

AN ABSTRACT OF THE THESIS OF

Christine A. Miller-Way for the degree of Master of Science  
in Oceanography presented on June 20, 1984

Title: The Response of a Marine Meiofaunal Assemblage to  
Experimental Manipulations of Sediment Microtopography

Redacted for privacy

Abstract approved: \_\_\_\_\_

Dr. Charles B. Miller

A number of recent studies have documented the important influence of biogenic microtopography on the small scale spatial distribution of meiofauna. Recent evidence has shown that physically generated sediment microtopography also affects the distribution of the meiobenthos. This study documented the relationship between sand ripples and the small scale distribution of meiofauna and investigated possible mechanisms producing this relationship. Meiofauna and sediment were sampled by the straw transect method and results analyzed using time series analysis techniques.

On January 12, 1983, meiofaunal sampling was conducted to confirm the nematode-sediment ripple relationship previously reported. The results indicated strong density periodicities in total meiofauna, nematodes, tardigrades, and harpacticoid copepods at the wavelength of the sediment ripples. These results confirm the nematode-ripple relationships previously documented and indicated the importance of

sediment ripples in affecting the small scale distribution of meiofauna.

During June 12-14, 1983, the spatial pattern of the sediment ripples was altered with an in situ wave box to demonstrate a causal link between sediment ripple spacing and meiofaunal density patterns. The wave box technique produced ripples of 10.0 cm wavelength in contrast to 6.0 cm wavelengths in an unmanipulated area. After 24 hrs, meiofauna samples were taken in the manipulated and control areas. Total crustaceans, gastrotrichs/turbellarians, and harpacticoid copepods showed a 10.2 cm wavelength in densities in the experimental series and a 6.0 cm wavelength in densities in the control series. Total meiofauna and nematodes showed no strong periodicities in the experimental series and weak periodicities at a 4.5 cm wavelength in the control series. These results indicated that different meiofaunal taxa are responding to different features of the sediment ripples.

During November 7-9, 1983, fecal pellets of the ghost shrimp Callinassa californiensis were added to the ripple system in a frequency pattern unrelated to the ripple spacing to isolate the direct and indirect influences of the sediment ripples. After 48 hrs, meiofaunal and organic carbon samples were taken in this experimental treatment, in a adjacent, similarly manipulated area in which no additions of fecal pellets were made, and in a control area. Total meiofauna and nematodes showed density periodicities at the frequency of the additions. Other meiofauna showed no density periodicities at the frequency of the additions and weak density periodicities which

were unrelated to sediment ripple spacing. These results indicated that nematodes are more sensitive to the micro-spatial distribution of organic matter than other meiofaunal taxa. Additionally, these results demonstrated that sediment ripples are not always the dominant influence on the small scale distribution of meiofauna.

On the basis of these results and reports in the literature, I concluded that different meiofaunal taxa are responding to different facets of their habitat. I hypothesized that the small scale distribution of nematodes was primarily influenced by the micro-spatial distribution of their food source, particulate organic matter, which is indirectly controlled by sediment ripples. In contrast, the distribution of other meiofauna appears to be directly influenced by a physical property or properties of the sediment ripples. I believe this property to be the micro-flow regime over a rippled sediment surface. The observed small scale distribution of the meiofaunal assemblage at my study site is a complex product of many different processes which include the direct and indirect influences of sediment ripples.

The Response of a Marine Meiofaunal Assemblage to  
Experimental Manipulations of Sediment Microtopography

by

Christine A. Miller-Way

A THESIS

submitted to

Oregon State University

in partial fulfillment of  
the requirements for the  
degree of

Master of Science

Completed June 20, 1984

Commencement June 1985

APPROVED:

Redacted for privacy

\_\_\_\_\_  
Professor of Oceanography in charge of major

Redacted for privacy

\_\_\_\_\_  
Dean of School of Oceanography

Redacted for privacy

\_\_\_\_\_  
Dean of Graduate

Date thesis is presented June 20, 1984

Typed by Christine A. Miller-Way for Christine A. Miller-Way

## Acknowledgements

I extend my sincere gratitude to Dr. Chip Hogue, who led me through the intricacies of meiobenthic research, participated in and suffered through every phase of this project, and made the research an enjoyable and learning experience.

I thank my major professor, Dr. Charlie Miller, who greatly improved my writing skills, and who, in his own way, taught me much about conducting and evaluating ecological research. I thank Dr. Jane Lubchenco, whose expertise contributed much to the synthesis of this research, and Dr. Chris Bayne, who gave me the opportunity to improve my teaching skills and provided perspective in a community often lacking in it.

Dr. Andrew Carey graciously made space and equipment in his laboratory available to me and Dr. Thomas Beasley provided financial assistance; for this assistance I am most grateful.

As in most research studies, many people have contributed to the success of this project. I thank Hal Batchelder, Gary Braun, Michel Boudrias, Mark Brzezinski, Terry Farrell, John Kern, Lynne Krasnow, Dreas Nielsen, Terry Risdon, Gene Ruff, Bill Savidge, Jon Shenker, and Jon Temte for their time, ideas, field assistance, computer skills, sympathetic ears, beer, and friendship. I would also like to thank Howard Jones for supplying his talent, equipment, time and space for the construction of the wave box. Special thanks to the myriad residents of 589 W. Olive St. and to Terry Risdon and Jesse Rodgers,

Lynne Krasnow, and Barbry and Chip Hogue for their hospitality and friendship during the latter phases of this project.

I appreciate the help of Mr. Bob Hawkins in drafting Figure 2. The Milne Computer Center of Oregon State University provided funds for the majority of the computer analyses conducted in this study.

My parents, Dr. Thomas Miller and Ms. Peggy Miller, have my gratitude for allowing me the mental and financial freedom to pursue my interests.

Finally, I thank Dr. Carl Way for often coerced field assistance, for editing, typing, and commenting on last minute manuscripts, for assisting in every phase of this research, for interrupting his own career so that I could continue mine, and for believing in me every step of the way.

## TABLE OF CONTENTS

|                     |    |
|---------------------|----|
| INTRODUCTION        | 1  |
| STUDY AREA          | 22 |
| EXPERIMENTAL DESIGN | 25 |
| RESULTS             | 33 |
| DISCUSSION          | 74 |
| CONCLUSIONS         | 87 |
| LITERATURE CITED    | 89 |

## LIST OF FIGURES

| <u>Figure</u> |  | <u>Page</u> |
|---------------|--|-------------|
| 1             | Location of study area in Yaquina Bay estuary, Newport, Oregon   | 23          |
| 2             | In situ wave box used in the manipulation of sediment microtopographical characteristics experiment (not to scale)   | 29          |
| 3             | Autocorrelation coefficients for sediment ripple heights on January 12, 1983, plotted from 0 - 50 lags   | 34          |
| 4             | Abundance per core versus distance for each taxon enumerated on January 12, 1983   | 38          |
| 5             | Autocorrelation coefficients for densities of all taxa enumerated on January 12, 1983, plotted from 0 - 50 lags  | 40          |
| 6             | Autocorrelation coefficients for sediment ripple heights in the manipulation of sediment microtopographical characteristics experiment, June 14, 1983, plotted from 0 - 25 lags          | 43          |
| 7             | Abundance per core versus distance for each taxon enumerated in the manipulation of sediment microtopographical characteristics, June 14, 1983   | 48          |
| 8             | Autocorrelation coefficients for densities of all taxa enumerated in the manipulation of sediment microtopographical characteristics experiment, June 14, 1983, plotted from 0 - 25 lags | 51          |
| 9             | Autocorrelation coefficients for sediment ripple heights on November 9, 1983, plotted from 0 - 25 lags   | 55          |
| 10            | Organic carbon levels versus distance for each treatment in the addition of organic matter experiment, November 9, 1983  | 59          |

| <u>Figure</u> |   | <u>Page</u> |
|---------------|---|-------------|
| 11            | Abundance per core versus distance for each taxon enumerated in the addition of organic matter experiment, November 9, 1983                                       | 64          |
| 12            | Autocorrelation coefficients for densities of all taxa enumerated in the addition of organic matter experiment, November 9, 1983, plotted from 0 - 25 lags        | 66          |
| 13            | Vertical distribution in the sediment of total meiofauna, nematodes, remaining meiofauna and organic carbon in experimental and control areas on November 9, 1983 | 70          |

