes, an unexpectedly large variance in 0 × samples, and nonhomogeneous variances between treatment levels

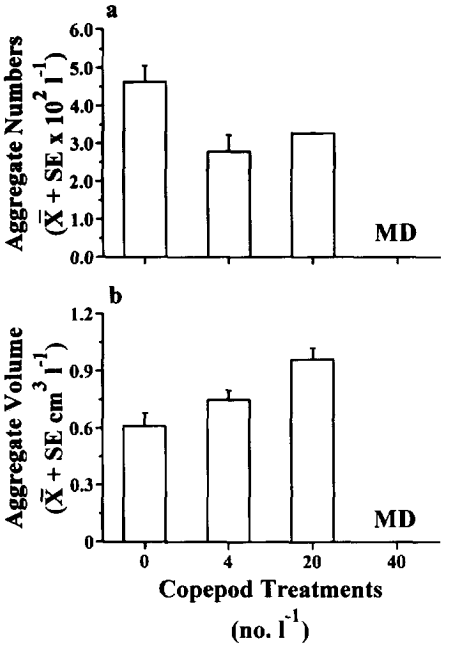

Fig. 3. The mean ($n = 2$–5) density (a) and volume (b) of aggregates formed in cylinders after 18 h of rotation in the October experiment. (MD = missing data).

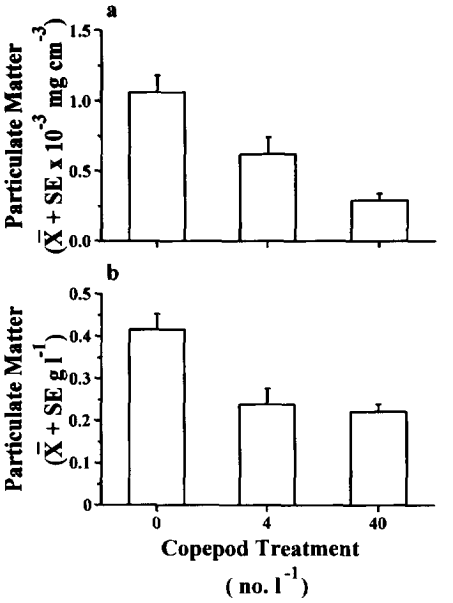

Fig. 4. The mean ($n = 4$) total particulate matter amounts associated with aggregates per cubic centimeter of aggregate (a) or liter of seawater (b) in the July experiment.

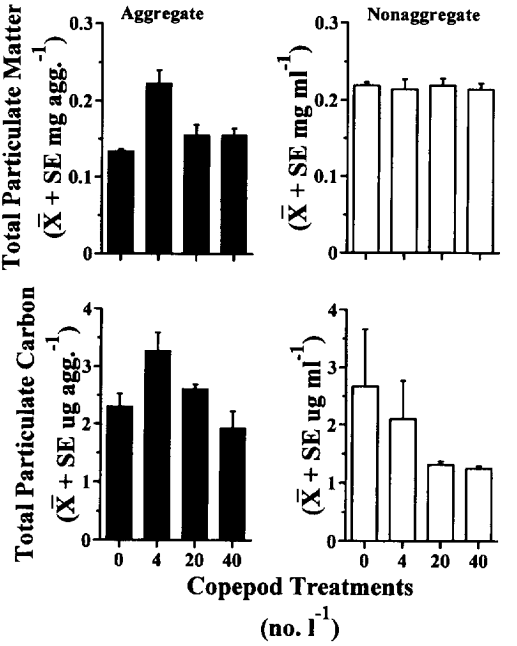

Fig. 5. The mean ($n = 3$–5) aggregate and nonaggregate total particulate matter and total particulate carbon amounts for each copepod treatment level in the October experiment.

contributed to the inability statistically to detect the 53% difference in TPC between 0 × and 10 × treatments. Aggregate TPM ($F = 14.35$; df = 3,10; $P \leq 0.001$) and TPC ($F = 3.98$; df = 3,10; P, 0.05) were significantly different between treatments, but differences could not be attributed solely to a copepod treatment effect. Aggregates in 1 × treatments contained significantly greater amounts of TPM than all other treatments and significantly greater amounts of TPC than the 10 × treatment level (Fig. 5), but TPM and TPC were not different between 0 × and 10 × treatments (Ryan's Q, $P \leq 0.05$). Both nonaggregate (7.9–6.1) and aggregate C:N ratios (7.9–7.2) remained substantially unchanged between treatments but were reduced from initial samples (12.3).

