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THE EFFECTS OF COMPLEX TROPHIC INTERACTIONS ON A MARINE MICROBENTHIC COMMUNITY[1]

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Abstract. The consequences of complex trophic interactions for the dynamics of a natural microbenthic community from an intertidal Australian seagrass bed were examined during experiments in January, March, April, and June 1989. Effects of meiofauna and protist density manipulations on bacterial numbers and division rates and microalgal biomass were determined over 6 d each month. Results varied among experiments, microbial groups, and vertical positions within the sediment. Meiofaunal effects increased bacterial division rates but not densities in January subsurface and March surface sediments. In June, enhanced meiofaunal densities decreased subsurface but increased surface bacterial densities. A complex, tri-trophic-level interaction among meiofauna, protists, and bacteria probably caused the increased bacterial densities in June surface sediments. Meiofauna had no discernible effect on bacterial densities and division rates in January surface and March subsurface sediments even though relatively small (<50%) differences between treatments could be detected with reasonable statistical power. Changes in microalgal biomass could not be attributed to experimental treatments, and meiofauna likely have a limited effect on microalgae in this intertidal seagrass habitat. Results indicate that the combined effects of meiofauna can alter microbial densities and growth rates and significantly affect microbenthic community structure. Spatial and temporal variability in the nature of trophic interactions will determine the cumulative effects of meiofauna on microbial communities.

Key words: bacteria; benthos; community ecology; indirect effects; meiofauna; microalgae; predation; protists; statistical power; thymidine; trophic interactions; Zostera capricorni.

INTRODUCTION

The structure and persistence of ecological communities can be influenced by complex trophic interactions (Paine 1980, Wilson 1986). In multispecies assemblages, complex interactions often produce indirect effects where the expected outcomes of pairwise species interactions are altered by the presence of other species in the community. Indirect effects are associated with a range of ecological phenomena including apparent competition (Holt 1977); keystone predation (Paine 1966); and higher order (Levine 1976), trophic cascade (Carpenter et al. 1985), and tri-trophic-level (Hurlbert et al. 1972) interactions. Changes in species abundance, richness, habitat utilization, distribution, physiology, and morphology all have been attributed to indirect effects (Kerfoot and Sih 1987). Although unambiguously assessing the relative importance of indirect effects in community development may be limited by current experimental methods (Strauss 1991), determining the magnitude and frequency of complex trophic interactions is critical to predict the assembly of natural communities.

Investigations of complex trophic interactions typically focus on a relatively small subset of consumer and resource species in a community. A majority of studies experimentally manipulate individual taxa that are suspected to produce measurable effects on one or more species. Unfortunately, the selection of which species to manipulate is not always straightforward. Numerical predominance or previous indications of significant direct effects are no guarantee that a species also will exhibit significant indirect effects (Strauss 1991). Even when a priori knowledge permits selection of taxa that should have significant community-wide effects, results of experiments where individual species are manipulated can be unpredictable (Kneib 1988, Martin et al. 1989). In a few studies investigators have manipulated larger groups of species or guilds defined mainly by trophic characteristics (Duggins 1981, Menge et al. 1986). The use of guilds may obviate difficulties in selecting individual taxa, but ambiguities in defining and placing species into meaningful guilds still exist (Simberloff and Dayan 1991). Experiments in which individual species or guild manipulations are employed also may oversimplify the actual trophic structure of communities and fail to identify the effects of important complex interactions (Kneib 1991). Inclusion of previously ignored species groups in studies of trophic interactions (Edwards et al. 1982), and intentional or unintentional editing of trophic structure

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(Paine 1988), have been shown to alter understandings about community development.

An alternative approach to the use of either individual species or guilds in studies of complex trophic interactions is to group species by other than exclusively trophic characteristics and measure experimental effects on as inclusive a community assemblage as possible. For example, instead of manipulating individual or select groups of pelagic copepod species to examine predation effects on microplankton, all macrozooplankton in the community would be manipulated. While similar to the convention of aggregating functionally or taxonomically related species (Briand 1983, Watzin 1983), the approach does not rely on the ability to distinguish specific relationships among species within a group. In the above example, the macrozooplankton manipulated might include trophically (bactivorous, herbivorous, etc.) and taxonomically (calanoids, cyclopoids, etc.) diverse species.

Although experiments in which amalgamated species groups are employed must be interpreted with caution (Bender et al. 1984) and may not provide details of individual species interactions necessary for current ecological theory (Paine 1988), there are a number of advantages to the approach. The trophic architecture of few communities is known completely, and experiments that manipulate species groups avoid the necessity of painstakingly identifying all possible trophic links. Focusing on amalgamated species groups also permits assessment of whether complex interactions affect overall community development and not just the dynamics of a small subset of species. Experiments that manipulate multispecies assemblages especially may be important to understanding the dynamics of marine systems where omnivory is prevalent and a single competitively dominant predator often does not exist (Schoener 1989, Posey and Hines 1991).

In this paper we examine the effects of complex trophic interactions on community dynamics by manipulating one or more of four sediment-dwelling species assemblages from an intertidal seagrass bed. Meiofauna, protists, bacteria, and microalgae numerically predominate in most marine soft-sediment habitats and comprised >90% of the benthic fauna within the seagrass bed. In shallow water systems, meiofauna, defined by taxonomic affiliation (e.g., Nematoda, Copepoda, Gastrotricha) and size (63–500 μm), are the most abundant metazoan fauna reaching densities of 3×10^6 individuals/m^2 (Coull 1988). Meiofauna as a group are polyphagous and feed on a range of benthic organisms including protists, bacteria, and microalgae (e.g., Hicks and Coull 1983, Heip et al. 1985). Spatial and seasonal density correlations (Montagna et al. 1983, Alongi 1988, Decho and Fleeger 1988*a*, Bak and Nieuwland 1989) as well as laboratory (Barsdate et al. 1974, Harrison and Mann 1975, Decho and Fleeger 1988*b*), field (Carman and Thistle 1985), and natural experiments (Meyer-Reil and Faubel 1980, Montagna 1984, Montagna et al. 1987, Montagna and Bauer 1988) all suggest significant trophic interactions between meiofauna and microbes. Protists are numerically abundant members of the microbenthos, with maximum reported densities reaching 5×10^{10} individuals/m^2 (Patterson et al. 1989). Heterotrophic protists also are polyphagous and consume a variety of microbes (Fenchel 1987, Patterson et al. 1989, Kemp 1990). Microbenthic bacteria and algae are the most abundant organisms in marine sediments and can reach densities of 2×10^{13} (Rublee 1982) and 2×10^{10} individuals/m^2 (Montagna et al. 1983), respectively. Bacteria and microalgae are primary members of most food webs and critical to the productivity of marine systems.

We designed experiments to test for the cumulative effects of meiofaunal, mainly nematode and copepod, and microfaunal, phagotrophic protist, consumers on the microbenthic community. Total meiofaunal densities were manipulated within enclosures, and the overall effects of direct and indirect interactions on bacterial numbers and division rates, microalgal biomass, and protistan densities were measured. Meiofauna were considered direct consumers of bacteria, microalgae, and protists and capable of indirectly affecting microbial populations by consuming phagotrophic protists. The goal was to determine whether meiofaunal predation on microbenthic assemblages could be detected and if complex trophic interactions within and among meiofaunal and microfaunal consumer groups affected the structure of microbial communities.