## LIST OF TABLES

| <u>Table</u> |  | <u>Page</u> |
|--------------|--|-------------|
| 1            | Summary of studies that have investigated the influence of biogenic microtopography on the small scale distribution of meiofauna.        | 21          |
| 2            | Summary of time series analysis results of the meiofaunal distributional study; January 12, 1983.  | 36          |
| 3            | Summary of time series analysis results of the manipulation of sediment microtopographical characteristics experiment; June 12-14, 1983. | 45          |
| 4            | Density data for all taxa enumerated in the manipulation of sediment microtopographical characteristics experiment; June 12-14, 1983.    | 47          |
| 5            | Summary of the time series analysis results of the addition of organic matter experiment; November 7-9, 1983.                            | 57          |
| 6            | Density data for all taxa enumerated in the addition of organic matter experiment; November 7-9, 1983.                                   | 63          |

The Response of a Marine Meiofaunal Assemblage to  
Experimental Manipulations of Sediment Microtopography

Introduction

While ecological studies of marine, soft-substrate, benthic communities have traditionally been descriptive, manipulative experimentation, has been used with increasing frequency in the study of soft-substrate communities (Peterson 1979, Woodin 1978, 1981). The experimental approach is useful because it can produce insights concerning factors important in structuring a community (Connell 1975, Paine 1977). Pielou (1969) pointed out that it is often futile to attempt conclusions about mechanisms underlying a distributional pattern by examining only the observed frequency distribution of the number of individuals per unit area. Bell (1979) states that "only through direct field or laboratory manipulations can we understand the dynamic elements responsible for producing meiofaunal patterns of abundance".

Experimental manipulations in the soft-sediment environment, however, often pose complex procedural problems. Virnstein (1978) and Peterson (1979) have reviewed the problems associated with caging studies in soft-sediment habitats. Disturbances of the flow regime often result in increased sediment deposition in the vicinity of the cage and inadvertant food additions (McCall 1977, Virnstein 1977, Hulberg and Oliver 1980, Woodin 1981). Through field manipulation,

Eckman (1979, 1983) has shown that the alteration of flow patterns by protruding structures can affect the distribution and abundance of meiofaunal-sized organisms by affecting benthic recruitment. Thus, experimental manipulations can often result in a complex alteration of the control situation and affect the distribution and abundance of organisms in ways other than those intended. Peterson (1980) concluded that only a limited number of experimental manipulations are possible in soft-sediment environments. He suggested adding individuals of various infaunal species as possible competitors, space occupiers or structural elements, excluding possible epibenthic predators, or adding food resources.

Recent studies (Bell et al. 1978, Woodin 1978, Reise 1981a,b, Bell and Coen 1982a,b, Bell 1983, Osenga and Coull 1983) have demonstrated the importance of biogenic structures such as plant roots and animal burrows in influencing the distribution and abundance of benthic fauna. Woodin (1978) experimentally demonstrated that the distribution of infauna around a polychaete tube was due to the physical presence of the tube and not to biotic effects or interactions. Thus, it seems reasonable to hypothesize that physically generated substrate structures may also affect the distribution and abundance of benthic fauna. However, little attention has been focused on this question. In fact, Gray (1974) concluded that the physical structure and contours of the sediment surface were unlikely to be of importance to the benthos in soft-substrate habitats.

Recent studies, however, have indicated that sedimentary bedforms may be important in influencing the distribution and abundance of macro- and meiobenthos. Eckman (1979, 1983) attributed the observed distribution and abundance of the small macrobenthos on an intertidal mudflat in Washington to active selection or passive transport to different areas on a rippled sediment surface. Harrison (1977) distinguished two distinct meiofaunal assemblages within a  $0.09 \text{ m}^2$  area, one in the trough and one on the crest of sand ripples. Schafer (1971) commented that at times, relatively large populations of Foraminifera were associated with either ripple crests or troughs in subtidal areas of the Gulf of St. Lawrence. Hogue (1982) noted that on the continental shelf of Oregon, nematode density fluctuations appeared to have the same periodicity as sediment ripples photographed at the site. Hogue and Miller (1981) observed similar periodicities in meiobenthic nematode densities and sediment ripples on an intertidal sandflat in Oregon. The authors hypothesized that sediment ripples affected the distribution of meiobenthic nematodes by affecting the micro-spatial distribution of the nematodes' food source.

Soft-sediment environments in which sediment ripples occur are very common subtidally and intertidally. The formation of ripples by storm waves off the Oregon coast has been observed in water depths as great as 200 m (Komar et al. 1972). Sanders et al. (1962) observed ripples with a 4-5 cm wavelength in Barnstable Harbor, Massachusetts. Bradley and Cooke (1959), Swedmark (1964), Newton (1968), Komar

(1974), Eckman (1979), Hogue (1982), and van Blaricom (1982) also anecdotally mention the presence of sand ripples in various habitats. I have observed many beaches along the Pacific Northwest coast that have sediment ripples. Shepard (1963) has stated that most beaches exhibit one or more of the several types of sediment ripples. However, on most beaches, sediment ripples occur in many orientations and with varying degrees of regularity and the observed pattern is complex (Shepard 1963). The statistical procedures used in this study, time series analysis, allows the separation of patterns in meiofaunal density due to the presence of sediment ripples from patterns due to other causes only in the case of simple, very regularly spaced ripples. Any mechanism for producing the observed distribution of meiofauna, however, could operate in any ripple system, however complex and irregular. A variety of other sedimentary bedforms such as sand ribbons, sand waves, and megaripples may also influence the spatial distribution of benthos in manners analogous to those described in this study for sediment ripples.

The relationship between the small-scale distribution of meiofauna and sediment microtopography in the form of sand ripples and the mechanism(s) by which this relationship occurs is the subject of this study. I used three experimental approaches to investigate the relationship of meiofauna to sediment ripple patterns. In the first, I conducted an experiment to confirm the nematode-ripple relationships documented by Hogue and Miller (1981) and assess the generality of this relationship with respect to all meiofaunal taxa. Second, I

manipulated the sediment ripple spacing to verify the causal link between ripple spacing and meiofaunal distributional patterns. Third, I added organic matter to the ripple system to test the hypothesis of Hogue and Miller (1981) stating that the observed distribution of nematodes was due to the distribution of their presumed food source, organic detritus. All experiments used the same sampling and statistical approach to the investigation of distributional relationships. The sampling method is termed "straw transect sampling", and consists of long series of small, contiguous core samples taken perpendicular to the ripple pattern. Results from straw transects were examined by time series analysis techniques. Specific details of the straw transect technique and statistical methods are presented in separate sections below, followed by detailed methodological sections on each of the experiments.

A short review of the distributional ecology of meiofauna follows.

