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Abundance and Horizontal Distribution of Meiofauna on a Northern California Beach[1]

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ABSTRACT: Distribution and abundance of meiofauna on a sandy beach in Big Lagoon, California, were studied during a 3-week period in the summer of 1996. Sediment cores were taken to a depth of 10 cm at three tidal levels. In addition to quantitative counts of meiofauna, exposure to air, percentage water content, and grain size composition were determined for each sample. Results of Spearman rank correlations revealed that median grain size, percentage exposure to air, and sediment saturation were strongly correlated to differences in meiofauna abundance at the mid and low water stations. Mean meiofauna abundance was 779 individuals per 100 cm^3 of sand. Nematodes and oligochaetes made up approximately 80% of the mean abundance at the midwater stations. Although polychaetes accounted for approximately 70% of the mean total meiofauna at the low water stations, the most numerically dominant group varied on different sampling days and included polychaetes, gastrotrichs, turbellarians, and nematodes. New distributional records for Northern California include *Nematoplana nigrocapitula* (Turbellaria, Proseriata), *Turbanella mustela* (Gastrotricha, Macrodasyida), and *Microcerberus abbotti* (Isopoda, Microcerberoidea).

VERY FEW BROAD STUDIES of meiofauna assemblages have been performed on West Coast sandy beaches (Wieser 1959, Narine 1977, Feder and Paul 1980, Gowing 1981). The majority of publications have been taxonomic descriptions of a single species or a particular group of meiofaunal organisms, such as solitary hydroids (Norenburg and Morse 1983), Turbellaria (Karling 1962, 1964, 1966, 1986, Kozloff 1965, Ax and Ax 1967, Schockaert and Karling 1970, Karling and Schockaert 1977, Ax and Sopott-Ehlers 1979, Sopott-Ehlers and Ax 1985), Nematoda (Hope 1967), Gastrotricha (Remane 1925, Wieser 1957*b*, Hummon 1966, 1969, 1972, Ruppert 1977, Todaro 1995), Archiannelida (Wieser 1957*a*, Gray 1968*b*, Martin 1977), Polychaeta (Gradek 1991), Oligochaeta (Erséus and Strehlow 1986), Tardigrada (McGinity 1969, Schuster and Grigarick 1970), and Copepoda (Gray 1968*a*).

The high-energy marine beach of Big Lagoon (41° 11′ N, 124° 07′ W) is located in Dry Lagoon State Park, approximately 30 miles (48 km) north of Eureka, California. Big Lagoon is located on the east side of a sandy beach that separates the lagoon from the ocean by approximately 200 m. Samples were taken from the highly exposed, steep-sloped (approximately 6%), marine side of the beach, approximately 0.5 miles (0.8 km) north of the southern tip of the lagoon. Highly exposed beaches with coarse sediment tend to have abundant meiofauna and sparse resident macrofauna populations (McLachlan 1977, 'Olafsson 1991), as is true for Big Lagoon beach.

The objective of this study was to document the meiofaunal composition of Big Lagoon beach and to examine the primary factors affecting their distribution. This study provides information regarding meiofaunal

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diversity, dispersion, and zoogeography previously unrecorded for Northern California.

MATERIALS AND METHODS

Meiofauna Sampling

Sand cores were taken during receding tides when the tidal height was approximately 0.0 ft. Sampling took place, as tides allowed, during a 3-week period from 21 May to 15 June 1996 along two transects. Each transect extended 40 m perpendicular to the water's edge during low tide; transect B was located 2 m north of transect A. Three stations were sampled along each transect at low, mid, and high water levels.

Eight surface sediment cores of 100 cm^3 were taken from each of the six sampling stations to a depth of 10 cm. In addition, four 100-cm^3 cores were taken from the high and mid water stations at a depth of 30–40 cm.

Meiofauna were extracted from sediment with a 63-μm sieve, using the magnesium chloride anesthetization-decantation method (Sterrer 1971). Six washes provided approximately 90% extraction efficiency of meiofauna. Counts of meiofauna were made while pipetting individual animals out of a petri dish. Metazoa were counted and identified to lowest recognizable taxon while viewed under a dissecting microscope.

