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The Relationship between Abundances of Meiofauna and their Suspected Microbial Food (Diatoms and Bacteria)[a]

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Samples were taken bi-weekly for one year at a sand site and a mud site in the North Inlet Estuary, Georgetown, South Carolina, for meiofauna, their suspected microbial food (bacteria and diatoms), and associated physical factors. Linear regression techniques were used to correlate food abundance and physical factors with the density of meiofaunal taxa. At both sites diatoms positively correlated with meiofauna taxa, but bacteria did not. Physical factors were not correlated with meiofaunal or microbial abundances at the sand site. Whereas, at the mud site meiofauna and diatom abundances were positively correlated with the depth of the redox layer and inversely correlated with temperature. Peaks of meiofaunal abundance did not follow peaks of food abundance. Analysis of copepods at the species level indicated that taxa response was due to the response of the dominant species. Even though some correlations existed, this study suggests that copepod species and meiofauna at the gross taxonomic level do not respond to changes in potential food abundance. Physical factors apparently influence both meiofauna and diatoms in the same fashion. However, bacterial abundance was not positively correlated with any of the factors studied.

Introduction

It has long been suspected that bacteria and diatoms are the principal microbial foods of meiofauna (Coull, 1973; Brown & Sibert, 1977; Gerlach, 1978; Tietjen, 1980). However, direct quantitative measurements of *in situ* feeding are rare (Tietjen, 1980), but certainly requisite if the trophic role of meiofauna in benthic ecosystems is to be resolved. Meiofaunal and microbial interactions do exist. For example, bacteria are known to affect the spatial distribution of interstitial gastrotrichs (Gray & Johnson, 1970), and diatoms have a similar effect on meiofauna in general (Lee *et al.*, 1977). Furthermore, Findlay (1981) has suggested that food might be critical in controlling the spatial distribution of meiofauna

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at the two sites investigated in this study. *In-vitro* studies demonstrate that copepods eat bacteria (Reiper, 1978; 1982) and diatoms (Lee *et al.*, 1976), as do nematodes (Alongi & Tietjen, 1980).

Food chains widely occur as pyramids (Elton, 1927). In aquatic systems the standing crop of producers (bacteria and algae) are quite small compared with consumers, but, turnover of the producers is more rapid. It is common for larger, slower growing organisms to be trophically coupled to smaller, faster growing organisms. For example, open ocean zooplankton peaks follow phytoplankton blooms and anchovy peaks follow zooplankton peaks (Smith & Eppley, 1982). This kind of stepwise trophic coupling also occurs in lakes between phytoplankton and zooplankton (Edmonson & Litt, 1982). If the meiofauna community has close trophic coupling with the microbial community, one would predict that peak meiofaunal abundances should follow (or lag) peaks of bacteria and diatom abundances.

The present study was designed to test for *in-situ* responses of the meiofauna community to fluctuations of abundance of the microbial community which may serve as a food source for the meiofauna.

Methods

Two subtidal sites in the North Inlet Estuary, Georgetown, South Carolina (33°20·0′N, 79°10·0′W) were occupied during this study. Physical descriptions of both the sand and mud sites are given in Coull & Vernberg (1975) and Coull & Fleeger (1977). Both sites were sampled every two weeks for one year (February 1981–January 1982).

At each station two cores (2·63 cm i.d.) for meiofauna were taken to the depth of the redox potential discontinuity (RPD) layer, which was visually estimated by the depth at which the sediment color turned from brown to black. Salinity was measured with a hand-held refractometer, and the sediment surface temperature by thermometer. Meiofaunal samples were immediately fixed in 4% buffered formalin containing rose bengal. In the laboratory these samples were passed through a 0·5 mm sieve and retained on a 0·063 mm sieve. The portion remaining on the 0·063 mm sieve was centrifuged in Ludox TM (de Jonge & Bouwman, 1977), sorted, enumerated and identified to major taxa. Copepods were identified to species.

At each site four additional cores (0·85 cm i.d.) were taken to a depth of 0·87 cm (to obtain a total volume of 0·5 cc) and placed in sterile jars with 4% buffering formalin. Two cores were used for diatom censusing and two for bacteria censusing. Bacteria were counted using acridine orange epifluorescence microscopy (Hobbie *et al.*, 1977). The details for use of this technique in marine sediments are reported by Montagna (1982). During the course of this study bacterial cells in the sand appeared larger than those in the mud site. To verify, cell volumes were calculated for one sample period (7 January 1982) by measuring cell lengths and assuming cocci were spherical and bacilli were cylindrical. Direct counts of diatoms were performed by microscopically examining subsamples mounted on a hemocytometer. Subsampling was performed by bringing the volume of the core up to 15 or 50 ml with water, and then examining 0·004 ml portions on the hemocytometer (Lund *et al.*, 1958). Twelve such examinations were necessary to obtain a variance within 20% of the mean (Cassell, 1965).