#### GENERAL ECOLOGY OF MEIOBENTHOS:

The term "meiobenthos" was first used by Mare (1942) and originates from the Greek word, "meion", meaning smaller. This group of animals, now referred to as the meiofauna, is functionally defined as those sediment-dwelling animals which pass through a 0.5 mm sieve but are retained by a 0.045 mm sieve. McIntyre (1969) divided the meiofauna into two groups: temporary forms consisting of the larvae of

the macrofauna which will eventually grow out of the meiofaunal size range; and permanent meiofauna. The latter group consists of members of the Nematoda, Kinorhyncha, Gastrotricha, Tardigrada, Gnathostumulida, Rotifera, Annelida (Archannelida, Oligochaeta, Polychaeta), Arthropoda (Harpacticoida, Mystacocarida, Ostracoda, Halacarida) and Turbellaria, in addition to specialized forms of the taxa Nemertina, Priapulida, Sipunculoida, Bryozoa, Tunicata, Hydrozoa, Gastropoda, Holothuroidea, and Solengastera. Swedmark (1964), McIntyre (1969), Coull (1973), Nicholas (1975), Fenchel (1978), and Coull and Bell (1979) have reviewed the biology and general ecology of these meiofaunal groups.

There is considerable diversity in the range of meiofaunal habitats. Some meiofaunal organisms are interstitial (moving between the sediment particles), others are burrowing (moving through or displacing sediment particles), and still others are epibenthic or phytal (inhabiting the substrate-water interface). This habitat diversity correlates with animal morphology: interstitial forms are small and vermiform to crawl through interstitial lacunae, burrowers are more robust and often have specialized adaptations for burrowing through sediments, and epibenthic/epiphytal forms are robust and specially adapted for crawling and/or swimming at the substrate-water interface. Feeding behavior is diverse among these animals, which include herbivores, carnivores, omnivores and deposit feeders.

While the meiobenthos is taxonomically diverse, nematodes and harpacticoid copepods are usually the two most abundant taxa (but see

Remane 1933, Wieser 1960, Jansson 1968, Hogue 1978). The ubiquity and numerical dominance of nematodes in meiobenthic populations has been repeatedly reported (see reviews by McIntyre 1969, Coull 1973, Coull and Bell 1979, Dye and Furstenburg 1981). Wieser (1960) found that nematodes constituted 89-99% of the total meiofaunal population in Buzzards Bay, Massachusetts. Sikora et al. (1977) found that nematodes constituted 67-98% (annual mean of 89%) of all meiofauna in a South Carolina estuary. Platt and Warwick (1980) concluded that nematodes represented 60-95% of all meiofauna from the littoral zone to the deep sea.

Meiofaunal densities are characteristically high, averaging  $10^6$   $m^{-2}$  worldwide (McIntyre 1969, Coull 1973, Gerlach 1978). However, there is considerable variability across habitats, seasons, latitudes, and water depths (range of  $5.0 \times 10^4$  to  $10.2 \times 10^6$   $m^{-2}$ ; McIntyre 1969). Several studies have supported the generality that average meiofaunal densities are higher in estuaries than in non-estuarine systems (McIntyre 1969, Dye and Furstenburg 1981). Population densities in estuarine habitats are generally highest in fine sediments with high detrital content and lowest in clean sands (Coull and Bell 1979, Dye and Furstenburg 1981). Numbers and biomass generally decrease from the littoral environment to the deep sea (McIntyre 1969, Coull and Bell 1979).

The importance of meiofauna in the benthic ecosystem has been a widely disputed topic. Some authors have suggested that meiobenthic species were consumed primarily by meiobenthic predators and thus not

available as a food resource to higher trophic levels (McIntyre 1969, McIntyre and Murison 1973 and references therein). In contrast, Sibert (1981) and Sikora et al. (1977) found that meiofauna were important constituents in the diets of many macrobenthic and epibenthic predators. Coull and Bell (1979) have noted a correlation between the habitat studied and the functional role ascribed to meiofauna. They concluded that most studies in sandy environments indicated that meiofauna were not food for higher trophic levels, whereas studies conducted in muddy or detrital substrates indicated meiofauna were important as food for higher trophic levels. The authors attributed this observation to the contrasting patterns of vertical distribution of meiofauna in these environments (see below).

Gerlach (1978) attempted to quantitatively evaluate the role of meiofauna in the food web of a sublittoral, silty-sand environment. Estimated average densities of meiofauna in this habitat were  $4 \times 10^6 \text{ m}^{-2}$ ; the standing crop biomass was approximately 0.22 g wet weight  $\text{m}^{-2}$ , which constituted approximately 3% of the total macrofaunal biomass. Meiofauna constituted only 20% of the food needs of the deposit feeding, subsurface macrofauna. However, Gerlach (1978) suggested that meiobenthos may indirectly increase the food resources of these larger forms by stimulating bacterial productivity. Experimental evidence supports this suggestion. For example, Lee et al. (1974) found that when all three components of their experimental system (the polychaete Capitella capitata, meiofauna, and bacteria) were together, total community respiration was three times greater

than the summed total respiration when only two components were present (C. capitata + bacteria, or meiofauna + bacteria). Tenore et al. (1977) corroborated this conclusion with similar experiments on the polychaete Nephtys incisa. Coull (1973) concluded that there were three major ecosystem pathways that include meiofauna: meiofauna as food for the next major benthic trophic level, the macrofauna; as food for nektonic forms; and as contributors to nutrient regeneration.

#### DISTRIBUTION OF MEIOFAUNA:

##### Factors Influencing the Large Scale Distribution of Meiofauna:

McIntyre (1969) concluded that the main factors controlling the large-scale distribution of meiofauna were temperature, salinity, and sediment grain size. Salinity fluctuations have generally been assumed to be the major limiting factor in the distribution of estuarine benthos (Levinton 1982 and references therein). Although the salinity of the overlying water and that of the interstitial water are not necessarily the same (Sanders et al. 1962), areas with less saline water will, in general, have less saline interstitial water and areas of higher salinity will have a higher interstitial salinity. Population density, species composition, and species diversity are all influenced by salinity. In general, meiofaunal densities and species diversity decrease as salinity decreases and in most cases a change in the faunal composition is associated with the diversity decrease (McIntyre 1969). Capstick (1959) observed significant differences in the species composition of the nematode fauna between the middle and

the less saline upper reaches of the River Blyth. Coull et al. (1979) observed that the harpacticoid copepod Nitocra lacustris was consistently associated with low salinity waters. The influence of salinity on the distribution of meiofauna is also demonstrated by vertical distribution data taken after a period of prolonged rain. Bush (1966) sampled the meiofauna of a sandflat after several hours of constant rain and found very few organisms in the top 3.5 cm of sediment; in the two samples taken after the rain, 99% and 69% of the meiofauna were found in the 8-14 cm depth interval, compared with 2% and 41% in the same depth interval after the next tidal cycle.

There is a considerable body of literature dealing with the influence of sediment grain size on the distribution of meiofauna (Coull 1970, Conrad 1976, and reviews by McIntyre 1969, Fenchel 1978). Wieser (1959), concluded from his study of the nematodes of Puget Sound that grain size was the major determinant of nematode distribution. The amount of pore space, determined by the sediment grain size, imposes a mechanical restriction on the movement of meiofauna. Swedmark (1964) postulated an upper size limit of 2-3 mm for true interstitial fauna. Wieser (1959) suggested that a mean grain size of 200  $\mu\text{m}$  served as the "barrier" which confined the true interstitial meiofauna to sediments of greater median grain size and the burrowing meiofauna to sediments of lesser mean grain size. However, Hulings and Gray (1976) found true interstitial fauna in habitats in which the mean grain size ranged from 125-500  $\mu\text{m}$ . In general, sediments in which the median particle diameter is below

125  $\mu\text{m}$  tend to be dominated by burrowing meiofauna (Coull and Bell 1979). Interstitial taxa (e.g. Tardigrada) are excluded from these substrates in which the interstitial lacunae are closed or severely restricted in size. In those taxa which have both interstitial and burrowing representatives (e.g. Nematoda), morphology differs between species characteristic of each habitat.

Additional properties of the sediment grain size distribution such as the degree of sorting and the degree of grain angularity have also been found to affect the distribution of meiofauna (Conrad 1976). Ward (1975) observed that the relative and absolute abundances of nematodes was affected by the degree of sediment uniformity, as measured by the mean grain size, the degree of sorting and the percentage of silt/clay.