Abiotic Factors

Percentage exposure to air during the week before sampling was determined for all stations. The tidal height for each sampling level was determined from the slope of the beach and the height of the tides for the 7 days before sampling and plotted using Harbor Master (1987). The percentage of time that the sampling stations were exposed to air was approximated from the tidal plot. The percentage exposure for the high water stations was estimated from direct observation. The high water stations were only submerged during times of an ocean swell, disallowing the standard method of calculation.

After the meiofauna was extracted, the sediment was rinsed with water to remove salt and then allowed to air-dry. The sediment was later placed in a 105°C oven for 48 hr to complete the drying and then reweighed. Water content of sediment was determined by subtracting the dry weight of the sediment from the wet weight and was expressed as a percentage of the total sample weight.

Dried sediment was passed through a series of six sieves, allowing grain size characteristics to be determined according to Giere et al. (1988).

RESULTS

Abiotic Factors

Exposure to air the week before sampling the high, mid, and low water stations averaged 98, 48, and 14%, respectively.

The mean physical characteristics for each of the six sampling stations are shown in Table 1. As expected, percentage water content was higher in sample cores taken closer to the water line. Water content in cores from the high water stations (A-1 and B-1) averaged 4.6% of the core weight. Water content of cores from the mid water stations (A-2 and B-2) averaged 7.9%. Cores taken from the low water stations (A-3 and B-3) were typically saturated at the time of collection, with a mean water content of 12.8%.

The median grain size of the high and low water stations was medium sand, and the median grain size of sediment from the low water stations was coarse-grained sand. Sediment from all stations was typically moderately sorted and the mean skewness was usually close to zero (Table 1), indicating that the majority of grain size fractions were similar in size to the median.

Sediment characteristics of the samples taken at 30 to 40 cm depth are shown in Table 2. All four samples were composed of coarse-grained sand.

Meiofauna Abundance and Distribution

Except for an occasional gastrotrich or turbellarian, nematodes and oligochaetes

TABLE 1

MEAN PHYSICAL CHARACTERISTICS FOR EACH OF THE SIX SAMPLING STATIONS ($n = 8$)

STATION	TIDAL LEVEL	MEDIAN GRAIN SIZE (μm)	Md[a] ϕ	Qd[b] ϕ	Skq[c] ϕ	WATER CONTENT[d] % wt
A-1	HW	525	0.93	0.92	−0.04	4.6
B-1	HW	540	0.89	0.89	−0.02	4.6
A-2	MW	620	0.69	0.92	0.18	8.6
B-2	MW	660	0.60	0.89	0.12	7.2
A-3	LW	1,050	−0.07	1.07	0.20	13.0
B-3	LW	1,072	−0.10	0.92	0.79	12.7
Mean	All	710	0.49	0.94	0.21	8.45

[a] Median particle diameter in phi units.
[b] Phi quartile deviation.
[c] Phi quartile skewness.
[d] Expressed as a percentage of sample weight.

TABLE 2

PHYSICAL CHARACTERISTICS FOR SAMPLES TAKEN AT 30–40 CM DEPTH

STATION	TIDAL LEVEL	MEDIAN GRAIN SIZE (μm)	MD ϕ	Qd ϕ	Skq ϕ	WATER CONTENT % wt
A-1	HW	1,020	−0.03	0.90	0.12	6.5
B-1	HW	895	0.16	0.83	0.08	2.3
A-2	MW	1,790	−0.84	−0.15	6.95	4.4
B-2	MW	1,750	−0.81	−0.08	1.85	5.4

NOTE: See explanation of symbols in Table 1.

were the only groups collected at the high water stations (A-1 and B-1) (Table 3). Nematode and oligochaete density averaged 3.6 and 2.5 individuals per 100 cm^3, respectively.

The highest meiofauna densities at the study site occurred at the mid water stations. Meiofauna densities at stations A-2 and B-2 averaged 942.9 and 940.9 individuals per 100 cm^3, respectively (Table 3). Nematodes and oligochaetes were the most abundant groups at the mid water stations, making up approximately 80% of the meiofauna (Figure 1). Turbellarians, ostracods, and harpacticoids typically made up 14 to 27% of the meiofauna at these stations (Figure 1).

The mean densities of meiofauna at low water stations A-3 and B-3 were 547.4 and 683.9 individuals per 100 cm^3, respectively (Table 3). Polychaetes at the low water stations outnumbered other meiofauna (Table 3), composing 68 to 72% of all specimens from the low water stations (Figure 1); the high standard deviations reflect the patchy distribution of polychaetes.