All data analyses were performed using Statistical Analysis System (SAS) software (Helwig & Council, 1979). Pearson product moment correlation coefficients (r) were calculated to correlate mean animal densities with mean microbe densities and physical

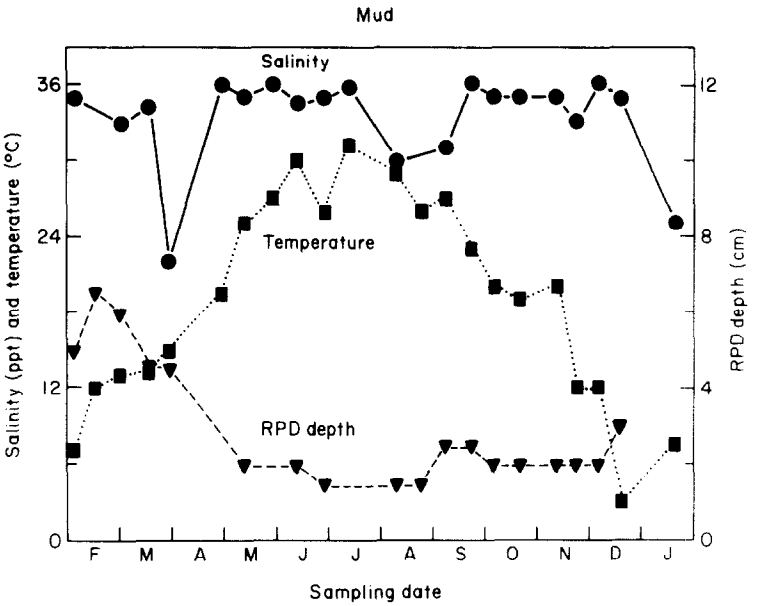

Figure 1. Physical regime at the mud site for one year from February 1981 to January 1982.

parameters ($n=24$ sample periods for each analysis). The data set was tested for lags between microbial and meiofaunal abundance by sliding the microbial axis ahead in two-week intervals, thus superimposing the microbial peaks on the meiofaunal peaks. This operation was performed three times, thus lag effects for a maximum period of six weeks were tested. We caution the reader that we can confidently reject the null hypothesis (the slope $=0$) at the 5% level for each correlation test, but, since there are many tests in this study the probability that a type I error (rejecting a true null hypothesis) occurs is very high. The following convention is used throughout the text: *significant at the 0·05 level, **significant at the 0·01 level, ***significant at the 0·001 level, and everything else is non-significant.

Results

Temperature is seasonal at both sites and the RPD depth is seasonal at the mud site (Figure 1); the relationship between season and the RPD depth is not distinct at the sand site (Figure 2). Salinity was constant throughout the year at both sites (Figures 1 and 2).

Annual mean microbial densities were greater at the mud site than the sand site (Table 1). Diatoms at the mud site were about twice as abundant than at the sand site, and bacteria were two orders of magnitude greater. On the date tested, bacterial cells were larger in the sand [$x=0\cdot907\ \mu m^3$ (95% CI$=0\cdot828$, $0\cdot994$)] than in the mud [$x=0\cdot210\ \mu m^3$ (95% CI$=0\cdot173$, $0\cdot256$)], t-test $P\leq0\cdot0001$. There were no significant correlations between the numbers of diatoms and the numbers of bacteria at either of the two sites. The only significant correlation between microbes and physical factors at the two sites was a positive correlation between diatoms and the RPD depth at the mud site (Table 2).

Total meiofauna densities were not significantly different between the two sites (Table 1). During a previous five year period (Coull & Bell, 1979) reported meiofauna density and biomass in the mud twice that of the sand at the same two sites. In the present study

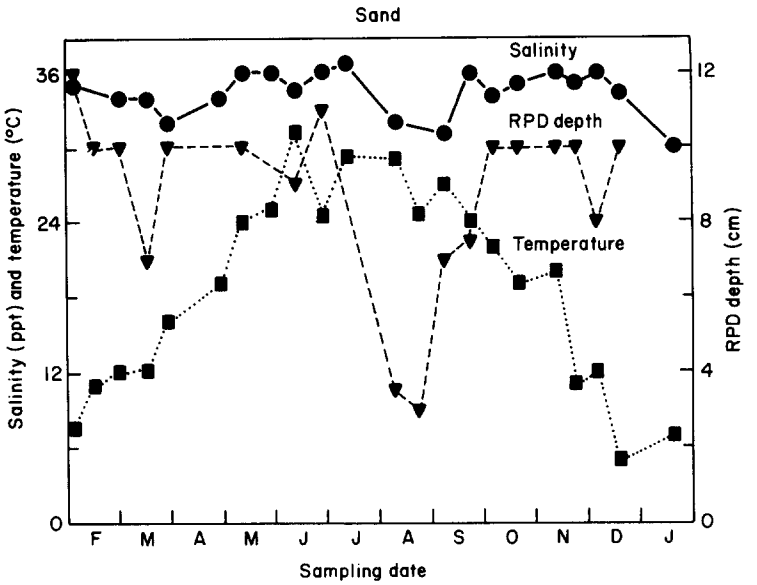

Figure 2. Physical regime at the sand site for one year from February 1981 to January 1982. Depth below sediment surface.