Methods

Study site

Experiments were conducted in an intertidal seagrass bed (*Zostera capricorni* Aschers) at Victoria Point, Queensland, Australia (27°35′ S, 153°19′ E). Victoria Point is part of Moreton Bay and experiences semidiurnal tides with an annual range of 2.6 m. The seagrass bed extended continuously from subtidal to intertidal depths, ending 30 m from the mean high water mark. *Halophila ovalis* (R. Br.) Hook often was interspersed among shoreward *Z. capricorni* culms. Study-site sediments were siliceous sand with ≈2% silt and 4% clay to a depth of 2 cm. Surface water temperatures during the study, determined at midday on an outgoing tide when >50 cm of water still covered the seagrass bed, ranged from 18.3 to 29.3°C.

Experimental design

The schedule of density treatments and sediment depths from which variables were measured in each of four experiments conducted between January and June 1989 is presented in Table 1. Experiments included both meiofaunal density and day treatments in a 2×3 factorial design. Meiofauna were manipulated to cre-

TABLE 1. An outline of initial treatments and depths in an Australian intertidal seagrass bed from which subsamples were taken to measure abundance, pigment, and growth rate variables in each experiment. (DD = decreased density, ID = increased density, S = shaded, NM = not manipulated, ND = not determined)

	Density treatments			Subsample collection depths (mm)		
Experiment	Meiofauna	Protists	Microalgae	Bacteria	Microalgae	Protists
January	DD, ID	ND	NM	0–2 8–10	ND	ND
March	DD, ID	ND	NM	0–2 8–10	0–2 8–10	0–2
April	DD, ID	DD	S	ND	0–2 8–10	0–2
June	DD, ID	DD	NM	0–3 7–10	0–3 3–7 7–10	0–3

ate decreased (DD) and increased (ID) density treatment levels corresponding to decreased and increased numbers of predators. Treatment levels were chosen to maximize the ability to detect predatory effects within a range of meiofaunal densities reasonably expected to occur in seagrass habitats. The DD level was not an absence of all meiofauna, but a significant reduction below normal ambient densities at the study site. Increased treatment densities varied among experiments, but were ≈3 times the ambient meiofaunal densities and within the range of values recorded from Victoria Point or similar seagrass beds. In at least two of the four experiments, protist numbers also were decreased below ambient densities at the beginning of the experiment. A shading treatment was used in April experiments to limit microalgal growth (see Alongi and Tenore 1985). Density treatments were established on the 1st d of each experiment and the effects on bacterial numbers and division rates, microalgal biomass, and protist numbers were monitored three times (days 2, 4, and 6) over the next 6 d. Samples were collected from multiple sediment profiles (Table 1) to account for depth-related differences in the numbers, composition, and/or physiological activity of bacteria (Moriarty et al. 1990), microalgae (Joint et al. 1982, Montagna et al. 1989), protists (Fenchel 1969), and meiofauna (Warwick and Gee 1984, Coull et al. 1989). The total sediment depth sampled was limited to 1 cm because meiofauna and protists were distributed superficially (see *Results: Effects of defaunation*).

The ability of microbial assemblages to grow and/or move through the sediments rapidly could confound the interpretation of experimental results. Bacteria are capable of dividing rapidly, and possibly compensate for predation losses through increased rates of population growth (Moriarty et al. 1985*a*). Vertical movements (Joint et al. 1982) and population growth (Admiraal et al. 1983) of microalgae also could mask potential predation effects. To account for differences in microbial population growth, bacterial growth rates were measured and microalgal growth rates were experimentally manipulated. The effects of microbial vertical movements, especially for microalgae, on experimental results were acccounted for by sampling from multiple sediment depths.

Experimental procedures

A plot of seagrass ≈3 m^2 was chosen haphazardly from within the study site 2 d prior to the start of each experiment. The plot was 5–15 m seaward of the leading edge of the seagrass bed and representative of areas covered with moderate density, thick-bladed *Z. capricorni*.

Initial meiofaunal and microbial field measurements were made on five sediment samples collected in an undisturbed area adjacent to the experimental plot using a 2.3 cm diameter corer (30 mL syringe). In March, April, and June samples were collected 1 d before the start of each experiment; in January, samples were collected on day 2. Bacterial numbers and division rates, microalgal pigment amounts, and protist numbers were determined for subsamples collected from various depths as outlined in Table 1. Except for June, meiofauna were enumerated from the same cores to a depth of 1 cm after subsample removal. The volume of subsample sediment removed in June necessitated the collection of additional cores to determine meiofaunal numbers.

The experimental plot was defaunated 1 d before the start of each experiment to produce a decreased meiofaunal density treatment. Defaunation consisted of lightly dragging the back of a level-head rake over sediment and seagrass blades. Service and Bell (1987) previously demonstrated that raking reduces meiofaunal densities in an intertidal sand habitat. To facilitate defaunation, raking was started just before low tide so that the ebbing tide carried resuspended sediment particles and fauna away from the experimental plot. Effects of the defaunation procedure on meiofauna, bacteria, microalgae, protists, and sediments were determined in separate experiments and selectively monitored during each predation experiment.

After raking and before meiofaunal recolonization could occur, 15 experimental chambers consisting of

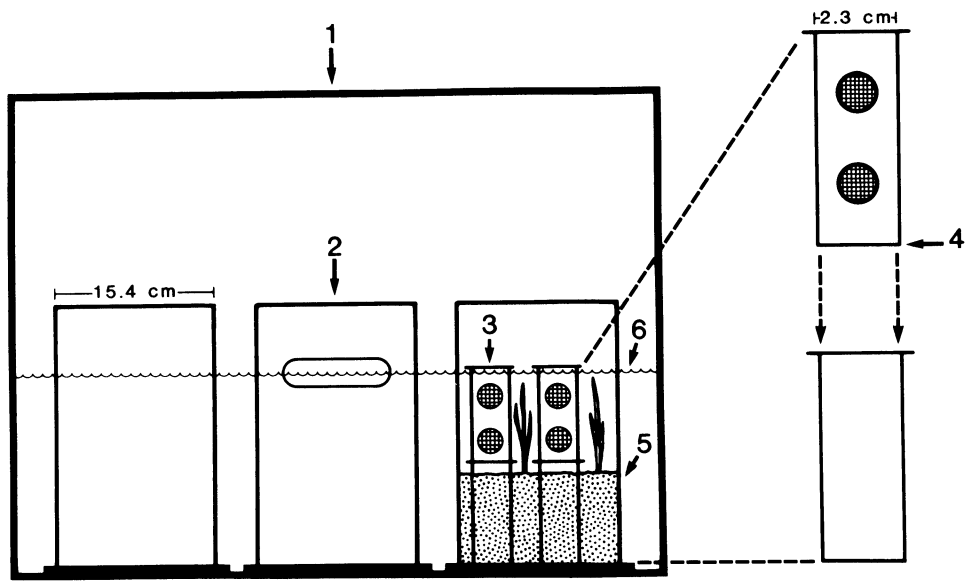

FIG. 1. Diagrammatic representation of the (1) flow-through seawater tank with (2) experimental chambers and (3) microcosms used in each experiment. Microcosms consisted of two syringes with the (4) luer [needle attachment] ends removed, which were placed into the (5) sediments within each chamber and remained above the (6) water line. For a complete explanation, see *Methods: Experimental procedures.*

15.4 cm diameter polyvinyl chloride (PVC) pipe 30 cm long (Fig. 1) were pushed 5 cm into the defaunated sediments. In January, chambers were haphazardly positioned within the defaunated seagrass plot. March, April, and June chambers were blocked in groups of three to account statistically for potential horizontal position effects. Each chamber had two exchange ports 5 cm from the top on either side and was conditioned in running seawater 5–7 d before experiments. In the field, exchange ports remained above the water level to prevent meiofaunal recolonization of sediments within the chambers. As soon as the experimental plot was exposed by the outgoing tide, each chamber, containing a plug of sediment and seagrass, was removed. A PVC plate was pushed under the bottom and strapped to chambers before transport back to the laboratory and placement in an external, flow-through seawater tank (Fig. 1). Seawater pumped from Moreton Bay was filtered through 63-μm mesh before entering the flow-through tank. Temperature, salinity, and light levels within the tank were similar to natural field conditions. In April the seawater tank was covered with shade cloth, allowing $\approx$2% light transmission, to reduce potential microalgal growth. Chambers were allowed to equilibrate for 24 h before further manipulating meiofaunal densities.