Turbellarians, nematodes, polychaetes, and gastrotrichs were each the most numerically abundant group, on different sampling days, at the low water stations. Although gastrotrichs made up 10 to 13% of the meiofauna from the low water station, they were the most abundant animals on three of the eight sampling days at both low water stations. Turbellarians were most abundant on 3 days at station A-3 and 2 days at station B-3. Polychaetes were most abundant on 1 day at station A-3 and on 3 days at station B-3. Nematodes were numerically dominant on 1 day at station A-3.

TABLE 3

MEAN DENSITIES (100 cm^{-3} ± SD) OF MEIOFAUNA TAXA AT EACH SAMPLING STATION ($n = 8$)

TAXON	TIDAL LEVEL HW A-1	HW B-1	MW A-2	MW B-2	LW A-3	LW B-3
Turbellaria						
Turbellaria (unidentified)	0.0 ± 0.0	0.0 ± 0.0	53.1 ± 54.9	41.2 ± 22.0	20.1 ± 23.5	22.6 ± 16.8
Acoela	0.0 ± 0.0	0.0 ± 0.0	2.5 ± 5.9	0.8 ± 1.0	6.0 ± 5.6	4.8 ± 6.0
Proseriata	0.0 ± 0.0	0.1 ± 0.3	77.0 ± 124.0	43.5 ± 37.1	31.5 ± 12.9	27.8 ± 19.5
Nematoplana nigrocapitula	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.7	0.1 ± 0.3	6.1 ± 6.5	31.5 ± 12.9
Cheliplana sp.	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.4 ± 1.7	2.6 ± 2.4
Nemertea (two species)	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.3	0.0 ± 0.0	0.1 ± 0.3
Nematoda (several species)	2.6 ± 3.2	4.5 ± 6.6	479.0 ± 268.8	515.0 ± 347.0	33.4 ± 25.0	13.5 ± 12.0
Gastrotricha						
Chaetonotida	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Turbanella	0.1 ± 0.3	0.0 ± 0.0	1.6 ± 1.9	0.5 ± 0.7	56.4 ± 51.5	90.0 ± 91.5
Polychaeta						
Protodrilus sp.	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.9	0.6 ± 0.9
Phyllodocida (two species)	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.3	0.4 ± 0.9	370.3 ± 941.1	489.5 ± 1092.3
Hesionides sp.	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 1.3	1.4 ± 3.6
Eusyllis larvae	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.3	0.3 ± 0.7	0.1 ± 0.3	0.0 ± 0.0
Oligochaeta	1.4 ± 3.6	3.62 ± 6.5	240.8 ± 120.3	288.0 ± 169.3	0.4 ± 0.7	0.8 ± 2.0
Crustacea						
Ostracoda	0.0 ± 0.0	0.0 ± 0.0	67.8 ± 84.9	38.8 ± 28.6	9.1 ± 18.2	8.3 ± 13.2
Harpacticoida	0.0 ± 0.0	0.0 ± 0.0	20.1 ± 23.5	12.3 ± 13.9	17.1 ± 33.5	13.4 ± 20.7
Harpacticoida nauplii	0.0 ± 0.0	0.0 ± 0.0	2.0 ± 3.3	1.3 ± 2.2	13.9 ± 13.8	14.8 ± 11.0
Halacaroidea	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 1.3	0.1 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Mean total	4.1 ± 1.4	8.3 ± 13.2	942.9 ± 493.5	940.9 ± 500.8	547.4 ± 994.6	683.9 ± 1128.7

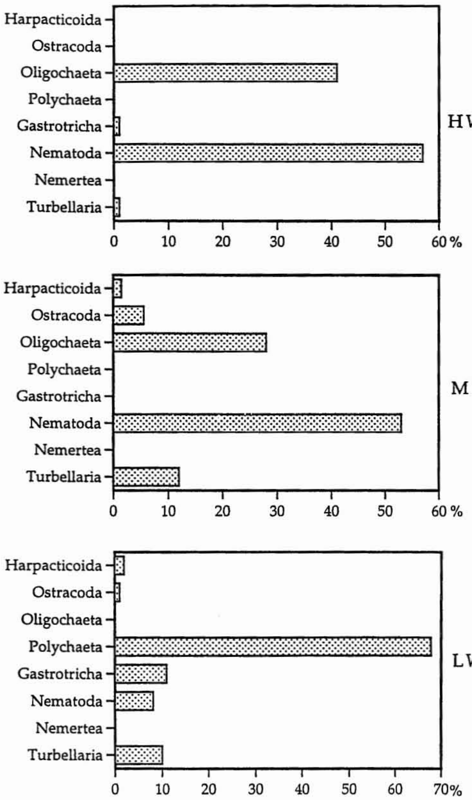

FIGURE 1. Mean percentage composition of meiofauna at the three tidal levels at Big Lagoon beach, California; 0–10 cm depth.