Grain size also affects the distribution of meiofauna by indirectly influencing the water content, and food and oxygen availability (McIntyre 1969). In general, water content, and food and oxygen availability form horizontal and vertical gradients; species can be restricted to certain tidal levels or sediment depths by their preference for particular environmental conditions. Coull et al. (1979) attributed the zonation patterns of many meiobenthic copepods in a South Carolina salt marsh to the degree of tidal exposure which controlled the sediment water content. The inverse relationship between grain size and sediment organic content has been widely documented (Newell 1965, Levinton 1982 and references therein). Sharma et al. (1978) concluded from sampling the nematode fauna from

three different sites with similar tidal levels on the Northern Pacific coast that the nematode faunal composition was determined by the quantity of organic matter. The effect of vertical gradients in water content and food and oxygen availability on the distribution of meiofauna will be addressed below.

Biological interactions also can affect the large-scale distribution and abundance of meiofauna (see reviews by McIntyre 1969, Coull and Bell 1979). Oakden (1980) reported that phoxocephalid amphipods from shallow sandy bottoms off the central California coast consumed nematodes and other meiofaunal-sized prey. Oliver et al. (1982) found that phoxocephalid amphipods were significantly more abundant in shallow, wave disturbed areas of Monterey Bay than in deeper regions. Hogue (1982) hypothesized that predation by amphipods was partially responsible for the differences in nematode faunal composition observed between shallow and deep water stations off the Oregon coast. Coull et al. (1979) attributed some of the differences observed in the zonation of meiobenthic copepods to the presence or absence of epifaunal predators whose distribution was influenced by tidal level. Teal (1962) found that crabs of the genus Uca, crush nematodes in the process of feeding. In some habitats these crabs are often sufficiently abundant to turn over large areas of the surficial sediments between each tidal cycle (McIntyre 1968), and they must have a marked effect on the distribution and abundance of meiofauna.

The large scale distribution of meiofauna appears to be also influenced by physical factors. Hogue (1982) found differences in the

nematode fauna in shallow and deep water stations off the Oregon coast. The changes in the faunal assemblages, reflected in the relative size and cuticular structure of nematodes, corresponded to patterns of sediment disturbance. The fauna characteristic of shallow water was dominated by small nematode species ( $\leq 1.1$  mm) possessing a highly modified cuticle with spines and annulations, while the deep water fauna was dominated by large nematodes ( $> 1.1$  mm) with smooth cuticles. Mean grain size, temperature, and the percentage of silt-clay did not vary systematically with depth. However, the division between the two groups of stations corresponded to the greatest depth at which sediments were disturbed by passing waves during much of the year. Thus, sediment disturbance was implicated as the determinant of this pattern. Hogue (1982) hypothesized that the small size and modified cuticle of the shallow water fauna probably enabled the nematodes to resist damage in this wave-disturbed habitat (Swedmark 1964) or to maintain their position in the face of sediment disturbance (Ward 1975).

#### Vertical Distribution of Meiofauna:

Meiofauna are generally limited to the upper few centimeters of substrate (see reviews by McIntyre 1969, Coull and Bell 1979, Dye and Furstenburg 1981). In estuarine detrital sediments located in South Carolina, 94% of all meiofauna were found in the upper 1 cm of sediment (Coull and Bell 1979). Sharma and Webster (1983) found the highest nematode density in the upper 2 cm of 6 cm cores on two

beaches near Vancouver, Canada. Other studies (Rees 1940, Perkins 1958, Wieser and Kanwisher 1961, Teal and Wieser 1966, Barnett 1968, Tietjen 1969, Platt 1977) have corroborated this result. Generally, the vertical distribution of meiofauna extends deeper in sandy sediments (see reviews by McIntyre 1969, Coull and Bell 1979, Dye and Furstenburg 1981). On a sandy beach in Florida, Bush (1966) found that though the meiofauna were concentrated in the upper 7-10 cm at the low-water to mid-beach they but were present at lesser densities to a depth of 46 cm.

Grain size may affect the vertical distribution of meiofauna indirectly by influencing sediment water content, and food and oxygen availability (McIntyre 1969). Fenchel et al. (1967) found that the volume of pore water was more important than either temperature or salinity in determining the meiofaunal distribution and abundance on a sand beach in the Oresund. Jansson (1968) found that among the meiofaunal taxa present at his study site, harpacticoid copepods were most sensitive to decreases in the amount of interstitial pore-water, while oligochaetes were not affected by similar decreases.

The position of the reduction-oxidation potential discontinuity (RPD) is also strongly influenced by sediment grain size and is important in controlling the vertical distribution of meiofauna. Wieser and Kanwisher (1961) concluded that sediment oxygen concentrations were the major determinant of the vertical and horizontal distribution of meiofauna in a Georgia salt marsh. This conclusion has been substantiated by McIntyre (1969) and Tietjen

(1969). Fenchel and Riedl (1970) and Boaden and Platt (1971) concluded that two distinct groups of interstitial meiofauna inhabit sandy marine sediments: one inhabits the surficial, oxic sediments, and the other inhabits the deeper, reducing sediments and is known as the thiebios. The boundary between these two layers is the RPD. The thiebios is dominated by gnathostomulids, while platyhelminthes, nematodes, annelids and gastrotrichs are also common (Fenchel and Riedl 1970). In contrast, the fauna of the surficial sediments is dominated by nematodes and harpacticoid copepods, while turbellarians, annelids, ostracods, and tanaids are also present in varying abundances (Fenchel and Riedl 1970). Reise (1981a,b) and Reise and Ax (1979) have disputed the existence of a true community associated with the reducing environment and believe that these organisms are merely an extension of the surface oxic biota that are associated with oxygenated microenvironments such as animal burrow walls. Powell et al. (1983) argued that the thiebios does exist, but redefined it as organisms with an ecological requirement for sulfide. Regardless of this current debate, the impact of sediment oxygen concentrations on the vertical distribution of meiofauna is clearly substantial.

Vertical migrations of meiofauna in the sediment have been noted in response to temperature, desiccation, rain, light, and tidal movement (Perkins 1958, Gray 1965, 1966, Dye and Furstenburg 1977, McLachlan et al. 1977). Gray (1965) showed that the archiannelid, Protodrilus symbioticus, normally found at the sediment surface because of its preference for areas with high oxygen tensions, can be

driven deeper into the sediment by drying of the surface sand. Renaud-Debyser (1963) documented changes in the vertical distribution of meiofauna in response to seasonal changes in temperature. Bush (1966) noted downward vertical migrations in response to a heavy rain on a sandy beach in Florida. Boaden (1968) observed vertical migrations in response to tidal fluctuations; a downward migration of meiofauna occurred on the outgoing tide and an upward migration occurred on the incoming tide.

Most studies have indicated that nematodes have greater depth penetration than other meiofaunal taxa. Smidt (1951) found that in sandy beaches of the Danish Waddensea, 96% of the harpacticoid copepods and 88% of the ostracods were found in the upper 2 cm of sand and neither occurred below 4 cm; but nematodes were found to depths of 6 cm, although 83% were present in the upper 2 cm. Perkins (1958) described a situation in which copepods and ostracods were confined to the top 4 mm of a fine sand deposit, but nematodes were found to 7 cm. Chandler and Fleegeer (1983) found that >95% of the harpacticoid copepods were restricted to the upper 1 cm of a muddy estuarine sediment but the center of the nematode depth distribution was 3 cm. This generalization has also been supported by other studies (Moore 1931, Mare 1942, McIntyre 1961, Fenchel and Jansson 1966, Dye and Furstenburg 1981).