TABLE 1. Annual mean abundances (per 10 cm²) and standard deviations for microbes and meiofauna at the two study sites

	Mud site	Sand site
Diatoms	$21{\cdot}0 \times 10^6$ ($\pm 7{\cdot}6 \times 10^6$)	$5{\cdot}39 \times 10^6$ ($\pm 2{\cdot}44 \times 10^6$)
Bacteria	269×10^9 ($\pm 91 \times 10^9$)	$8{\cdot}64 \times 10^9$ ($\pm 3{\cdot}09 \times 10^9$)
Nematodes	304 (±89)	270 (±43)
Copepods	33 (±15)	14 (±9)
Nauplii	32 (±15)	27 (±14)
Ostracods	9 (±8)	2 (±2)
Gastrotrichs	— —	187 (±54)
Ciliates	17 (±7)	28 (±9)
Turbellarians	18 (±8)	18 (±7)
Polychaetes	33 (±11)	23 (±8)
Total Meiofauna	469 (±127)	579 (±109)

the mud site was numerically dominated by nematodes (65%), whereas, at the sand site there was co-dominance by nematodes (47%) and gastrotrichs (32%). Gastrotrichs do not occur at the mud site.

At the mud site total numbers of meiofauna exhibited a general seasonal trend, being higher in winter and lower in summer [Figure 3(c)]. Diatom abundance was bimodal with peaks occurring in February–March (winter) and July–August (summer) [Figure 3(b)]. Three peaks in bacterial cell abundance were evident, one each occurring in winter, spring and autumn [Figure 3(a)], but there was no summer peak. Bacterial density was never positively correlated with the density of any meiofaunal group (Table 2). Diatom densities were positively correlated with nematode and turbellarian densities (and therefore, total

TABLE 2. Results of correlation analyses of meiofauna with microbial and physical factors at the two sites. Key to tabled values: + = positive correlation at the 0·05 level; − = negative correlation at the 0·05 level; and 0 = no correlation, $P > 0{\cdot}05$

	Mud site					Sand site				
	Microbes[a]		Physical factors[b]			Microbes[a]		Physical factors[b]		
	D	B	S	T	R	D	B	S	T	R
Diatoms		0	0	0	+		0	0	0	
Bacteria			0	0	0			0	0	0
Nematodes	+	0	0	−	+	+	0	+	0	0
Copepods	0	0	0	0	+	0	0	0	0	0
Nauplii	0	0	0	0	0	0	0	0	0	0
Ostracods	0	0	0	+	+	0	−	0	0	0
Ciliates	0	0	0	0	0	+	0	0	0	0
Turbellarians	+	0	0	0	+	0	0	0	0	0
Polychaetes	0	0	0	−	+	+	0	0	0	0
Gastrotrichs	do not occur					0	0	−	0	0
Total meiofauna	+	0	0	−	+	0	0	−	0	0

[a]Abbreviations for microbes: D = diatoms; B = bacteria.
[b]Abbreviations for physical factors: S = salinity; T = temperature; R = Redox layer depth.

meiofaunal numbers). Temperature and RPD depth were inversely correlated with nematodes, ostracods, polychaetes and total numbers.

At the sandy site there was no distinct seasonality in either microbial [Figures 3(d) (e)] or meiofaunal abundances [Figure 3(f)]. Diatom abundance was positively correlated with nematodes, ciliates and polychaetes (Table 2). Gastrotrichs, a dominant taxa, were not correlated with diatoms, thus neither were total meiofauna numbers. Bacterial densities were not correlated with any meiofaunal taxon density except for a weak negative correlation with ostracods. There were no correlations between temperature and RPD depth with abundances of meiofaunal taxa. However, salinity was correlated with the co-dominants (nematodes and gastrotrichs), thus yielding a correlation with total meiofaunal numbers.

No significant correlations were found between microbes and 2, 4 and 6 week lags of meiofaunal density at either site. Thus, a lag effect, where density of a potential food source (bacteria or diatoms) had a positive influence on the succeeding population densities of meiofauna, did not exist. This was confirmed by a graphical analysis which could identify lags as long as 26 weeks (Wood & Foot, 1981). Meiofaunal densities were most often positively correlated with diatom densities and where no lags were employed (6 of 144 tests).