Although the mean number of individuals at the mid water stations was nearly double that at the low water stations, the numbers of meiofauna groups represented at the mid and low water stations were similar. However, the number of groups that composed a major percentage of the total meiofauna was significantly lower at the mid water stations (Figure 1). Nematodes and oligochaetes made up 80% or more of the meiofauna in 75% of the samples taken from the mid water stations. At the low water stations, two groups composed 80% or more of the meiofauna in 50% of the samples. In the other 50% of samples at the low water stations, it took three or more groups to make up 80% or more of the meiofauna.

Samples Taken at 30–40 cm Depth

Despite having larger sediment size, the four samples taken at 30 to 40 cm depth at the high and mid water stations had meiofauna densities similar to those of the surface samples. Meiofauna densities at high water stations A-1 and B-1 were 13 and 42 individuals per 100 cm^3. At the mid water stations, 411 meiofauna organisms were collected from station A-2, and 745 individuals were collected from station B-2.

Correlations between Meiofauana and Abiotic Factors

Data from the mid and low water stations were combined to determine Spearman rank correlation coefficients (r_s) for abiotic factors and number of meiofauna. Data from the high water stations were excluded from this analysis because of the short time of submergence and correspondingly low counts of meiofauna.

Median grain size, percentage exposure to air the week before sampling, and percentage water content were strongly correlated with meiofauna abundance (Table 4). As noted earlier, the low water stations were made up of predominately larger sand grains than were the mid water stations. Gastrotrichs and polychaetes were significantly positively correlated with median grain size diameter ($r_s = 0.56$, $P < 0.001$; $r_s = 0.60$, $P < 0.001$, respectively). Nematodes, oligochaetes, ostracods, and harpacticoids were significantly negatively correlated with median grain size diameter ($r_s = -0.68$, $P < 0.001$; $r_s = -0.81$, $P < 0.001$; $r_s = -0.57$, $P < 0.001$; $r_s = -0.31$, $P < 0.05$, respectively). Gastrotrichs and polychaetes also had significant negative correlations with percentage exposure to air the week before sampling ($P < 0.001$) and significant positive correlations with percentage water content of sediment ($P < 0.01$, $P < 0.001$, respectively). Conversely, nematodes, oligochaetes, and ostracods had significant positive correlations with percentage exposure to air the week before sampling ($P < 0.001$) and significant negative correlations with percentage water content ($P <$

TABLE 4

SPEARMAN RANK CORRELATION COEFFICIENTS (r_s) OF ABIOTIC FACTORS AND NUMBERS OF MEIOFAUNA AT THE MID WATER AND LOW WATER STATIONS (A-2, B-2, A-3, B-3)

TAXON	% WATER CONTENT	MEDIAN GRAIN SIZE (μm)	GRAIN SIZE SORTING (Qd ϕ)	% EXPOSURE TO AIR
Turbellaria	−0.13 ns	−0.30 ns	−0.18 ns	0.26 ns
Nematoda	−0.69***	−0.68***	−0.44**	0.81***
Gastrotricha	0.53**	0.56***	0.27 ns	−0.72***
Polychaeta	0.69***	0.60***	0.20 ns	−0.77***
Oligochaeta	−0.72***	−0.81***	−0.51**	0.83***
Ostracoda	−0.61***	−0.57***	−0.40*	0.65***
Harpacticoida	−0.11 ns	−0.31*	−0.36*	0.32*
Total meiofauna	−0.47**	−0.53**	−0.36*	0.63***

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant ($P > 0.05$); $n = 32$.

0.001). Turbellarians were not significantly correlated with any of the abiotic factors measured in this study.