The fine scale vertical distribution of meiofaunal species appears to be temporally consistent. Joint et al. (1982) observed that meiobenthic copepod species always maintained the same vertical

distribution with respect to one another, even during movements in response to tidal fluctuations. Hogue (1982) found that nematodes retained the same relative vertical position with respect to each other from January through May, even though the center of distribution for each species was deeper within the sediment during January than in May. Sharma and Webster (1983) found no significant difference in the relative vertical distribution of the nematode fauna during a one year study of two intertidal habitats near Vancouver, Canada.

#### Factors Influencing the Small-Scale Distribution of Meiofauna:

Meiofauna exhibit patchy distributions, even in sediments which appear homogenous (Gray and Rieger 1971, Hogue 1978, and see reviews by Coull 1973, Coull and Bell 1979). Many processes potentially can generate small-scale aggregations of meiofauna. Gray and Johnson (1970), Giere (1975), Andrews and Nichols (1976), Hummon et al. (1976), and Lee et al. (1977) believed that the patchy distribution of meiofauna was due to the patchy distribution of their food. Gerlach (1977) demonstrated the attraction of nematodes to scattered dead and dying organisms on a Bermuda beach. Bush (1966) has noted turbellarian migration toward carrion on a Florida beach. Lee et al. (1977) observed the selective recruitment of nematodes at patches of algal aggregates in the sediment. Fenchel (1970) observed a patchy distribution of ciliates around decaying material that showed high bacterial counts. Habitat preference experiments with marine meiofauna indicated that some forms will select sands having an

organic coating, usually bacterial in origin (Gray 1966, 1967a, Gray and Johnson 1970). Many meiofaunal species can distinguish between sands containing different species of bacteria and are attracted to and inhabit sands where the preferred bacteria dominate the microbial assemblage (Gray 1966, 1967a,b, 1968, Gray and Johnson 1970). Gray (1966) found that the bacterial assemblage was responsible for the observed field distribution of the archiannelid, Protodrilus symbioticus.

Reproductive processes have also been cited as a potential cause of small-scale aggregation in meiofauna (Heip 1975, Coull and Bell 1979). Most meiofauna lack a larval dispersal phase (Swedmark 1964, McIntyre 1969, Coull and Bell 1979), so reproduction could result in an aggregations of juveniles. Heip and Engels (1977) noted gregariousness in adult harpacticoid copepods; male copepods and non-gravid female copepods occurred together, whereas gravid females were randomly distributed.

Competition and predation may also affect the small-scale distribution of meiofauna. Jansson (1968) suggested that competition for space could best explain the relative vertical distribution of oligochaetes and turbellarians on a Swedish beach. Joint et al. (1982) suggested that the isolated, fine-scale, vertical stratification of two nematode species with identical feeding structures was due to competition for a food resource. Woodin (1976) and Bell (1979) have suggested that interactions between juvenile macrofauna and meiofauna may influence the abundance of both groups.

Bell and Coull (1979) demonstrated that experimental decreases in density of juveniles of the polychaete Streblospio benedicti were associated with density increases of permanent meiofauna. In control areas, S. benedicti juveniles increased while permanent meiofauna decreased. Boaden and Erwin (1971) and Thistle (1979) have also attributed observed small-scale aggregation of harpacticoid copepods to biotic interactions.

#### Association of Meiofauna with Biogenic Structures:

Meiofaunal association with biogenic substrate structures (e.g. plant roots, macrofauna burrows and tubes) may also affect the small-scale distribution of meiofauna. In general, meiofaunal association with biogenic structures results in increased meiofaunal density by the provision of favorable microhabitats associated with the biogenic structure. Table 1 summarizes those studies which have focused on investigating relationships between meiofaunal distributional patterns and biogenic structures. Explanations for meiofaunal aggregations around biogenic structures include 1) food accumulation sites (Lee et al. 1977, Bell et al. 1978, Osenga and Coull 1983), 2) enhanced microbial populations associated with structure due to altered chemical reactions or diffusion gradients (Myers 1977, Aller and Yingst 1978, Aller 1980, Reise 1981b), 3) oxic microhabitats (Teal and Wieser 1966, Osenga and Coull 1983, Reise 1981a), 4) reduced physical stress (Bell and Coen 1982b), and 5) increased habitat complexity (Bell and Coen 1982b). Biogenic

structures also may provide spatial refugia from biological or physical disturbance and/or predation (Lee et al. 1977, Woodin 1978, Thistle 1979, Eckman et al. 1981).

Table 1: Summary of studies that have investigated the influence of biogenic microtopography on the small scale distribution of meiofauna.

| Biogenic Structure  | Relationship with Meiofauna  | Hypothesized Cause  | Habitat                             | Reference             |
|---|--|---|-------------------------------------|-----------------------|
| <b>Vegetational:</b>  |  |   |                                     |                       |
| <i>Spartina</i> roots   | Increased nematode abundance in root area  | Creation of oxygenated micro-environment  | Ga. salt marsh                      | Teal and Wiener 1966  |
| "   | No consistent relationship between root density and total meiofaunal abundance   | Roots impose limits on the burrowing abilities of meiofauna   | High Ga. salt marsh                 | Bell et al. 1978      |
| "   | Positive correlation between live root density and nematode abundance  | Creation of oxygenated micro-environment or increased food supply from microbial growth stimulated by root exudates   | Low Ga. salt marsh                  | Osenga and Cault 1983 |
| <b>Faunal:</b>  |  |   |                                     |                       |
| <i>Abarenicola marina</i><br><i>Nereis virens</i><br>burrows      | Positive association between burrow walls and gnathostomulids  | Creation of oxygenated micro-environment  | North Sea tidal flats               | Reine 1981a           |
| <i>Uca pugnax</i><br>burrows                                      | Positive association of nematodes with burrows   | Increase in fecal pellets and associated microbial activity around burrows  | High Ga. salt marsh                 | Bell et al. 1978      |
| "   | Negative association of harpacticoid copepods with burrows   | Sediment reworking by <i>Uca</i>  | "                                   | "                     |
| <i>Manayunkia aestuarina</i><br>tubes                             | Initial increase and subsequent decrease in density of the nematode <i>Spirina</i> sp. and the copepod <i>Stenhalia bifida</i> as the volume of tube density increased | Increase was manipulation artifact<br>Decrease due to interference from feeding activities of <i>Manayunkia</i> or from limits imposed on copepod burrowing abilities | S.C. salt marsh                     | Bell 1983             |
| "   | No relationship between tube density and other meiofauna.  | None given  | "                                   | "                     |
| <i>Diopatra cuprea</i><br>tube caps                               | Physical presence of tube resulted in increased density of macro- and meiofaunal sized fauna   | Creation of refuge from disturbance by foraging macrofauna  | Vn. mudflat                         | Woodin 1978           |
| "   | Higher densities of total meiofauna on tube caps than in equivalent volumes of sediment  | Increased water exchange provided greater nutrient and oxygen renewal   | Fla. estuary                        | Bell and Coen 1982a   |
| "   | Presence of algae on tube caps resulted in increased abundance of copepods, ostracods, and polychaetes   | Creation of additional micro-habitats and/or amelioration of habitat physical stress  | Fla. estuary                        | Bell and Coen 1982b   |
| "   | No relationship between tube density and meiofaunal abundance  | Absence of trend believed to be due to limited range of tube densities examined   | "                                   | "                     |
| <i>Chaetys laticostellus</i><br><i>Streblospio</i> sp.<br>burrows | Increased abundance of harpacticoid copepods when tubes present  | Creation of refuge from disturbance and/or predation  | San Diego Trough<br>Depth of 1220 m | Thistle 1979          |

### Study Area

The study area was located in a small, sheltered embayment in the Yaquina Bay estuary (Fig. 1). It is immediately adjacent to the Oregon State University Marine Science Center, Newport, Oregon ( $44^{\circ} 37.5' N$ ,  $124^{\circ} 02.6' W$ ). The tidal regime is characterized by two high tides and two low tides of unequal duration and amplitude in a 24.8 hr period. At the study site the estuary is well mixed most of the year. The study site is an intertidal sand flat (+1.0 MLLW) with moderately well sorted ( $\sigma=0.27$ ), fine to medium sand (sensu Shepard 1954). Median grain sizes range from 2.18 to 2.40 $\phi$  (Kulm and Bryne 1966). Calcium carbonate constitutes less than 1% of the sediment by weight at the site (Kulm and Bryne 1966).