At the mud site, densities of the six dominant meiobenthic copepods (mean annual abundance per 10 $cm^{-2} \pm$ S.D.) were: *Halicyclops coulli* Herbst ($13{\cdot}9 \pm 21{\cdot}7$) [Figure 4(a)], *Pseudobradya pulchella* (Sars) ($13{\cdot}1 \pm 16{\cdot}6$) [Figure 4(b)], *Enhydrosoma propinquum* (Brady) ($12{\cdot}6 \pm 19{\cdot}3$) [Figure 4(c)], *Microarthridion littorale* (Poppe) ($10{\cdot}4 \pm 10{\cdot}7$) [Figure 4(d)], *Halectinosoma winonae* Coull ($6{\cdot}4 \pm 10{\cdot}3$) [Figure 4(e)] and *Paronychocamptus wilsoni* (Coull) ($6{\cdot}1 \pm 10{\cdot}6$] [Figure 4(f)]. Three species had co-occurring peaks in June–July: *H. coulli, E. propinquum,* and *M. littorale. Halectinosoma winonae* and

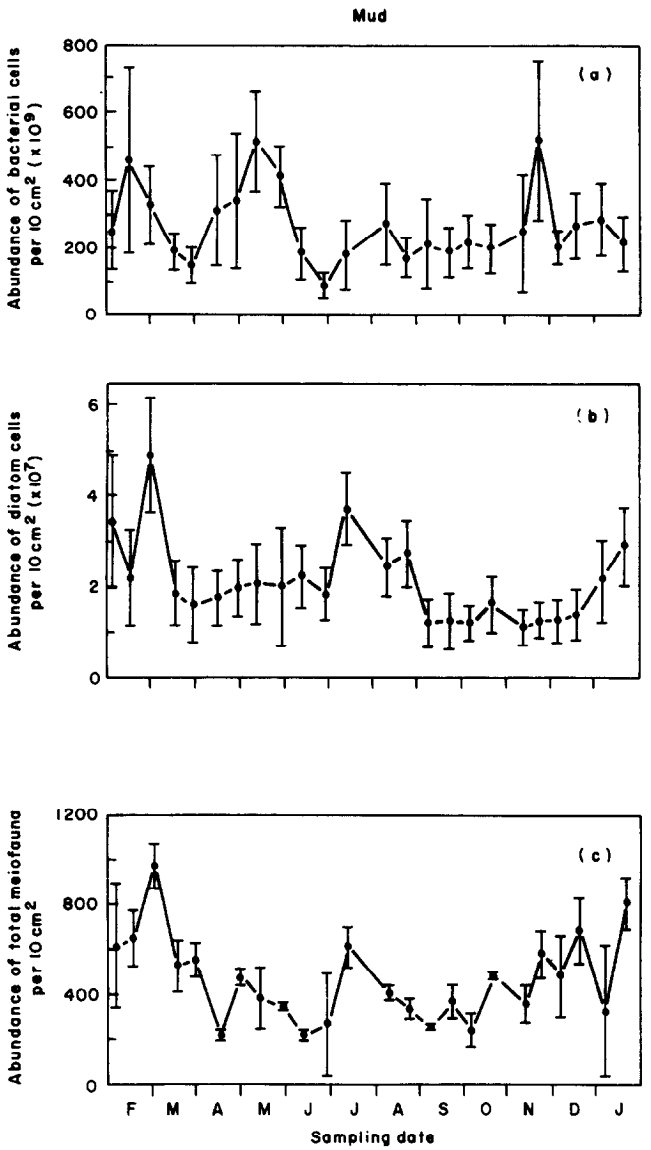

Figure 3. Abundance patterns of diatoms, bacteria and total meiofauna during one year at the mud and sand sites (error bars equal ± one standard deviation).

Pseudobradya pulchella had peaks in fall; and *Paronychocamptus wilsoni* was the only species with both spring and fall peaks. None of the copepod species abundances were correlated with either diatom or bacterial abundance (Table 3). For physical variables *Halicyclops coulli* was negatively correlated with RPD depth, and positively correlated with temperature; *E. propinquum* was also negatively correlated with RPD depth. The only correlation of the six copepod species and lagged microbial densities was with *Paronychocamptus wilsoni* and bacteria after a four week lag period.