Density treatments were created by adding known numbers of meiofauna to 2.3 cm diameter microcosms (30 mL syringe) placed within each chamber on the 1st d of each experiment (Fig. 1). Microcosms consisted of a base syringe pushed into the sediment between seagrass culms and fitted with a top syringe. The top syringe extended above the water line to inhibit movement of fauna into or out of microcosms. Sixteen holes, 1 cm in diameter and covered by 100-μm nytex mesh, above the sediment surface allowed adequate seawater exchange between microcosms and the surrounding environment. Meiofauna for additions were collected from sediments adjacent to the experimental plot by treating a predetermined number of cores with the general anesthetic $MgCl_2$ ($\approx$72 g/L) and then shaking and decanting through 500- and 63-μm sieves. All material, including meiofauna, retained on the 63-μm sieve was rinsed into a flask and brought to a known volume. Increased density treatments representing $\approx$3 times ambient numbers were pipetted into one microcosm within each experimental chamber.

To eliminate the potential effects of adding particulate material and meiofauna to ID treatments, an equivalent amount of similar-sized material without live meiofauna was added to DD treatments. A predetermined number of sediment cores were collected from just outside the experimental plot, double-sieved (500 and 63 μm), and the 63-μm fraction retained and dried overnight at 60°C. The dried particulate material was rehydrated and added to DD treatment microcosms in volumes equivalent to ID treatments ($\approx$30 mL).

On each sampling date the seawater tank was drained to facilitate processing of five microcosms per density treatment. Sediments from each depth profile sampled (Table 1) were mixed gently with a spatula and placed in a 2-mL syringe (luer-loc [needle-attachment end] removed) for extraction of 0.1–0.4 cm^3 subsamples. Bacterial numbers and division rates, chlorophyll *a* and phaeopigment concentrations, and protist numbers were

determined from subsamples. To verify that two density treatments were established and maintained, meiofaunal numbers, except in June, were determined to a depth of 1 cm from the sediment remaining in each microcosm. June meiofaunal numbers were enumerated only at the beginning of the experiment from separate defaunated cores or material used to increase densities.

Monitoring treatment effects

Bacterial numbers from 0.1-cm^3 subsamples collected as described above were counted by epifluorescence microscopy (Hobbie et al. 1977). Microcosm subsamples were preserved in 2% formaldehyde and refrigerated until processing. Before counting, sediment was transferred into vials with 5 mL of sterile water and sonicated (1 min pulsed at 60 W) to remove cells from sand grains. All material except sand grains was retransferred to sample vials and homogenized by rotary stirring (1 min at 333 Hz) to disperse cells and organic material. Aliquots (50 μL) were collected from the homogenized subsample, stained with acridine orange, and counted. In January a total of 50 fields on two filters were counted per subsample. The number of fields was reduced after analysis of variance (ANOVA) indicated that 20 fields on one filter was sufficient to account for sample variability.

Bacterial division rates were measured by the incorporation of [5-methyl-^{3}H] thymidine into DNA (Moriarty and Pollard 1981). One blank and two assays were run for each microcosm. Sediment subsamples (0.1-cm^3) were placed in sterile polypropylene screw-top tubes into which 60–75 mL of 0.2-μm filtered seawater and 25–40 mL of thymidine solution (1–2 nmol of thymidine, specific activity 370–925 kBq/nmol) were then added. Isotope dilution experiments (see Pollard and Moriarty 1984) indicated that the amount of thymidine added was adequate to prevent dilution problems. Blank incubations were stopped immediately after the addition of thymidine by adding 8 mL of cold ethanol (80% volume/volume). Assays were run for 20 min, a time interval short enough to minimize possible disturbance effects from the sampling procedure (Moriarty and Pollard 1990). Labeled DNA was extracted for counting by dialysis (Pollard 1987). Bacterial division rates and doubling times were calculated as described by Moriarty (1990) assuming an average theoretical factor of 5×10^{17} cells/mol of thymidine incorporated into DNA.

Chlorophyll *a* and phaeopigment concentrations were measured from 0.2–0.4 cm^3 subsamples immediately treated with 6 mL of 90% acetone (with $MgCO_3$) and refrigerated. After 24 h of cold storage, samples were sonicated (1 min at 60 W), centrifuged (5 min at 59 000 m/s^2) and pigment determinations made on the supernatant using a Hitachi (Model number U-2000) spectrophotometer. Amounts of chlorophill *a*, an estimate of live microalgal biomass, and phaeopigments, an estimate of degraded plant material, were determined from the equations of Parsons et al. (1984).

Protists were extracted and enumerated from 0.2–0.4 cm^3 subsamples following the Percoll–sorbitol procedure of Alongi (1986). Samples were centrifuged only once instead of three times. While one centrifugation led to an underestimate of ciliate numbers, flagellate estimates were not improved by repeated extractions.

Meiofauna were removed from sediment samples for counting using a modified shake and decant procedure (Weiser 1960). More than 98% of all individuals were extracted from samples after five decantings. All major meiofaunal taxa were enumerated under a dissecting microscope at 25× magnification.

Sediment dry masses were determined from 0.4-cm^3 subsamples that had been dried for >24 h at 60°C and weighed to the nearest 1.0 mg.

Statistical analyses

All statistical procedures were run on either a DEC/VAX microcomputer using Release 5.18 of SAS (SAS Institute 1985) or an IBM/PS2 Model 70 using Version 6.03 of SAS for Personal Computers (SAS Institute 1988). The general linear model (GLM) procedure was used for all ANOVAs. Data were transformed when necessary to satisfy the assumptions of ANOVA, but all results presented represent untransformed means. Block effects were removed from March, April, and June ANOVA models first. Day and density treatment effects were tested over appropriate mean-square error terms for the mixed model design. A total of five microcosms constituted the number of replicates per treatment level. When day and density interactions were not significant, Ryan's Q (Day and Quinn 1989) was used to compare main-effect treatment means. Statistical power and determination of effect size for tests run on experiments were calculated as described by Sokal and Rohlf (1981). Power was set at 80%, a reasonable level if making a Type II error is considered approximately twice as costly as making a Type I error (Peterman 1990). Effect sizes were calculated a priori (Peterman 1990) using the observed variation in January to June field samples.

Results

Effects of defaunation

Preliminary experiments indicated that the defaunation procedure increased sediment densities (Fig. 2e) and mainly affected the surface layers. The top 2 mm of sediment was significantly denser after defaunation ($F_{1,8} = 13.68$, $P < .01$), and visual inspection indicated a loss of lighter sediment particles, possibly detritus, during raking. There was no significant effect of defaunation on dry-mass sediment densities at 1 cm depth ($F_{1,8} = 0.90$, $P > .05$).