Figure 1: Location of study area in Yaquina Bay estuary, Newport, Oregon.

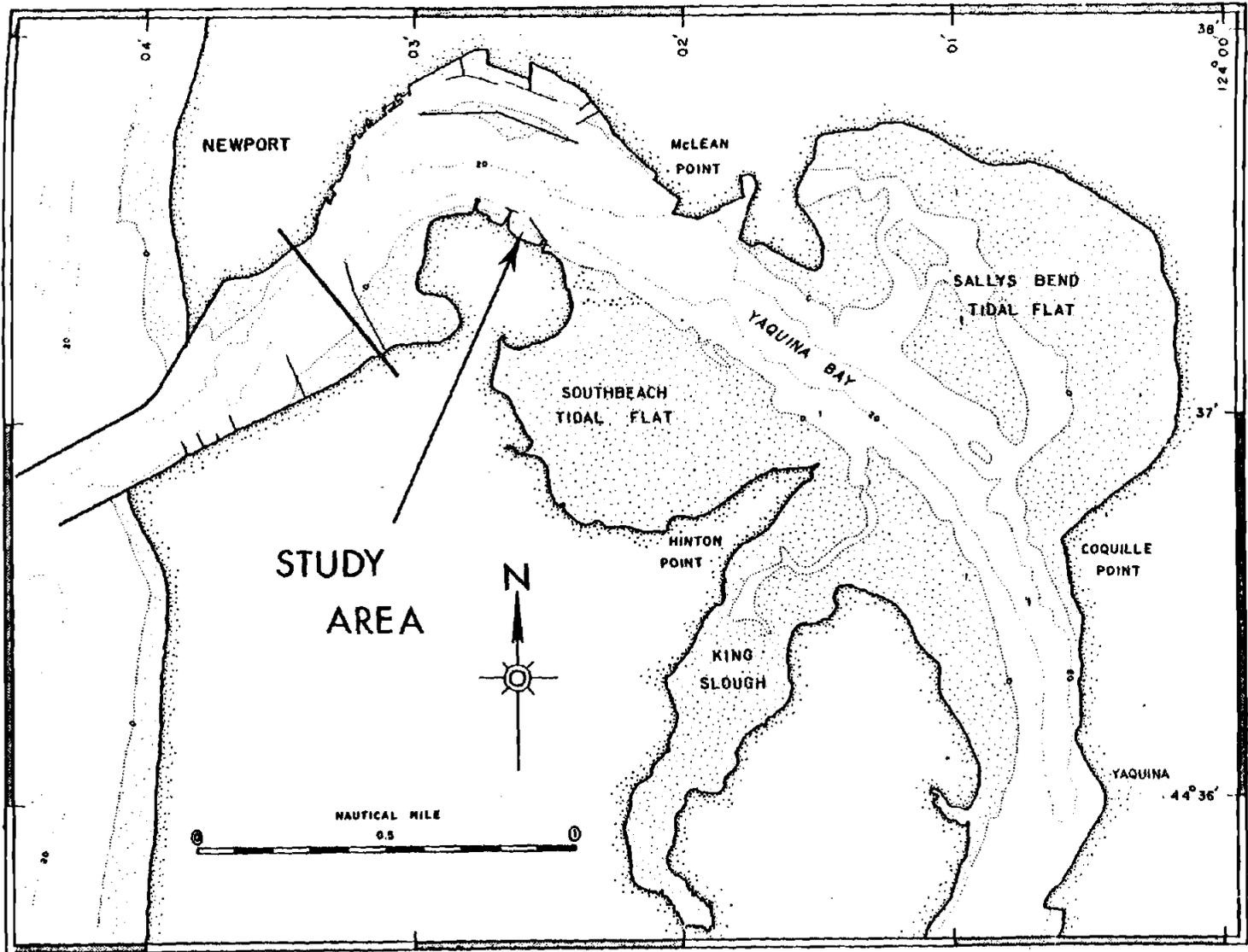


Figure 1

## Experimental Design

### SAMPLE COLLECTION AND TREATMENT:

Transects were created by inserting a series of plastic soda straws, (6 mm internal diameter) 4 cm vertically into the sediment to obtain cores. Transects were oriented perpendicular to the sediment ripples. Transect length varied between experiments. Core samples, sand and meiofauna, were preserved in 10% formalin and stained with rose bengal immediately following collection. After sampling, photographs of the transects were taken and the location of ripple crests and troughs and the approximate height of each crest were mapped. In the laboratory, samples were processed by a technique developed by Feller (1980). Samples were placed in a 500 ml beaker and sediments were suspended with a jet of water. The suspension was allowed to settle for 3-5 s and the supernatant decanted through a 38.5  $\mu\text{m}$  mesh sieve. This procedure was repeated three times for each sample. All of the material collected on the sieve was sorted under a dissecting microscope (22x) to the major taxon level. This procedure is known to work well for the extraction of meiofauna from sediment samples in sandy habitats (Eckman 1979, Feller 1980). Periodic checks of the tailings indicated an extraction efficiency of 86 to 100%.

Straw transects for analyses of organic matter were taken concurrently with meiofaunal samples in the addition of organic matter experiment. These transects were taken immediately adjacent ( $\leq 1$  cm)

and parallel to the faunal transects. Upon collection the sample was capped and stored at 10°C until analysis. Preceding analysis, samples were dried to a constant weight at 60°C for 3 hrs, powdered with a mortar and pestle, and redried (Byers et al. 1978). A quantitative estimate of the organic carbon content was obtained by measuring the percent carbon present with a Perkin-Elmer CHN Analyzer. As the number of possible analyses was limited, analyses were conducted primarily on samples from the experimental transect.

#### STATISTICAL ANALYSIS:

The techniques of time series analysis were used to detect periodicities in the data. In this, as in many ecological applications of time series analysis, space rather than time is the independent variable. References for the calculations employed and descriptions of these procedures can be found in Jenkins and Watts (1968), Platt and Denman (1975), and Chatfield (1980). The raw data were log-transformed (to better meet the assumption of Normality), filtered using a three sample running mean to emphasize variations in abundance at scales greater than 2 cm, and then detrended (to better meet the assumption of stationarity). The detrending procedure involved subtracting the value predicted from a linear regression of counts on position from the actual filtered value.

Autocorrelation coefficients were computed for lags  $k=1,2,\dots,N/4$ , where  $N$  is equal to the number of samples, and were

calculated for all meiofaunal taxa or groupings enumerated, for sediment ripple height, and for all organic carbon values available. This information was presented in autocorrelograms, plots of autocorrelation coefficients versus lag number. There is no consensus as to what constitutes a statistically significant value of an autocorrelation coefficient. If a time series of N observations is completely random, 19 of 20 autocorrelation coefficients can be expected to lie between  $\pm 1.96 N^{-1/2}$ . Thus individual values outside this interval were accepted as significantly different from 0.0 ( $\alpha=0.05$ ). Power spectra were estimated using the Fourier cosine transform of the autocorrelation coefficient weighted with a Bartlett lag window, and smoothed with a bandwidth of either 0.0833 cycles  $\text{cm}^{-1}$  (data from January 1983) or 0.1000 cycles  $\text{cm}^{-1}$  (all other experiments)(see Jenkins and Watts 1968 for details).