At the sand site densities of the four dominant copepod species (mean annual abundance

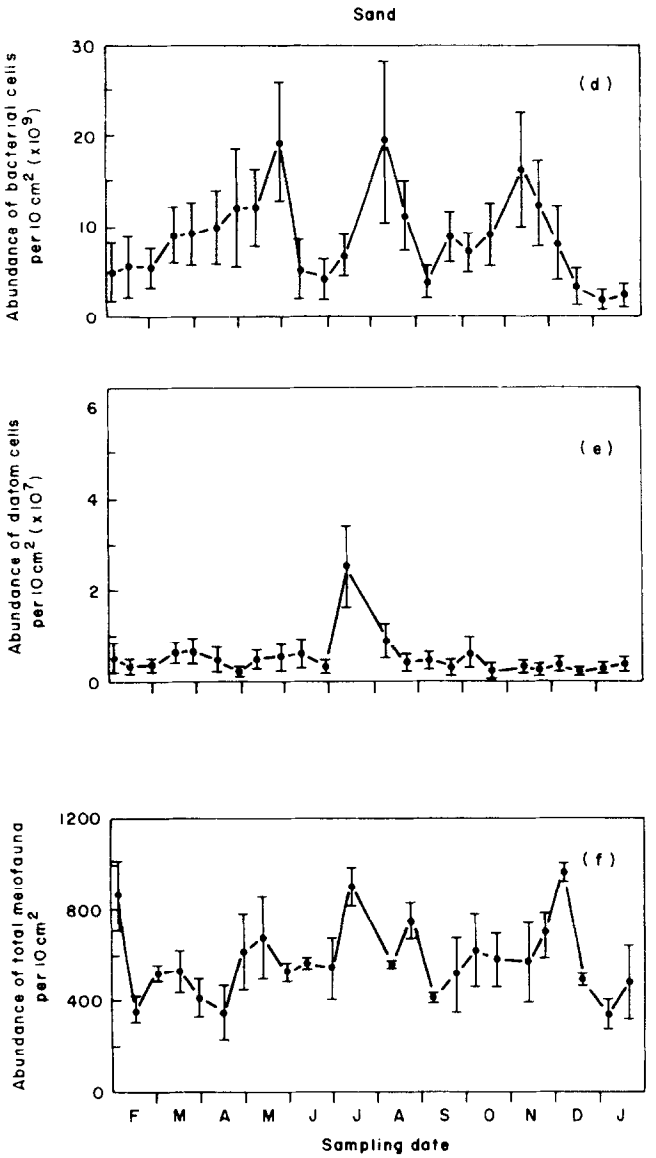

Figure 3.—continued.

per 10 $cm^{-2} \pm$ S.D.) were: *Thompsonula hyaenae* (I. C. Thompson) (7·3 ± 17·5) [Fig. 5(a)], *Halectinosoma winonae* (3·7 ± 11·5) [Fig. 5(b)], *Leptastacus macronyx* (T. Scott) (3·3 ± 3·8) [Figure 5(c)] and *Arenostella spinicauda* Wilson (3·2 ± 6·2) [Figure 5(a)]. The August peak of *H. winonae* at the sand site preceeds the fall and winter peaks which occur at the mud site. *Halectinosoma winonae* behaved like a typical mud-dweller at the sand site being positively correlated with temperature and negatively correlated with the RPD depth. *Halectinosoma winonae* is also strongly correlated with the standing stock of diatoms (Table 3), and even more strongly correlated with diatom densities of the previous two weeks.