Taxonomic Summary

Three orders of Turbellaria were recognized in the samples, including members of the Acoela, Proseriata, and Rhabdocoela. The proseriate *Nematoplana nigrocapitula* was found in samples from the mid and low water stations. *Nematoplana nigrocapitula* has been reported from San Juan Island, Washington, as well as Tomales Bay and Pacific Grove, California (Ax and Ax 1969). Also identified in the low water station samples were several specimens of the kalyptorhynch rhabdocoel *Cheliplana* sp.

There appeared to be several groups of nematodes in the samples, based on differences in appearance. Qualitative sampling from depths greater than 30 cm at the mid water station yielded members of the nematode family Epsilonematidae.

One unidentified chaetonotid and a single specimen of *Turbanella* cf. *hyalina* (Gastrotricha, Macrodasyida) were collected, but the majority of the gastrotrichs appeared to be *Turbanella mustela*. *Turbanella mustela* was most abundant at the low water stations, where its average density was 56.4, with 90.0 individuals per 100 cm^3 (Table 3).

Three genera of phyllodocid polychaetes, *Eusyllis*, *Pisione*, and *Hesionides*, were collected. Because of the difficulty in differentiating between *Eusyllis* and *Pisione* when viewed under the dissecting scope, these genera were counted under the category "Phyllodocida spp." Most of these individuals appeared to be *Eusyllis*.

A single species of Isopoda was found at Big Lagoon beach. Twenty-eight individuals of *Microcerberus abbotti* (Microcerberoidea) were collected from the two mid water station samples taken at 30 to 40 cm depth. *Microcerberus abbotti* has been found in central and southern California (Lang 1961, Schultz 1969), and a subspecies, *M. abbotti juani*, has been described from San Juan Island, Washington (Coineau and Delamare Deboutteville 1967).

DISCUSSION

Comparison with Other West Coast Studies

Temperature, granulometry, salinity, oxygen availability, substratum porosity, and water saturation are thought to be major abiotic factors affecting the large-scale distribution patterns of meiofauna (Giere et al. 1988). Although relatively few studies have been done on meiofauna from intertidal sandy beaches on the West Coast of North America, three quantitative studies (Narine 1977, Feder and Paul 1980, Gowing 1981) allow for comparisons with my work (Table 5). Two of these studies (Narine 1977,

TABLE 5

MEIOFAUNAL DATA FROM SANDY BEACHES ON THE WEST COAST OF NORTH AMERICA

LOCATION	DEPTH (cm)	MEAN GRAIN SIZE (μm)	TYPE OF COUNT[a]	TOTAL MEIOFAUNA	NEMATODA	COPEPODA	TURBELLARIA	OLIGOCHAETA	POLYCHAETA	OTHERS	REFERENCE
Younger Lagoon Santa Cruz, California	0–40	460	a	817	159 (20%)	190 (23%)	127 (16%)	84 (10%)	231 (28%)[c]	26 (3%)	Gowing (1981)
Salinas State Beach Monterey Bay, California	0–50	500–1000	b	5,510–11,023[b]	(42%)	(43%)	(11%)	(< 5%)	(< 5%)	(< 5%)	Narine (1977)
Mineral Creek Flats Port Valdez, Alaska	0–5	420–700	a	1,512	1,010 (67%)	372 (25%)	2.5 (0.2%)	0	29 (2%)	98 (6%)	Feder and Paul (1980)
Big Lagoon beach Big Lagoon, California	0–10	820	c	779	260 (33%)	16 (2%)	88 (11%)	133 (17%)	216 (28%)	68 (9%)	This study

NOTE: Abundances given per 10 cm^2. Data for Mineral Creek compiled from primary data matrix, excluding protozoa and those organisms with mean abundances less than 1.

[a] a, mean annual; b, September 1974 to January 1975; c, mid and low water level, 21 May–8 June 1996.

[b] Mean abundances given for winter and summer.

[c] Predominantly archiannelids.

Gowing 1981) were performed in relatively close proximity to one another in Monterey Bay, California (36° 47′ N, 121° 47′ W and 36° 56.9′ N, 122° 4′ W). The third study (Feder and Paul 1980) occurred much further north, on a tidal flat in Port Valdez, Alaska.