#### INDIVIDUAL EXPERIMENTAL STUDIES:

##### Confirmation of Meiofaunal Distributional Patterns:

On January 12, 1983, one series of 300 meiofaunal samples was collected at low tide from the study site. Although a 300 core transect was sampled, 200 samples were determined to be adequate for the elucidation of a pattern after inspection of the data. Collection and sample treatment procedures followed those outlined under Sample Collection and Treatment.

### Manipulation of Sediment Microtopographical Characteristics:

A wooden wave box was constructed for installation on the beach at the study site so that sediment microtopography could be manipulated. The box measured 3.0 m in length, 1.5 m in width, and 1.0 m in height and was open on the top and bottom (Fig. 2). Drainage holes (Fig. 2) minimized eddies and turbulence within the box which were found to disrupt the ripple pattern. The box was sunk to approximately 30 cm in the sand, and weighted to prevent the box from floating away during high tide. The box was situated with the open end higher intertidally.

It was observed by Hogue and Miller (1981), and confirmed by me, that sediment at the study site is in motion only when the water depth is 30 cm or less. Thus ripple manipulation was begun when the water depth in the box was sufficient to move the sediment with the manipulating device, a movable hinged panel of wood (Fig. 2), and terminated when the water depth exceeded the box height. This best mimicked the manner in which beach ripples at the site were naturally created and modified. Upon termination of ripple manipulation, a fourth side (Fig. 2) was added to the box to prevent ripple disruption during the active portions of the following tidal cycle. The wave box consistently produced ripples of approximately 100 mm wavelength.

The habitat manipulation experiment was conducted on June 12-14, 1983. The wave box was positioned on low tide the morning of June 12, and manipulation of the ripple pattern was done on the subsequent

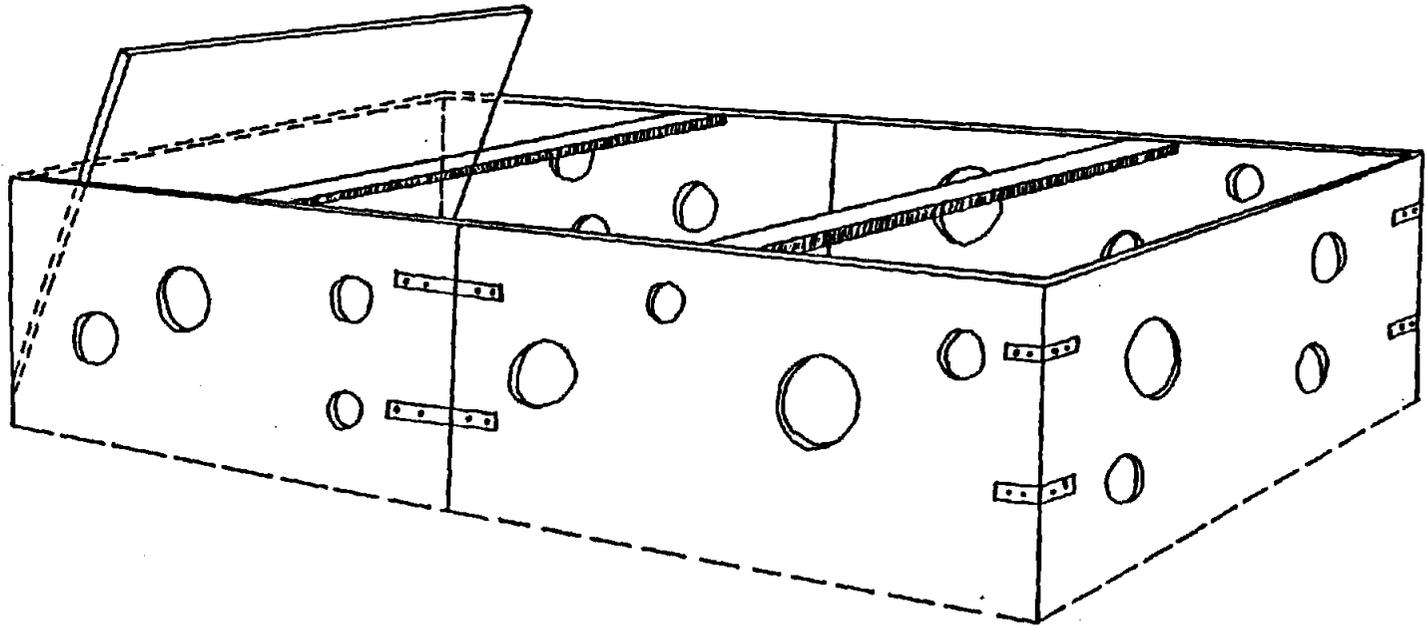


Figure 2: In situ wave box used in the manipulation of sediment microtopographical characteristics experiment (not to scale).

incoming tide. After one complete tidal cycle, sampling was conducted by the straw transect method. In this experiment two transects, each consisting of 180 samples, were taken for meiofaunal analyses. The experimental transect was taken within the box and the control transect was taken outside of the box, approximately 1.0 m away. Time constraints precluded sampling all transects during one low tide; consequently the series within the box was taken at low tide on June 13 and the control series was taken at low tide on June 14. During this time, the wave box was left in position. Transects within the wave box were positioned in the center of the box area to preclude possible edge effects.

Addition of Organic Matter to the Ripple System:

As another approach, organic material was added to the sediment at regular intervals. The spacing was unrelated to the spatial pattern of the ripples. Specifically, I wanted to determine whether the meiofaunal distributional patterns were due to the micro-spatial distribution of organic material or due to some property of the sediment ripples themselves. In the experimental treatment, freshly collected organic material, consisting primarily of fecal pellets, was deposited in furrows every 11 cm to a depth of 2 cm. Organic matter was added by first using a 15 cm, V-shaped, metal scoop to lift out a wedge of sediment 2 cm in height. An assistant then added organic matter to fill up approximately one-half of the newly created trough. The wedge of sediment was then replaced and the surface smoothed to

simulate previous ripple contours. This procedure was repeated, forming a swath 1.5 m in length and 15 cm in width with organic additions every 11 cm.

To test for possible artifacts resulting from this manipulation, an adjacent transect was created in an identical manner with the exception that no organic matter was added to the troughs before replacement of the sediment wedge. This was the experimental-control treatment.

A third area immediately adjacent to other two transects was used as a control. The combined width of the three treatments was no greater than 1.0 m to minimize the chance of sampling different habitats. Thus, the experiment consisted of three treatments: experimental, experimental-control, and control. Two days after the establishment of the treatments, two transects, each consisting of 200 cores, were sampled within each treatment, one for meiofaunal abundance analyses and one for organic carbon analyses. The experiment was conducted from November 7-9, 1983. Sample collection and treatment followed procedures outlined previously.

The vertical distribution of meiofauna and organic matter in the experimental treatment was also investigated. Four short sample series, each 5 samples in length, were collected from an area with and without organic matter additions. Cores were inserted 4 cm into the face of a trench excavated perpendicular to the horizontal transect, with the next core being placed directly underneath the previous core,

until a five core series had been collected.

The organic matter added to the ripple system at the study site consisted of fecal pellets collected from the surface of the sand on the day of the experiment. Fecal pellets were the most abundant particulate material accumulating in the ripple troughs at the study site (personal observation) and were produced by the ghost shrimp, Callianassa californiensis.

## Results

### Confirmation of Meiofaunal Distributional Patterns:

Regularly spaced, asymmetrical sand ripples of approximately 1 cm height were present over the entire study site on Jan. 12, 1983. No other irregularities were observed in the sediment surface. The mean wavelength of the sediment ripples on this date was 5.3 cm ( $s = 0.43$  cm). The autocorrelation of ripple heights along the sample transect clearly showed this periodicity: coefficients peaked at multiples of 9 lags (Fig. 3, Table 2), corresponding to a horizontal distance of 5.4 cm. The power spectrum for the ripple heights peaked at a frequency of  $0.187 \text{ cycles cm}^{-1}$  (Fig. 3), indicating a significant proportion of the total variance in the data was due to periodic fluctuations occurring at a 5.3 cm wavelength.