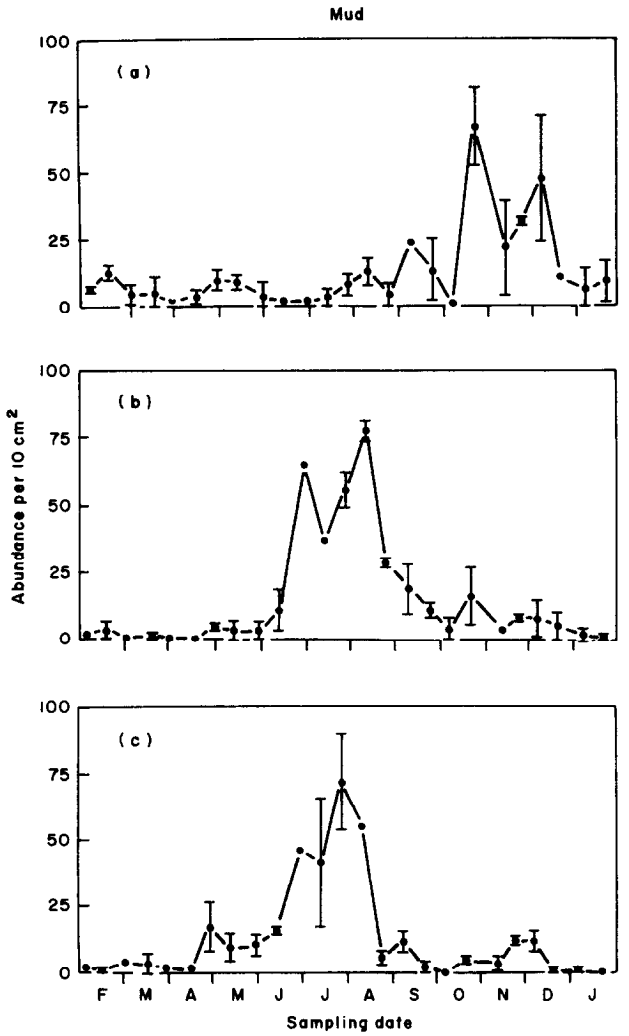

Figure 4. Abundance patterns of six dominant copepod species during one year at the muddy site; given in order of mean annual dominance: (a) *Pseudobradya pulchella*, (b) *Halicyclops coulli*, (c) *Enhydrosoma propinquum*, (d) *Microarthridion littorale*, (e) *Halectinosoma winonae*, and (f) *Paronchocamptus wilsoni*.

Discussion

Studies which examine biological interactions over a one-year period are always susceptible to the possibility that the study was performed during an unusual year. Whereas it is usually impossible to know the year-to-year variability of a given taxon at any study site, we have available 10 years of data on major taxa and copepod species composition at these two sites (Coull, unpubl.). The densities we report herein are lower than those previously encountered (Coull & Vernberg, 1975; Coull & Fleeger, 1975; Coull & Bell, 1979), but are consistent with the overall trend for 9·5 years (Coull, unpubl.). Unfortunately there are no previous data on microbial abundances to correlate with the previous meiofauna data. Meiofauna seasonality is not the point of this paper and due to the known year-to-year variability (Coull, unpubl.) discussion of it for one year would be foolhardy. Therefore,

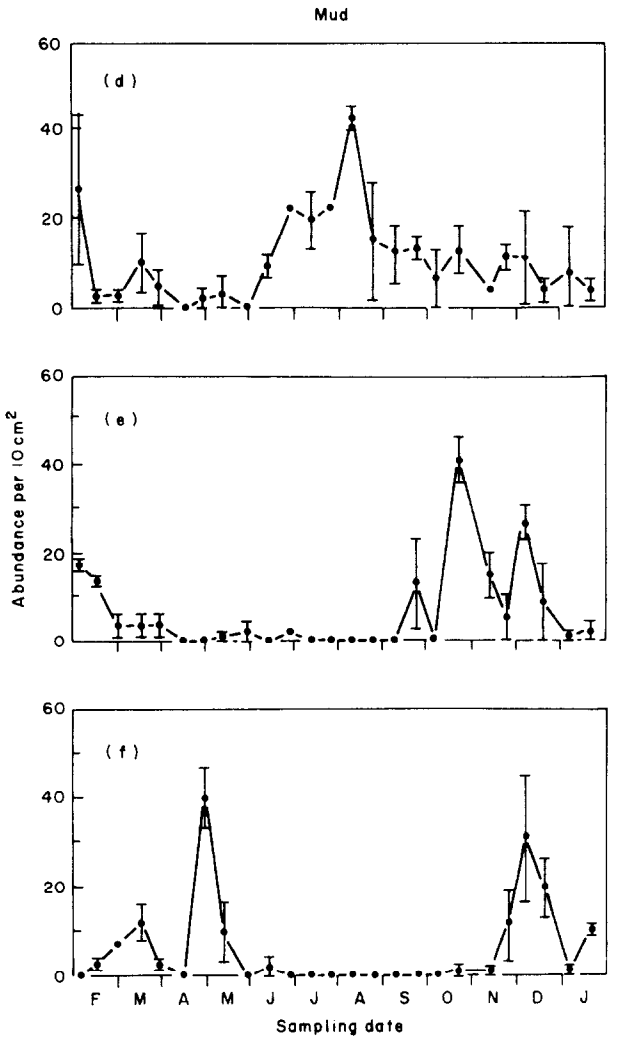

Figure 4.—continued.

our goal is to present the first annual data relating meiofauna abundances with microbial abundances, where both have been sampled simultaneously. The specific seasonal trends (i.e. fall peaks, summer peaks, etc.) are irrelevant, what is important is the relationship between meiofauna and their potential food over an annual period.