July bacterial densities (Fig. 6a) varied significantly and were dependent on both the presence or absence of visible aggregates and copepod treatments (Likelihood ratio $\chi^2 = 4.93$; df = 2; $P \leq 0.001$). Nonaggregate bacterial densities consistently were ca. 3-times greater than aggregate bacterial densities and declined steadily between 0 × and 10 × treatments (Fig. 6a). Aggregate bacterial numbers declined by 31% between 0 × and 1 × treatments but increased by 64% between 1 × and 10 × treatments (Fig. 6a). The trend for a decrease in nonaggregate and an increase in aggregate bacterial densities between 0 × and 10 × treatments resulted in a net no change in total bacteria per liter of seawater ($F = 1.35$; df = 2,9; $P \geq 0.05$). There was only a 6% difference in total bacterial densities between initial samples (Fig. 1) and 10 × treatments (Fig. 6a). Although overall numbers remained unchanged, densities of bacteria per cm^3 of

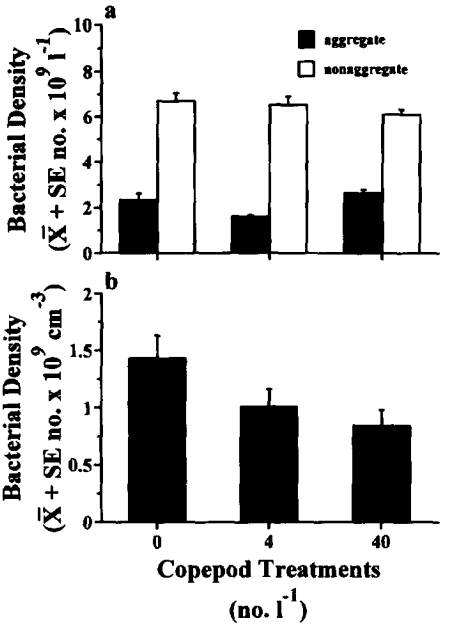

Fig. 6. The mean ($n = 4$) nonaggregate and aggregate bacterial densities per liter (a) or cubic centimeter of aggregate (b) in the July experiment.

aggregate actually declined with increased copepod abundance (Fig. 6b). The decline in bacterial densities per unit volume of aggregate was marginally significant ($F = 4.24$; df = 2,9; $P \leq 0.0505$). There were fewer bacteria cm^{-3} on $10\times$ compared to $0\times$ aggregates (Ryan's Q, $P \leq 0.05$).

Copepod treatment effects on bacteria also were detected in the October experiment (Fig. 7). Nonaggregate bacterial densities (Fig. 7a) declined significantly between copepod treatments ($F = 10.94$; df = 3,10; $P \leq 0.002$). There were fewer bacteria in the water column in $10\times$ compared to all other treatments (Ryan's Q, $P \leq 0.05$). Bacterial densities per aggregate (Fig. 7b) also decreased significantly between copepod treatments ($F = 4.17$; df = 3,10; $P \leq 0.05$). Fewer bacteria were found on $10\times$ compared to $0\times$ or $1\times$ aggregates (Ryan's Q, $P \leq 0.05$). The increased bacterial density in $1\times$ treatments (Fig. 7b) was not significantly different from $0\times$ or $5\times$ levels. The inadvertent loss of cylinder photographs for the $10\times$ treatment precluded analysis of aggregate bacterial densities per liter of seawater or cm^3 of aggregate, but the decrease in bacterial density per aggregate and increase in the size of aggregates (Fig. 3b) suggest that bacterial densities per cm^3 of aggregate also declined between copepod treatments.

4. Discussion

Results indicated that meiobenthic copepods can have significant trophic and nontrophic effects on the formation of marine aggregates. The presence of only a few

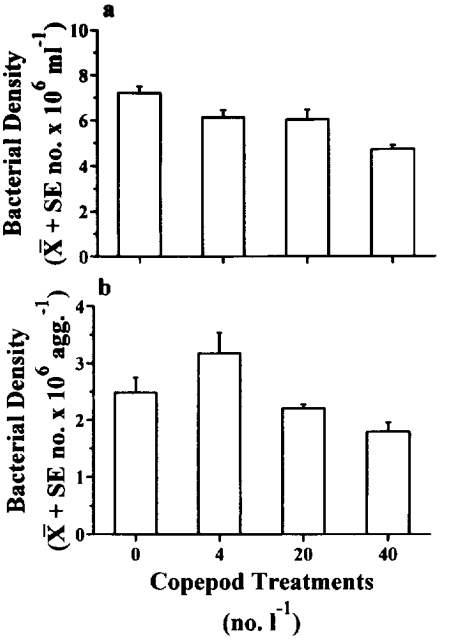

Fig. 7. The mean (n = 3–5) nonaggregate (a) and aggregate (b) bacterial densities in the October experiment.