Sediment defaunation also resulted in statistically

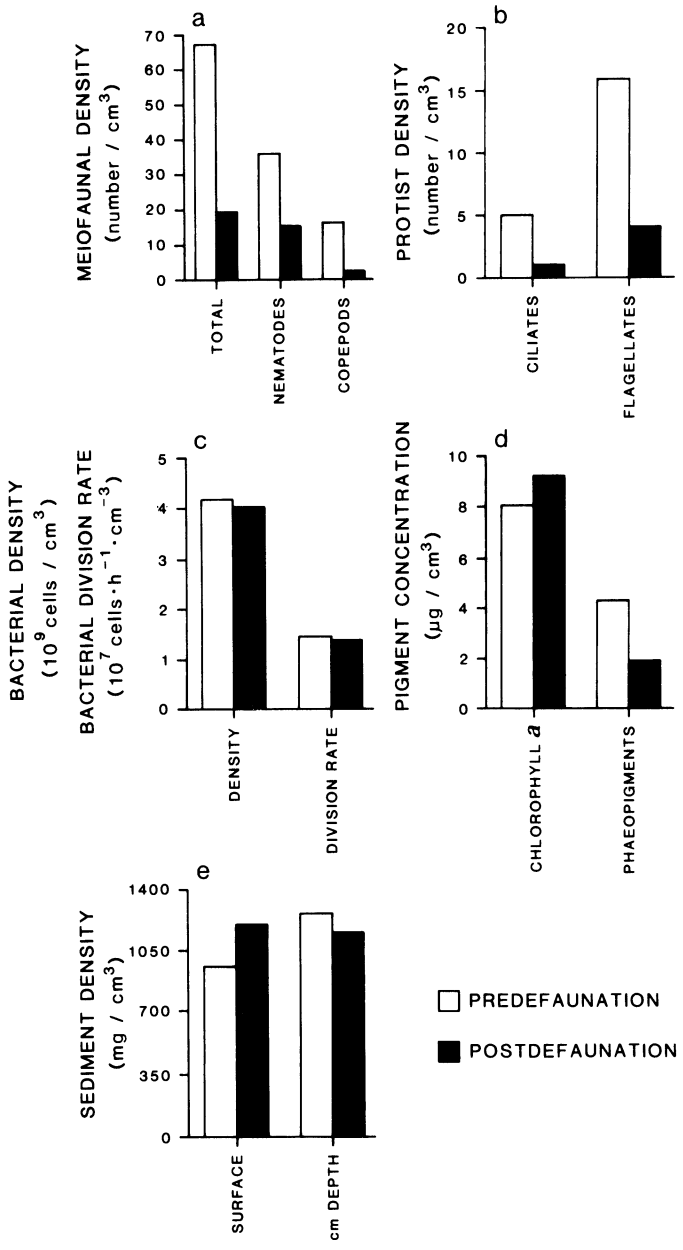

FIG. 2. The mean effects of defaunation on (a) meiofauna, (b) protists, (c) bacteria, (d) microalgal pigments, and (e) sediment densities. $n = 5$.

significant reductions in nematodes ($F_{1,8} = 11.62$, $P < .01$), harpacticoid copepods ($F_{1,8} = 67.09$, $P < .0005$), total meiofauna ($F_{1,8} = 18.43$, $P < .005$), and ciliates ($F_{1,8} = 6.53$, $P < .05$), but not flagellates ($F_{1,8} = 5.21$, $P > .05$) (Fig. 2a and b). The 71% decrease in total numbers of meiofauna present after raking mainly resulted from a 58% reduction in nematodes and an 89% reduction in copepods (Fig. 2a). The greater copepod compared to nematode reductions in post-defaunation samples probably resulted from differences in the vertical distribution of taxa. In undisturbed sediments 88% of all meiofauna resided above 1 cm depth. More than 86% of all copepods but only 45% of all nematodes also were found within the top 0.5 cm. Raking only impacted the very surface sediment layers, and over half the nematode population would not have been affected by the defaunation procedure. Similar to copepods, >71% of all other meiofaunal taxa were distributed above 0.5 cm. Over 86% of the ciliates and 97% of the flagellates also were within the surface 0.3 cm. An 80% reduction in ciliates and, although not statistically significant, a 75% reduction in flagellates occurred after defaunation (Fig. 2b).

Defaunation did not affect bacterial or microalgal

TABLE 2. A comparison of mean (n = 5) meiofaunal and protist densities (numbers/cm^3) among decreased (DD), ambient (AD), and increased (ID) density treatment levels in each experiment in an Australian intertidal seagrass bed. Ambient density values are from field samples, DD and ID values are from experimental microcosms collected 2 d after defaunation, 1 d after meiofaunal additions.*

	Experiment											
	January			March			April			June		
Species group	DD	AD	ID	DD	AD	ID	DD	AD	ID	DD	AD	ID
Meiofauna†												
Nematodes	12	32	54	19	44	97	19	50	69	62	154	371
Copepods	1	8	32	0	12	53	4	19	39	28	52	400
Total	15	49	102	21	72	181	26	86	125	104	256	963
Protista‡												
Ciliates		ND§			ND		6	4	10	25	22	21
Flagellates		ND			ND		2	16	5	10	28	8

* Density differences are determined by ANOVA and Ryan's Q (α = .05). Means that are not significantly different within months share a common underline.

† Meiofauna were enumerated from cores to 1 cm depth except in June, when increased density levels were determined from the actual addition volume.

‡ Protists were determined from the top 2–3 mm of sediment in each core.

§ ND = not determined.

assemblages (Fig. 2c and d). There were no statistically significant decreases in bacterial numbers ($F_{1,8}$ = 0.02, P > .05) or division rates ($F_{1,8}$ = 0.05, P > .05) after raking. Defaunation also did not affect chlorophyll a concentrations ($F_{1,8}$ = 0.98, P > .05), but phaeopigment amounts did decrease significantly in post-raked surface sediments ($F_{1,8}$ = 11.4, P < .01).

Meiofaunal treatments

Significantly different meiofaunal treatment densities were established in each of the four experiments (Table 2). For nematodes, copepods, and total meiofauna, ID treatment densities were at least three times DD densities. Numbers in DD treatments were significantly less than natural field densities, except for nematodes in March and copepods in June. In April, ID treatments were not significantly different from natural field densities for each meiofaunal group.

Protist densities were affected by the defaunation procedure (Fig. 2b) but were not altered further by treatment additions (Table 1). The significant reduction in ciliates after defaunation was not maintained during experiments. There was no significant difference between field and treatment ciliate densities by day 2 in either April or June (Table 2). Flagellate numbers were reduced significantly below natural field densities in April and June (Table 2), although densities were not reduced statistically by defaunation in earlier experiments (Fig. 2b).