The mud site salinity exhibited no clear influence on meiofauna densities, while the temperature–RPD interaction did (Table 2). When temperature increased, the depth of the RPD decreased, the anoxic zone moved toward the surface and animal abundances decreased. This apparently accounted for the low densities of meiofauna in the summer at the mud site [Figure 3(c)]. While this generalization was true for four of the eight meiofauna taxa tested (nematodes, copepods, ostracods and polychaetes) it was also true for total meiofaunal density. By contrast no major meiofaunal taxon was positively correlated with bacterial density and only two of eight groups were correlated with diatoms densities (Table 2); diatoms were also responding to RPD depth (Table 2). Thus, at the muddy site, both meiofauna and diatoms were positively correlated with depth of the RPD

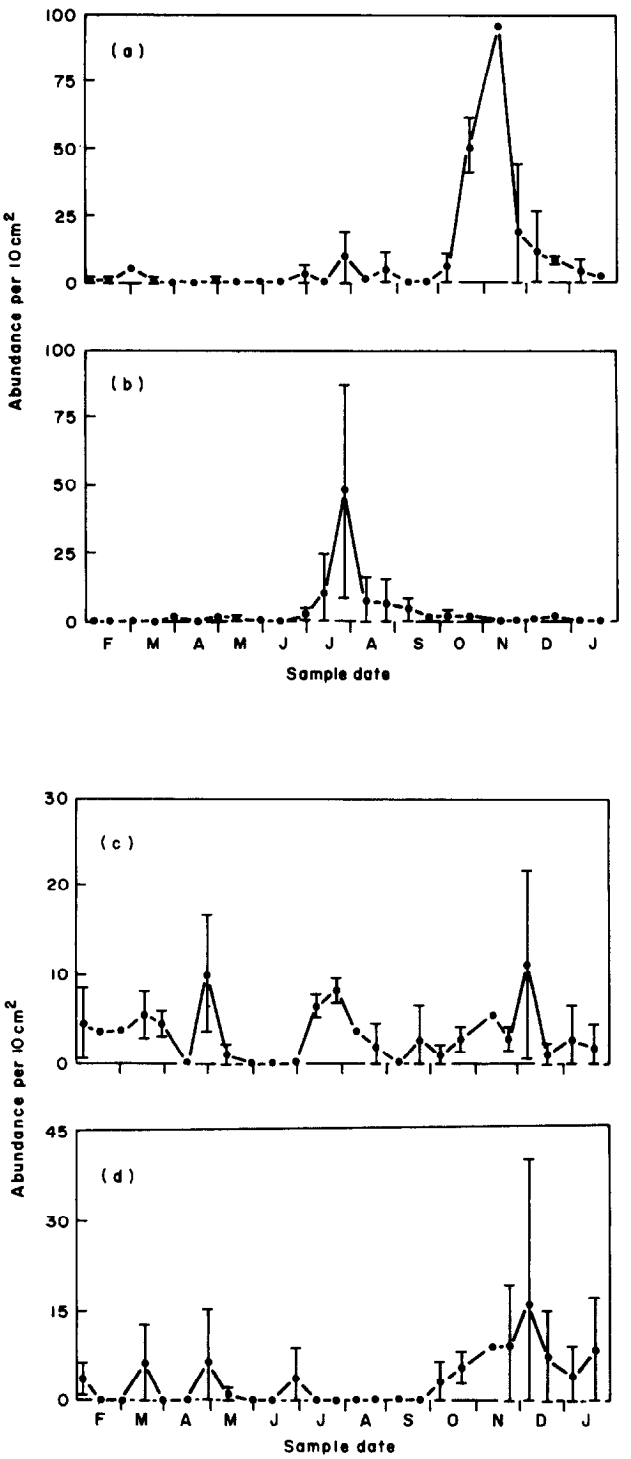

Figure 5. Abundance patterns of four dominant copepod species during one year at the sandy site; given in order of mean annual dominance: (a) *Thompsonula hyaenae*, (b) *Halectinosoma winonae*, (c) *Leptastacus macronyx*, and (d) *Arenostella spinicauda*.

TABLE 3. Correlation coefficients and significance level for copepod species correlation with microbes and physical factors at both sites (if no significance level is indicated then the value is non-significant)

Site and species	Microbes		Physical factors		
	Diatoms	Bacteria	Salinity	Temperature	Redox depth
Mud:					
Pseudobradya pulchella	−0·356	+0·051	+0·151	−0·170	−0·266
Halicyclops coulli	+0·120	+0·267	−0·28	+0·566**	−0·482*
Enhydrosoma propinquum	+0·197	−0·092	+0·057	+0·602**	−0·440
Microarthridion littorale	+0·194	−0·332	+0·016	+0·254	−0·244
Halectinosoma winonae	−0·194	−0·087	+0·240	−0·353	+0·059
Paronychocamptus wilsoni	−0·131	−0·196	+0·152	−0·409	+0·018
Sand:					
Thompsonula hyaenae	−0·211	+0·299	+0·097	−0·055	+0·195
Halectinosoma winonae	+0·714***	+0·121	−0·034	+0·546**	−0·794***
Leptastacus macronyx	+0·154	+0·139	+0·170	−0·264	−0·051
Arenostella spinicauda	−0·313	−0·054	+0·067	−0·553**	+0·202

*Significant at the 0·001 level.
**Significant at the 0·01 level.
***Significant at the 0·05 level.

layer (Table 2). If diatoms were a limiting resource one might expect meiofauna peaks to be correlated with lags in the abundances of diatoms. This did not occur, and diatoms at the mud site were correlated with meiofauna taxa only when lags were not employed. A strong inference is that physical factors, temperature and RPD depth, and not potential food densities are controlling the meiofauna at the mud site. Furthermore, these physical factors appear to be a dominant force regulating abundance patterns of both meiofauna and diatoms at the mud site.