copepods per liter consistently resulted in fewer but larger marine snow particles. Copepods can cause a reduction in the density of aggregate particulate matter and may influence nonaggregate total carbon amounts, but the effects were inconsistent. At densities of just 40 individuals l^{-1} harpacticoid copepods were able either to dilute the concentration of aggregate bacteria or actually reduce both aggregate and nonaggregate bacterial densities.

Harpacticoid copepods in the water column could influence aggregate numbers and sizes directly through the release of muco-polysaccharides. Increased amounts of transparent exopolymer material (TEM) in the water column increase the probability that plankton stick together upon collision forming aggregates and increase aggregate scavenging of other flocs, fecal pellets and debris (Decho, 1990; Kiørboe and Hansen, 1993; Passow et al., 1994). An increase in the coalescence efficiency and scavenging of smaller particles would produce fewer, larger aggregates as in our experiments (Fig. 2 and Fig. 3). The release of TEM also may affect the small-scale hydrodynamics within chambers and physically promote formation of larger aggregates (e.g., Jenkinson, 1986). A number of sediment-dwelling harpacticoid copepod species directly release mucus material through various body pores for a variety of purposes that include the formation of diapause cysts (Williams-Howze, personal communication) and feeding sacs (Hicks and Coull, 1983). The ability of the *S. alterniflora*-associated copepods used in our experiments to release mucus directly is unknown.

Copepods also may affect aggregate numbers and sizes indirectly by increasing the availability of dissolved organic material (DOM) and nutrients either through foraging

or excretion (sensu Jumars et al., 1989). Increased amounts of DOM and nutrient may stimulate microbial assemblages to release exopolymers and affect the formation of aggregates. Zooplankton activities can provide nutrients for bacterial growth in laboratory experiments (Peduzzi and Herndl, 1992) and nutrients released by calanoid copepods also can stimulate epibiotic bacterial activity (Carmen, 1994). Epibiotic bacteria associated with high-density (100 individuals l^{-1}) zooplankton assemblages may contribute significantly to pelagic carbon flow (Carmen, 1994), but there is no evidence to suggest that harpacticoid copepods even at 40 individuals l^{-1} release sufficient amounts of DOM to affect either nonaggregate, aggregate or epibiotic bacterial activities. If an increase in nutrient availability occurred in copepod treatments, it did not result in a detectable increase in either nonaggregate or aggregate bacterial densities.

A second line of evidence suggests copepods may not be affecting aggregate numbers and sizes solely by increasing amounts of TEM. If copepods increased coagulation efficiencies and particle scavenging then the amount of particulate matter associated with aggregates should increase. Instead the density and amounts of particulate matter actually declined between copepod treatments in the July experiment (Fig. 4). In October aggregate formation increased TPM l^{-1} over initial values (Fig. 1 and Fig. 5), but TPM aggregate^{-1} did not increase as expected if copepod-generated mucus influenced the accumulation of aggregate particulate matter. Harpacticoid copepod activities appear able to cause an increase in aggregate size without an increase in the accumulation of TPM. Copepod movements on and/or between aggregates may prevent the physical compaction of aggregates and explain the increase in size. Although biological processes are recognized as an important influence on the aggregation and disaggregation of marine snow particles (Alldredge and Silver, 1988; Kepkay, 1994), the physical actions of fauna are expected to break-up aggregates (Alldredge et al., 1990). Contrary to expectations we observed that harpacticoid copepod activities produced an increase in aggregate size.

The influence of meiobenthic copepods on aggregate size also has implications for particle settlement and the flux of material between pelagic and benthic habitats. Large, rapidly sinking aggregate and fecal particles are believed to predominate the flux of organic matter reaching the sea floor (Fowler and Knauer, 1986; Alldredge and Silver, 1988). Aggregate physical characteristics will affect the rate at which particles sink through the water column and can be affected by zooplankton and other fauna. Alldredge et al. (1990) proposed that animal grazing activities contribute significantly to the disaggregation of marine snow. The resultant production of smaller, less dense aggregates would slow particle settlement. We found that harpacticoid copepod activities produced larger, not smaller, less dense aggregates. The increased size and decreased density also should increase the time aggregates and any associated fauna remain in the water column. Meiobenthic copepod activities appear capable of reducing the rate of water column particle flux.