Meiofaunal treatment effects

Bacterial densities.—Changes in bacterial densities provided modest evidence of a direct meiofaunal predation effect. Bacterial numbers varied among days, and significant interactions between density and day treatments occurred in March, (0–2 mm depth: $F_{2,12}$ = 3.91, P < .05), and June (0–3 mm; $F_{2,12}$ = 6.14, P < .025; 7–10 mm: $F_{2,12}$ = 7.37, P < .001). Meiofaunal predation in March and June surface sediments was not responsible for the significant density and day interactions because bacterial numbers actually were greater in ID compared to DD treatments (Fig. 3c and e). Only in June subsurface sediments were bacterial numbers relatively greater in DD treatments (Fig. 3f), indicating a direct predation effect. Subsurface bacterial densities also increased between days 2 and 6 in both June treatments (Fig. 3f). Horizontal position within the seagrass bed in both March and June experiments did not affect bacterial density (ANOVA block effect, P > .05).

Bacterial division rates.—Meiofaunal treatments significantly affected bacterial division rates in both January subsurface ($F_{1,12}$ = 8.90, P < .01) and March surface sediments ($F_{1,12}$ = 16.75, P < .005). Division rates were significantly greater (Ryan's Q, P < .05) in ID compared to DD tratments on days 2 and 4 (Fig 4b and c). In March surface sediments a rise in day-4 division rates probably contributed to the greater bacterial densities in ID treatments by day 6 (Fig. 3c). A significant day effect also occurred in June experiments (0–3 mm depth: $F_{2,8}$ = 21.14, P < .001; 7–10 mm: $F_{2,8}$ = 56.24, P < .0005), resulting in a two- to four-fold decrease in rates beween day 2 and day 6 (Fig. 4e and f). The effects of horizontal position on bacterial rates of division within the experimental plot were not significant (ANOVA block effect, P > .05).

Doubling times for bacteria generally were faster in surface sediments and were similar between density

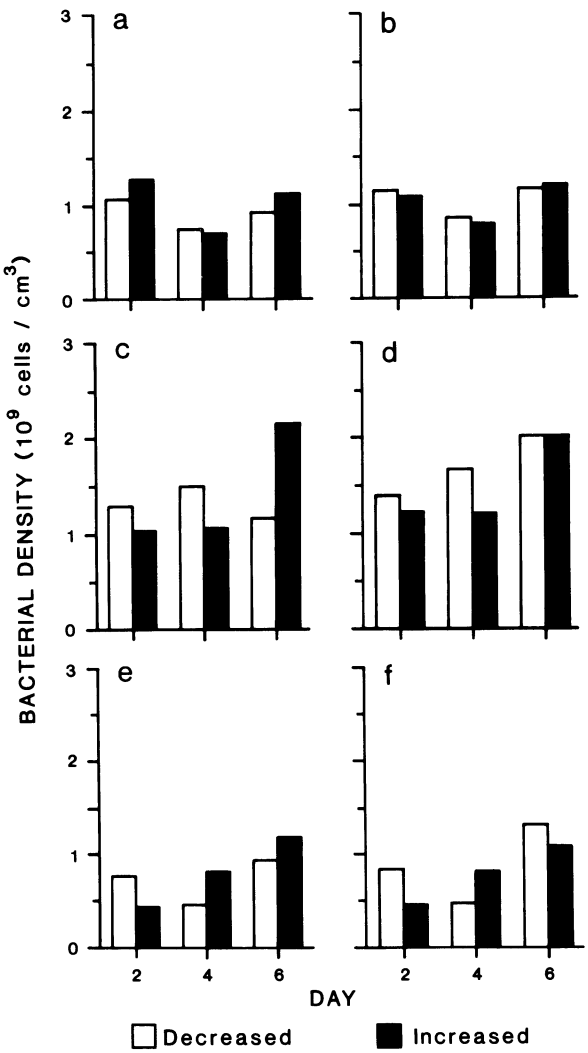

FIG. 3. Differences in mean bacterial abundances between meiofaunal density treatments (decreased, increased) over three sampling dates in each of three experiments. $n = 5$ in each experiment. (a) January, 0–2 mm sediment depth; (b) January, 8–10 mm; (c) March, 0–2 mm; (d) March, 8–10 mm; (e) June, 0–3 mm; (f) June, 7–10 mm.

treatments. On average, surface populations doubled every 3 d compared to 7 d for subsurface populations (Table 3). In one third of the comparisons (Table 3), ID treatment populations doubled >20% faster, but only in January subsurface and March surface sediments were the decreased doubling times consistent with increased division rates (Fig. 4b and c).

Pigment concentrations.—Increased meiofaunal numbers had either a positive or no effect on chlorophyll *a* and phaeopigment amounts. There were no significant interactions between density and day treatments in any experiment. In June, chlorophyll *a* concentrations at all depths were affected by density treatments (0–3 mm depth: $F_{1,12} = 10.22$, $P < .01$; 3–7 mm: $F_{1,12} = 6.89$, $P < .05$; 7–10 mm: $F_{1,12} = 9.35$, $P < .01$), but amounts were significantly greater in ID compared to DD treatments (Fig. 5e, f, and g). Increased meiofaunal densities produced significantly greater phaeopigment concentrations in April ($F_{1,12} = 11.57$, $P < .01$) and June ($F_{1,12} = 11.08$, $P < .01$) surface sediments (Fig. 6). Shading had no discernible effect on either chlorophyll *a* or phaeopigment amounts or on the outcome of experiments. Surface and subsurface concentrations of both pigments were similar between March unshaded (Figs. 5a and b and 6a and b) and April shaded experiments (Figs. 5c and d and 6c and d). Horizontal position within the seagrass bed affected phaeopigment amounts in April surface sediments (ANOVA block effect: $F_{4,8} = 4.28$, $P < .04$) and June 3–7 mm sediments (ANOVA block effect: $F_{4,8} = 7.41$, $P < .01$).

Protist density.—Meiofauna affected protist densities in both April and June experiments. Increased meiofaunal densities had no effect on ciliates in April (ANOVA, $P > .05$), but flagellate numbers were significantly greater in DD treatments by day 6 ($F_{2,8} = 18.6$, $P < .05$; Fig. 7b). In June, both ciliate ($F_{1,12} =$

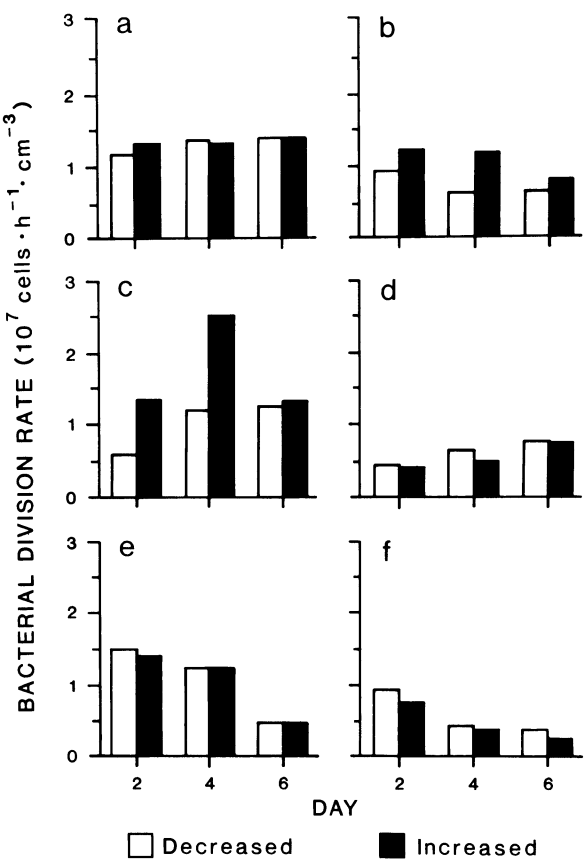

FIG. 4. Differences in mean bacterial division rates between meiofaunal density treatments (decreased, increased) over three sampling dates in each of three experiments. $n = 5$ in each experiment. (a) January, 0–2 mm sediment depth; (b) January, 8–10 mm; (c) March, 0–2 mm; (d) March, 8–10 mm; (e) June, 0–3 mm; (f) June, 7–10 mm.