The study by Feder and Paul (1980) represents a habitat and an assemblage much different from those of the three California studies. The far north location of Mineral Creek Flats, Alaska, was subjected to a mean annual air temperature of 10°C and to wet snow that froze on the study site in the winter. The low-energy environment of the tidal flat habitat had a low concentration of dissolved oxygen below 30 mm sediment depth, and 90% of the total meiofauna was restricted to the upper 30 mm of sediment. Sediment at Mineral Creek Flats was very poorly sorted and consisted of coarse to medium sands with a mean particle size that ranged from 420 to 700 μm. Meiofauna consisted of mostly nematodes and harpacticoid copepods, as well as many "temporary" meiofaunal individuals. Nematode abundance was highest in August and lowest in January; polychaete abundance peaked in May and was lowest in November.

Although the mean grain size of sediment from Mineral Creek Flats is similar to that of the California study sites, the lower temperature and protected tidal flat habitat almost certainly contributed to the differences in relative abundance of meiofauna. The highest temperatures of the California studies occurred at Younger Lagoon, with a mean air temperature of 22°C in September 1976. During September 1974, Salinas State Beach had a mean air temperature of 16°C. Air temperatures were not recorded at Big Lagoon beach, but mean air temperature at a beach approximately 10 miles (16 km) from Big Lagoon during the study period was 17°C.

Comparisons of mean abundance of meiofauna between my study and others must be viewed with caution because of potential differences in sampling technique. In particular, it is important to note that the 0 to 10 cm sampling depth used on Big Lagoon beach was too shallow to collect many meiofauna. Samples taken from the mid water stations at 30 to 40 cm depth, show that meiofauna abundance at that depth is probably similar to abundance in the upper 10 cm of sediment. If the abundance of meiofauna in the upper 50 cm of sediment at Big Lagoon beach is assumed to be proportionally equal to that in the upper 10 cm of sediment, the mean abundance would far surpass that of Younger Lagoon, but it would still fall short of the mean abundance found at Salinas State Beach.

Nematodes and copepods are generally the two most commonly occurring groups of meiofauna. Nematodes often compose more than 50% of the meiofauna (Coull and Giere 1988). It is interesting to note the strikingly low abundance (2% of the meiofauna) of copepods on Big Lagoon beach, particularly in contrast to the other West Coast studies. Nematodes and copepods made up approximately 85% of the total meiofauna at Salinas State Beach, but those groups composed only 43% and 35% at Younger Lagoon and Big Lagoon, respectively.

Despite differences in sampling depth, mean grain size, and relative percentage of copepods, the relative percentages of other meiofaunal groups at Younger Lagoon beach are similar to those at Big Lagoon beach (Table 5). Although there were very few oligochaetes or polychaetes found in the Salinas study, these groups were found in similar percentages at Younger Lagoon and Big Lagoon. However, most of the polychaetes found at Younger Lagoon were the archiannelid *Protodriloides chaetifer*, whereas polychaetes at Big Lagoon included one species of archiannelid (*Protodrilus* sp.) and three species of phyllodocids. Correlations of meiofauna abundance with abiotic factors were also similar in the Big Lagoon and Younger Lagoon studies. In both studies, numbers of harpacticoids, nematodes, and oligochaetes were correlated with percentage exposure to air. In addition, both studies showed a positive correlation between the water content of the sediment and the abundance of nematodes and oligochaetes. Gowing (1981) proposed that the significant negative correlation between total meiofauna abundance and water content, and the significant positive correlation between abundance and exposure to air in her Younger Lagoon study suggest that oxygenation of sand is an important factor of meiofauna abundance. Similar correlations were revealed at Big Lagoon.

Although several meiofaunal groups at Big Lagoon were significantly correlated with median grain size (Table 4), this was true only for harpacticoids and nematodes at Younger Lagoon. These two beaches have fairly different median grain size (Table 5), and the sediment at Big Lagoon was moderately sorted whereas sediment at Younger Lagoon was well sorted.

CONCLUSIONS

Although the marine interstitial environment has persisted through geological time, local habitats persist over shorter periods of time because of fluctuations in water movement (Ruppert 1977). The seasonal variation of water movement can directly affect the interstitial environment through erosion and siltation and by changing the energy dynamics of a local habitat (e.g., the formation of sand bars) (Ruppert 1977). As a result, my study and other short-term ecological studies of marine meiofauna do not reflect the long-term effects of seasonal changes in water movement on meiofauna composition and the factors that influence their distribution. However, this work does provide some general insight into the physical factors that influence the abundance and horizontal distribution of surface meiofauna.

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