In July nonaggregate bacterial densities were affected by aggregate formation and aggregate bacterial densities were affected by a copepod-influenced increase in aggregate size. Total bacterial numbers l^{-1} remained unchanged while nonaggregate bacterial densities decreased from initial water column values by up to 34.5% (Fig. 1 and Fig. 6a). Results suggest bacteria found on aggregates were scavenged from the water column and

that both nonaggregate and aggregate bacterial populations either were not growing or growing at a rate equal to cell losses. In the field reduced aggregate bacterial growth rates typically occur only after nutrients and organic matter become depleted (Alldredge and Gotschalk, 1990; Müller-Niklas et al., 1994). It is possible the period of rapid bacterial growth and increased mortality was missed given the length, 18 h, of our sampling interval. Kepkay and Johnson (1988) reported peak bacterial densities on particles within 5 to 10 h after initiation of experiments after which protists supposedly reduced densities back to initial values. Protists are a significant source of mortality for bacteria (Capriulo et al., 1991), but we did not examine whether protists affected bacterial densities in our experiments. If protists were unaffected by copepod treatments, foraging by protists may explain the 12.5% difference in total bacterial densities between treatment levels. Although evidence from the July experiment does not suggest major direct effects by copepods on either bacteria or protists, copepods indirectly decreased aggregate bacterial densities by increasing aggregate size. Aggregate bacterial densities were diluted, fewer bacteria cm^{-3} aggregate, because the same bacterial numbers were present on larger aggregates. A reduction in the concentration of aggregate bacteria could have implications for the scavenging of nutrients by aggregates and bacterial population growth rates on aggregates.

Meiobenthic copepods exhibited what can only be interpreted as a direct effect on both nonaggregate and aggregate bacterial populations in the October experiment. Compared to initial densities nonaggregate bacterial populations increased by 8.2% in $0\times$ and decreased by 29.3% in $10\times$ copepod treatments (Fig. 1 and Fig. 7a). These results suggest that the nonaggregate bacterial population was growing at a rate greater than any losses from natural cell mortality or protist predation and that copepods directly contributed to the reduction in bacterial densities in $10\times$ treatments. Aggregate bacterial densities also declined with increased copepod densities (Fig. 7b). If the October trend in aggregate numbers and sizes remained consistent over all treatment levels, total bacteria l^{-1} in the $10\times$ copepod treatment would have declined by 21.2% below initial densities. Bacterial densities in copepod treatments also did not increase or exhibit other indications of possible complex trophic interactions between copepods, protists, and bacteria (sensu Walters and Moriarty, 1993). Direct consumption of bacteria by copepods is the most likely explanation for the decline in both nonaggregate and aggregate bacterial densities.

The overall effect of benthic copepods on aggregate dynamics ultimately will depend on the frequency, density, and duration of harpacticoid excursions into the water column. Studies indicate that various physical and biological factors influence the frequency and numbers of harpacticoids entering the water column (Palmer, 1988; Walters, 1991). In shallow subtidal environments where the nightly migration of large numbers of copepods from both sediment and seagrass habitats is common (Walters, 1988, 1991), effects on aggregate dynamics may be significant. The limited numbers of sediment-dwelling copepods typically suspended into the water column in intertidal saltmarsh habitats (Palmer and Gust, 1985) may have a minimal affect on stem-associated aggregates. Meiobenthic copepods in controlled conditions are able to remain in the water column for long (hours) periods (Bell et al., 1989), but in the field resettlement can be rapid (Walters and Bell, 1994). Behavioral observations of copepod-aggregate

interactions also suggest the association is only temporary for certain species (Shanks and Edmondson, 1990; Walters, personal observation). The duration of any association between benthic copepods and pelagic aggregates is likely to be species-specific and depend on factors such as habitat affiliation and ontogenetic stage that also influence a copepod's presence in the water column (Palmer, 1988; Walters, 1991). Once advected into the water column, individuals of a copepod species that seldom leave the benthic environment may tend to remain associated with an aggregate. In comparison, copepod species, from either subtidal or intertidal vegetation, might be more likely to move between aggregates because of superior swimming abilities. A better understanding of the causative factors that determine the presence of benthic copepods in the water column and the duration of copepod–aggregate interactions is critical to determine the overall impact of meiobenthic copepods on marine snow aggregate dynamics.

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