TABLE 3. Bacterial doubling times (in days) for decreased (DD) and increased (ID) density treatments on each day of each experiment. Data are means ± 1 SD (n = 5).

Experiment	Day	Treatment	Depth 0–2 mm	Depth 8–10 mm
January	2	DD	2.92 ± 1.40	4.06 ± 1.66
		ID	2.87 ± 0.71	3.50 ± 2.28
	4	DD	1.75 ± 1.00	4.24 ± 1.05
		ID	1.43 ± 0.22	1.97 ± 0.47
	6	DD	2.10 ± 0.69	5.78 ± 2.45
		ID	2.44 ± 0.95	4.50 ± 0.55
March	2	DD	6.57 ± 2.05	9.78 ± 2.58
		ID	3.07 ± 1.77	11.47 ± 7.23
	4	DD	3.69 ± 0.96	8.49 ± 5.30
		ID	1.30 ± 0.40	7.98 ± 3.30
	6	DD	2.79 ± 1.66	9.21 ± 5.08
		ID	5.21 ± 2.99	8.51 ± 2.55
			0–3 mm	7–10 mm
June	2	DD	1.87 ± 0.92	2.88 ± 0.51
		ID	0.92 ± 0.30	1.96 ± 0.22
	4	DD	1.13 ± 0.20	3.66 ± 1.57
		ID	2.14 ± 0.84	6.86 ± 1.24
	6	DD	6.08 ± 1.13	16.73 ± 11.34
		ID	6.74 ± 2.27	14.21 ± 2.50

20.97, $P < .001$) and flagellate numbers ($F_{1,12} = 4.67$, $P < .05$) were reduced significantly in ID treatments (Fig. 7c and d). There was no effect of horizontal position on either ciliate or flagellate numbers (ANOVA block effect, $P > .05$).

Experimental power

The ability to recognize experimental differences statistically was evaluated by calculating the effect sizes necessary to produce detectable treatment differences (Table 4). For a majority of the experimental variables, differences of < 50% could be detected with 80% power at the .05 level of significance. Differences in the March 0–2 mm depth phaeopigment amounts and the April flagellate numbers probably would not be detected given the large, > 100%, effect sizes (Table 4).

DISCUSSION

Our results demonstrate that the cumulative effects of trophic interactions between meiofauna and microbes (1) can decrease bacterial densities and increase population growth rates, (2) may involve complex, tritrophic-level interactions among meiofauna, protists, and bacteria, and (3) can produce undetectable or neutral community responses. The microspatial distribution of both meiofauna and microbes within the sediments influenced results in each experiment. For example, the limited vertical distribution of benthic protists meant that complex interactions among meiofauna, protists, and microbes were restricted to the surface sediments. Differences in microbial responses between experiments likely reflected the natural seasonal increases and decreases in meiofaunal density. Ambient meiofaunal densities increased by an order of magnitude between the January and June experiments. A possible complex interaction among meiofauna, protists, and bacteria was detected only during June experiments when ambient meiofaunal densities were greater than all other dates.

Direct effects of meiofauna

Meiofauna directly affected bacterial densities in June subsurface sediments. Bacterial numbers were reduced in increased density (ID) compared to decreased density (DD) treatments, even though the trend was reversed on day 4, and densities in ID treatments increased between days 2 and 6. The reduction in bacterial densities probably resulted from the cumulative effects of meiofaunal predation. Alternative microbial predators, in particular protists, were uncommon below the sediment surface. Changes in natural cell senescence or mortality coincident with meiofaunal density differences also were unlikely. The limited numbers of harpacticoid copepods and other meiofaunal taxa below 0.5 cm depths in the seagrass bed implicated nematodes as the taxon most responsible for subsurface reductions in bacterial abundance.

Previous studies concluded that nematode predation has a minimal effect on benthic bacterial assemblages (Alongi 1985, 1988, Tietjen and Alongi 1990). The inability of past studies to detect nematode effects may be attributed to the use of individual or relatively few species and/or no consideration of microspatial differences in predator and prey distributions. Results of experiments that manipulate individual nematode spe-

TABLE 4. The percentage decrease (one-tailed) that could be detected with 80% power for each experimental variable. Calculations are based on the variation determined from initial January, March, April, and June field samples. (ND = not determined).

Experiment	Variable	Depth 0–2 mm	Depth 3–7 mm	Depth 8–10 mm
January	Bacterial density	53.8		38.4
	Bacterial division rate	11.6		49.5
March	Bacterial density	28.4		29.3
	Bacterial division rate	34.8		52.9
	Chlorophyll *a*	72.9		24.5
	Phaeopigments	101.4		24.6
April	Chlorophyll *a*	22.7		41.7
	Phaeopigments	35.3		55.7
	Ciliates	51.9		ND
	Flagellates	104.0		ND
		0–3 mm	3–7 mm	7–10 mm
June	Bacterial density	18.1	ND	17.8
	Bacterial division rate	26.2	ND	71.6
	Chlorophyll *a*	15.9	21.9	28.2
	Phaeopigments	32.3	17.8	42.3
	Ciliates	57.9	ND	ND
	Flagellates	35.3	ND	ND

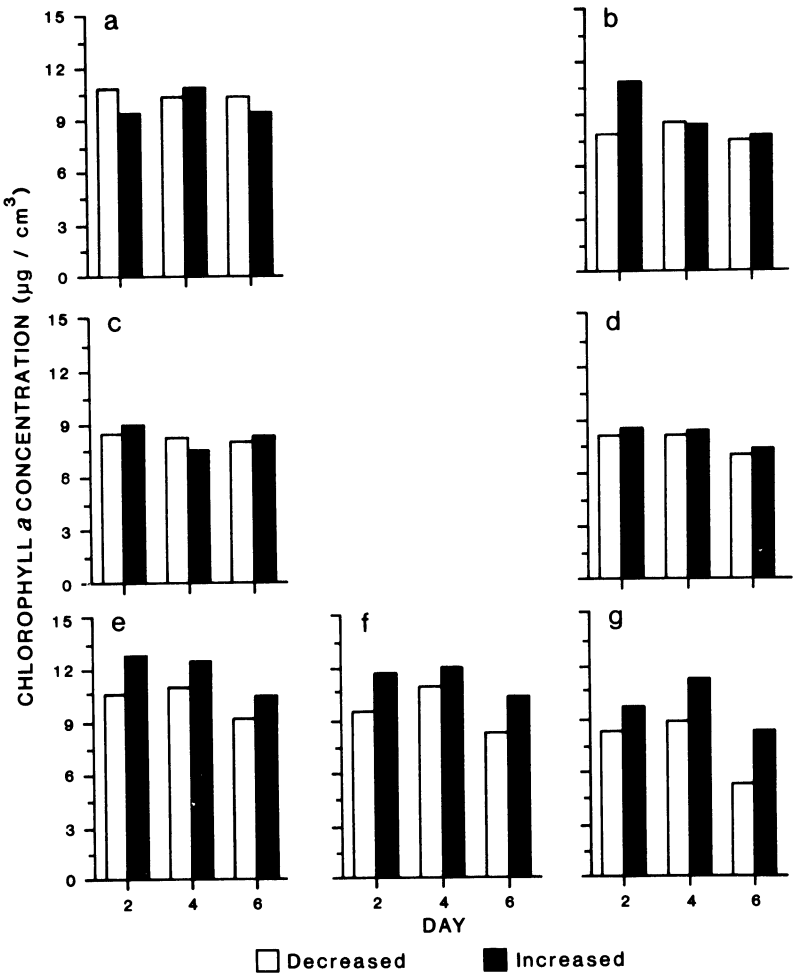

FIG. 5. Differences in mean chlorophyll *a* concentrations between meiofaunal density treatments (decreased, increased) over three sampling dates in each of three experiments. $n = 5$ in each experiment. (a) March, 0–2 mm sediment depth; (b) March, 8–10 mm; (c) April, 0–2 mm; (d) April, 8–10 mm; (e) June, 0–3 mm; (f) June, 3–7 mm; (g) June, 7–10 mm.