In the more hydrodynamically active sand site, the physical factors measured were not correlated with the fauna (Table 2), even though Hogue (1978) reported that gastrotrich density peaked in the warmer months of 1976–1977 at the same site. Since the microbes did not appear to be responding to the physical factors measured at the sand site, the positive correlations between the three meiofauna taxa and diatoms may well be trophically related (Table 2). However, we found no correlation of meiofauna with lags in diatom densities. Perhaps individual species trends were masked by the trends of total numbers within a taxon. For example, copepods were correlated only with RPD depth at the mud site; however, when examining the data at the species level we also found inverse correlations with temperature for two of the six dominant species.

In both the mud and sand sites correlations between meiofauna density and suspected food, or with lag periods of suspected food were rare (8 cases of 102 tests). Perhaps species identifications of diatoms or bacteria would have provided significant correlations. In general, species identification of the benthic copepods demonstrated that the response of that taxon was due to the response of a dominant (or co-dominant) species (Tables 2 and 3). An exception was *H. winonae* at the sand site which behaved like a species would if it were regulated by food limitation. Although *H. winonae* is found at both sites it is primarily a mud dwelling species (Coull & Vernberg, 1975). Perhaps mud is the optimal habitat for this species, but it is capable of switching to sand when food (diatoms) is abundant.

Diatom densities were higher at the mud than sand site, similar to what Tietjen (1968)

reported for chlorophyll pigments. Assuming the conversion coefficients given by Luria (1960), the bacterial biomass on 7 January 1982 at the mud site was 6·57 mg C 10 cm^{-2} (95% CI = 5·15, 8·40), and in the sand 0·170 mg C 10 cm^{-2} (95% CI = 0·145, 0·199). So, whereas cell abundance in the mud is 167× greater than the sand [Figures 3(a) and (b)], cell biomass is only 39× larger. Bacterial biomass at the mud site was an order of magnitude greater than that reported in similar habitats in North Carolina, U.S.A. (Rublee, 1982). This reflects order of magnitude differences in cell counts, probably due to differences in extraction procedures. At both of our study sites positive correlations were found for meiofauna with diatoms but not with bacteria. The only significant correlation between meiofauna and bacteria was negative with ostracods. By contrast, Meyer-Reil & Faubel (1980) found inverse correlations for total meiofaunal biomass with bacterial biomass. Their data base consisted of nine different stations from the Kiel Fjord and Kiel Bight, sampled at two different times. Since sediment bacterial density is strongly correlated with grain size (Dale, 1974) and grain size varied with stations, different stations were a confounding factor in their study.

It is also possible that the groups studied (meiofauna, diatoms and bacteria) operate at different spatial and temporal scales. Generation times can potentially be on the order of hours for bacteria (Meyer-Reil, 1977), days for diatoms (Admiraal *et al.*, 1982) and weeks or months for meiofauna (Gerlach, 1971). The time scale used in this study (2 weeks) is adequate to measure meiofauna response, but not short enough to identify the shorter-periods of microbial fluctuations. In this study meiofauna ranged in size from 63–500 μm, benthic diatoms between 20–200 μm, and the bacteria averaged 1·1 μm in length. Microorganisms are usually found in localized patches on the surface of sandgrains (Meadows & Anderson, 1966; 1968). Meiofauna appear to have similar spatial scales to that of their suspected microbial food, and may even share similar spatial resource axes with benthic diatoms.

The data in this paper are consistent with the hypothesis that food resources are not the only limiting factor for meiofauna taxa. If food was limiting then one would have predicted meiofauna peaks following peaks in microbial abundance throughout the year; this was not the case. However, conclusions from correlation studies must always be considered cautiously because all possible variables cannot be measured, confounding factors may be present, and correlation does not, *a priori*, guarantee cause and effect. For example, predation can regulate meiofauna communities (Bell & Coull, 1978), but was not measured in this study.

All the positive correlations we found with food occurred with diatoms, not with bacteria. Whereas, in coastal waters off Georgia (Hanson *et al.*, 1981) and Spain (Tenore *et al.*, 1982) nematode abundance was positively correlated with ATP measures of microbial biomass (which includes algae and protozoa as well as bacteria). This apparent contradiction could, of course, be site or habitat specific. If generalizations are to be made regarding microbial-meiofaunal interactions similar work is necessary in a variety of sites and habitats.

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