cies are unlikely to be comparable to the effects of natural assemblages, which often have >100 species. For some communities, multi-species effects may represent the additive responses of individual predators (Van Buskirk 1988), but too little is known about complex interactions among nematode predators to suggest the same is true for meiofauna. Microspatial differences in nematode abundance (Heip et al. 1985) and the vertical distribution of feeding groups (Jensen 1983) typical in most marine habitats also will influence experimental results. Attempts to document predation effects by in toto sampling of a 5-cm sediment column may obfuscate differences that occur within only a few millimetres. The slower growth rates in some subsurface bacterial assemblages (Novitsky 1987; Fig. 4) also will accentuate predatory effects that may be obscured in combined samples of surface and subsurface sediments.

Another direct effect of increased meiofaunal numbers was the stimulation of bacterial division rates in January subsurface and March surface assemblages (Fig. 4b and c). Doubling times in ID treatments were faster during all except the last day in March (Table 3). The shorter doubling times, 1.3 to 4.5 d, in ID treatments did not result in increased bacterial densities, and implied that mortality maintained densities below DD treatment levels on at least 2 of 3 d (Fig. 3b and c). Because protists were restricted to surface sediments in the study site, increased bacterial mortality in January can be attributed directly to predation by meiofauna. Mortality differences between treatments in March surface sediments possibly included the effects of protistan predators. Unfortunately, numbers of ciliates and flagellates were determined only from day 6 in March, but greater protist densities in DD treatments suggest that protists were not responsible for treatment differences in bacterial mortality.

Relative differences in bacterial abundances and division rates between field sites or sampling dates are considered an indication of predation effects (Moriarty

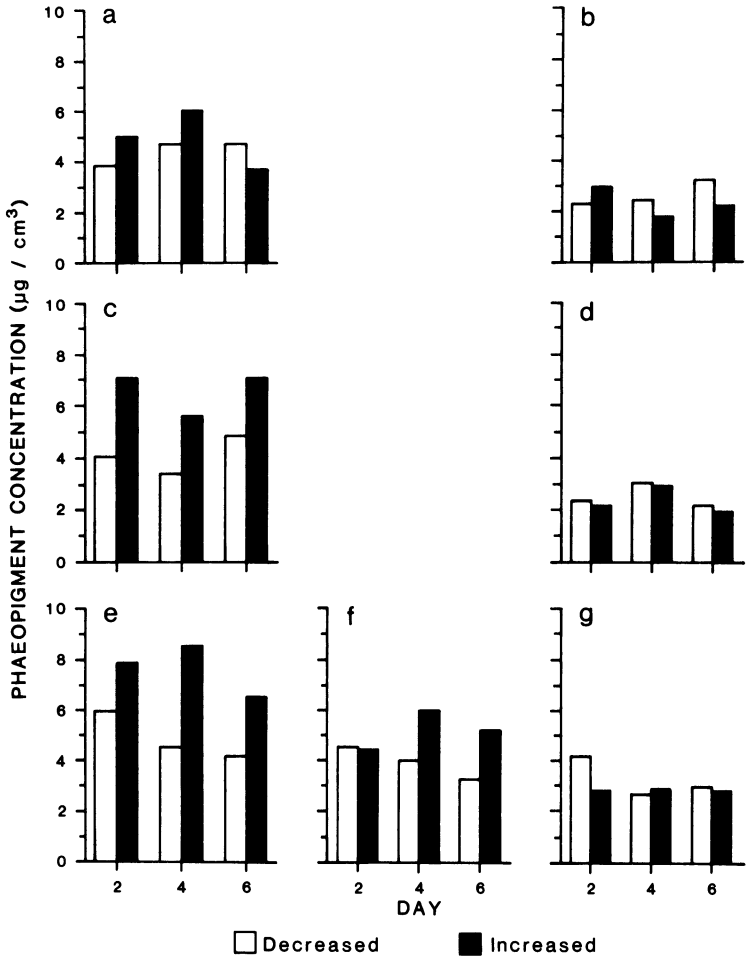

FIG. 6. Differences in mean phaeopigment concentrations between meiofaunal density treatments (decreased, increased) over three sampling dates in each of three experiments. $n = 5$ in each experiment. (a) March, 0–2 mm sediment depth; (b) March 8–10 mm; (c) April, 0–2 mm; (d) April, 8–10 mm; (e) June, 0–3 mm; (f) June, 3–7 mm; (g) June, 7–10 mm.

et al. 1985*b*, 1990, Montagna et al. 1987, 1989). It is argued that if bacterial densities do not increase when division rates are rapid, then the population is experiencing some source of increased mortality. Unfortunately, field evidence from bacterial abundances and division rates alone is insufficient to assess directly how predation is affecting population densities and growth rates. Complex trophic interactions among predators and prey can produce unexpected density changes (Ambrose 1984, Commito and Shrader 1985), and we discuss the effects of a possible complex interaction between meiofaunal and microbial assemblages in the next section. Predation also has inconsistent effects on population growth, and numerous factors are capable of influencing growth rates. Terrestrial nematodes can stimulate or retard bacterial growth rates (Abrams and Mitchell 1980, Anderson et al. 1983, Ingham et al. 1985), and stimulation of bacterial growth may be unrelated to actual predation on bacteria (Abrams and Mitchell 1980, Ingham and Coleman 1983). Disturbance, either physical or biological, also results in an increase in bacterial growth rates that is unrelated to predation (Findlay et al. 1990*a*, *b*). For these reasons, field observations alone are unable to differentiate among the numerous factors affecting population growth.

In the present study the relative differences in bacterial abundances and growth rates between treatments in January subsurface and March surface sediments are attributed easily to meiofaunal predation. The increased bacterial division rates in ID treatments should have produced increased densities. Alternative factors that might influence densities and growth rates either were controlled experimentally, e.g., the addition of similar amounts of particulate material to all treatments, or were not statistically significant, e.g., disturbance (defaunation) had no impact on bacterial growth rates (Fig. 2c).

Complex trophic interactions

Results from June surface sediments suggest the possibility of a complex, tri-trophic-level interaction among

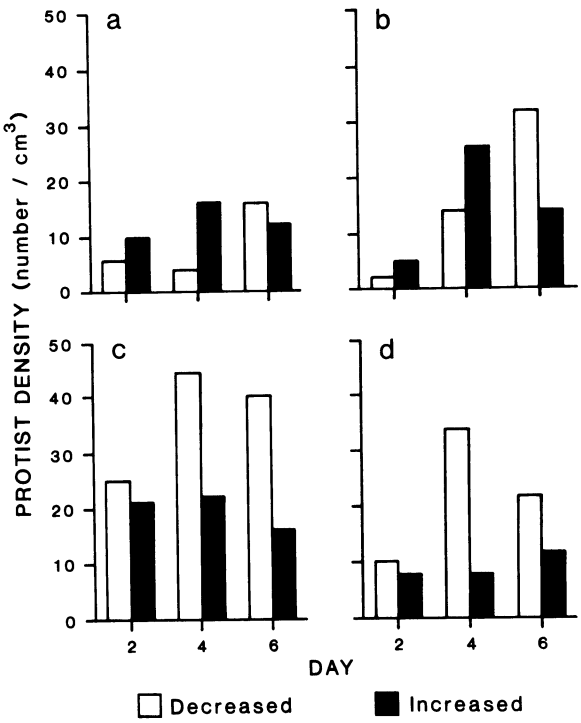

FIG. 7. Differences in mean protist numbers found in surface sediments between meiofaunal density treatments (decreased, increased) over three sampling dates in each of two experiments. $n = 5$ in each experiment. (a) April, ciliates; (b) April, flagellates; (c) June, ciliates; (d) June, flagellates.

meiofauna, protists, and bacteria. Bacterial densities unexpectedly increased in treatments containing enhanced numbers of meiofauna, and the greater bacterial abundance resulted from decreased mortality and not from increased division rates (Figs. 3c and 4c). Decreased bacterial mortality in ID treatments may be explained by the significant reduction in ciliates and flagellates (Fig. 7c and d). Protists are major microbial predators in pelagic environments (Sherr and Sherr 1986), but densities in some benthic habitats are too low to affect microbial abundances significantly (Kemp 1988, Epstein and Shiaris 1992). Natural densities of benthic protists likely are decreased by meiofaunal predators, particularly harpacticoid copepods (Rieper 1985). Our experiments indicate that meiofauna may affect bacterial populations indirectly by reducing protist densities, but the inability to control protist numbers beyond day 0 permits only an incomplete evaluation of potential complex interactions. Predator–predator interactions can produce unexpected prey population increases (Commito and Ambrose 1985, Kerfoot 1987, Mills et al. 1987), and interactions among meiofauna, protists, and bacteria remains the most parsimonious explanation for increased bacterial abundances in June surface sediments.

Evidence of a possible complex trophic interaction among meiofauna, protists, and microalgae was contradictory. The enhanced June surface concentrations of chlorophyll *a* in ID treatments (Fig. 5e) were consistent with a possible decrease in herbivory and suggestive of an indirect predation effect, but increased phaeopigment (Fig. 6e) and subsurface chlorophyll *a* concentrations (Fig. 5f and g) were not. The significantly greater phaeopigment amounts, products of pigment degradation, in ID treatments implied increased and not decreased foraging on surface microalgae. Subsurface chlorophyll *a* concentrations also were greater in ID treatments, and protists, critical to the explanation of an indirect predation effect on bacteria, were not distributed in subsurface sediments.

A stimulation of microalgal vertical movements and/or growth rates might explain the enhanced surface concentrations of chlorophyll *a* in June ID treatments. Greater chlorophyll *a* concentrations at all depths in ID treatments suggested that meiofauna did not increase microalgal vertical movements. Microalgal growth rates were not measured, but can range between 0.07 and 1.12 divisions/d in intertidal mudflat habitats (Admiraal et al. 1982). In April experiments, microalgal growth was inhibited by the use of shade cloth, and no meiofaunal treatment effects were detected. Although growth rates of 1.12 divisions/d should have produced a detectable increase in chlorophyll *a* concentrations, such rates would not explain the observed treatment differences in June experiments. An enhancement of algal growth resulting from the release of nutrients during increased bactivory in ID treatments also is unlikely; bacterial mortality was reduced in June surface sediments. Increased chlorophyll *a* amounts in June ID treatments remain unexplained.

Neutral or undetectable effects

Neutral or undetectable effects of meiofaunal predation were observed in a number of experiments. Bacterial numbers and growth rates were not affected by enhanced meiofaunal densities in January surface and March subsurface sediments. Microalgal pigment concentrations also were unaffected in March and April experiments. The inability to document significant effects may reflect a lack of statistical power, inconsistent experimental procedures, or a real inability of meiofauna to influence microbial assemblages at the community level.

Assessing the power of statistical analyses can provide support for null experimental results (Toft and Shea 1983), but there are limitations to the use of power analysis in ecology. Determination of a reasonable effect size and the excessively large sample sizes required by ecological experiments are cited as major difficulties in power analysis (Rotenberry and Wiens 1985, Young and Gotelli 1988). An alternative approach to arbitrarily selecting an effect size and attempting to collect the appropriate number of samples is to determine the detectable effect size given observed sample variability and a specified level of power, similar to the a priori power analysis of Peterman (1990). Evaluation of effect

size magnitudes then could be used to determine whether a nonsignificant result was ecologically meaningful. In benthic bacterial assemblages, where densities of 10^9 cells/cm^3 and rapid population growth are common, a nonsignificant experimental result when a 50% difference in abundance could be detected (an increase of from 2.0×10^9 to 3.0×10^9 cells/cm^3) can be interpreted as ecologically meaningful. For January to June experiments in which null hypotheses were not rejected, effect sizes typically were $<50\%$. Experiments permitted detection of ecologically reasonable differences between treatments at the .05 level of significance with 80% power. Large effect sizes, $>70\%$, were observed only for March surface pigments and April flagellate numbers, and suggest these results should be interpreted with caution.

Experimental procedures were consistent between dates, but ambient meiofaunal densities were not. Density differences cannot explain the occurrence of depth-related neutral results within a date, but may explain some of the dissimilarities in results between dates. Experiments were not replicates of each other, but were designed to determine both the range and frequency of possible trophic effects in natural communities. Natural meiofaunal assemblages typically exhibit yearly fluctuations in density (e.g., Coull 1985). It is reasonable to expect that trophic effects would be most noticeable during periods when consumers are most numerous. Between January and June, field meiofaunal densities increased by $>500\%$, from 49 to 256 individuals/cm^3. Treatment levels reflected the changes in field densities, and ID treatments increased by almost an order of magnitude between January and June (Table 2). The occurrence of neutral results in experiments with relatively lower ambient meiofaunal densities suggests that both the magnitude and type of trophic effects on microbial communities may be density dependent.

Our neutral results, reasonable power of statistical tests, and consistent experimental procedures all suggest that predation by meiofaunal assemblages is not always able to affect microbenthic communities. Although studies have documented significant predator effects in marine soft-sediment communities (Wilson 1990), dramatic changes in prey populations may not be common (Hall et al. 1990*b*). Recent investigations suggest that predation effects may be limited or nonexistent in soft-sediment systems (Kneib 1988, Hall et al. 1990*a*). Confidence in results that report nonexistent predation effects will be influenced by the ability to identify adequately all multispecies interactions likely to affect a community. Experiments that manipulate individual species or guilds may be confounded by an incomplete understanding of community trophic structure (Kneib 1991). Because we manipulated the entire meiofaunal assemblage, our results are not compromised by a failure to identify important species interactions and suggest that trophic relationships do not always influence microbenthic community dynamics. The occurrence of neutral effects means that the frequency with which trophic interactions are capable of affecting benthic assemblages will be critical in community development.

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