Enumerated meiofaunal taxa included nematodes, harpacticoid copepods, and tardigrades. Gastrotrichs and copepod nauplii were present in the samples, but were not counted because of their low densities. Total meiofaunal densities, therefore, are the sum of nematodes, harpacticoid copepods and tardigrades. Nematodes were the numerically dominant taxon in all samples. Mean densities per core were low for all taxa: 6.1, 4.9 and 2.1 for nematodes, tardigrades and harpacticoid copepods, respectively, corresponding to densities per  $10 \text{ cm}^2$  of 217.1, 173.9, and 76.1.

Figure 3: Autocorrelation coefficients for sediment ripple heights on January 12, 1983, plotted from 0 - 50 lags. Inset shows corresponding power spectrum. Note the clear regularity of ripple spatial pattern.

Figure 3

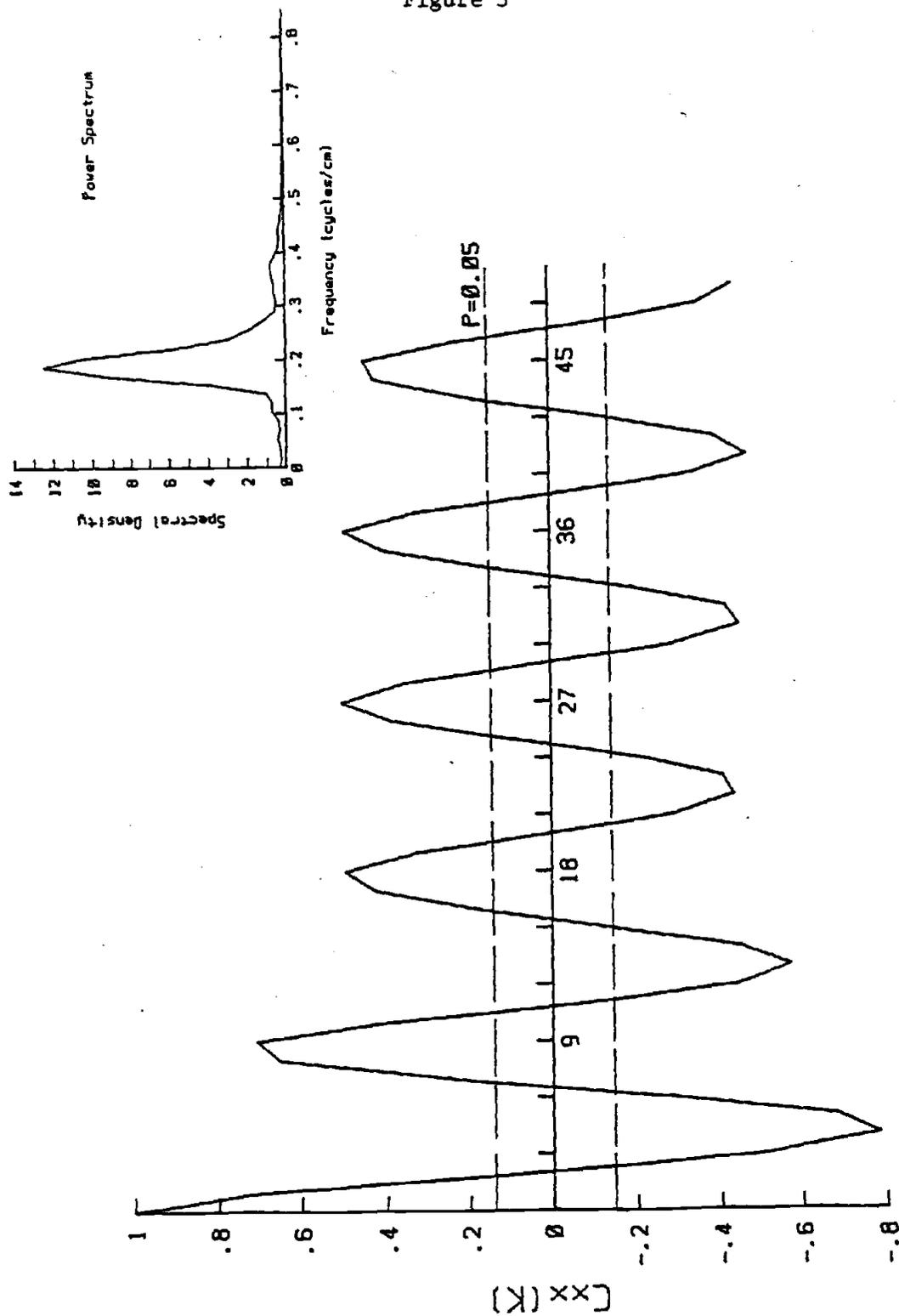


Table 2: Summary of time series analysis results of the meiofaunal distributional study; January 12, 1983.

| Variable              | Information from autocorrelogram                                | Dominant frequencies indicated by the power spectrum | Dominant periodicity of data |
|-----------------------|---|--|------------------------------|
| Sediment ripples      | Local maxima at regular 9 lag multiples; 9*, 18*, 27*, 36*, 45* | 0.187 cycles/cm                                      | 5.3 - 5.4 cm                 |
| Total meiofauna       | Local maxima at 9*, 18*, 27, 37*, and 46* lags                  | 0.170 cycles/cm<br>0.374 cycles/cm                   | 5.4 - 5.8 cm                 |
| Nematodes             | Local maxima at 10*, 15, 21, 31, and 44 lags.                   | 0.153 cycles/cm<br>0.323 cycles/cm                   | 6.0 - 6.5 cm                 |
| Tardigrades           | Local maxima at 9*, 17*, 27, 30, and 35 lags.                   | 0.119 cycles/cm<br>0.187 cycles/cm                   | 5.3 - 5.4 cm                 |
| Harpacticoid Copepods | Local maxima at 9*, 18*, 27*, 36*, and 45* lags.                | 0.187 cycles/cm                                      | 5.3 - 5.4 cm                 |

\*Indicates significance at  $P \leq 0.05$

A total of 23 cycles (ripple crest to ripple crest) were sampled along the transect. All meiofaunal taxa showed distinct density periodicities (Fig. 4, Table 2). Three-to four-fold differences in density were observed between areas of high and low densities for all taxa (Fig. 4). Areas of peak density did not occur exactly in ripple troughs or crests for any taxon; peaks in taxon density tended to be offset 1-2 cores (0.6-1.2 cm) toward the leading side of ripple crests (Fig. 4). The spacing between density peaks was not always exact, varying by approximately 2 cores (1.2 cm).

The observed density periodicities of all meiofaunal taxa present was related to sediment ripple spacing. Density fluctuations in total meiofauna, and harpacticoid copepods were very close to ripple height periodicities, all showing strong periodicity of approximately 5.4 cm wavelength (Fig. 5, Table 2). The major features of the autocorrelograms for these taxa closely match the major features of the ripple height correlogram (Table 2, compare Fig. 3 and Fig. 5). Periodicity in nematode and tardigrade densities, although present, was not as strong and regular as for other taxa. In addition, nematode density periodicity also was less strongly related to ripple height periodicity, being approximately 6.0 cm in wavelength (Fig. 5, Table 2). Thus, on January 12, 1983, sediment ripples appeared to be the dominant influence on the micro-spatial distribution of all meiofaunal taxa.

Figure 4: Abundance per core versus distance for each taxon enumerated on January 12, 1983. Ten cores = 6 cm.

Figure 4

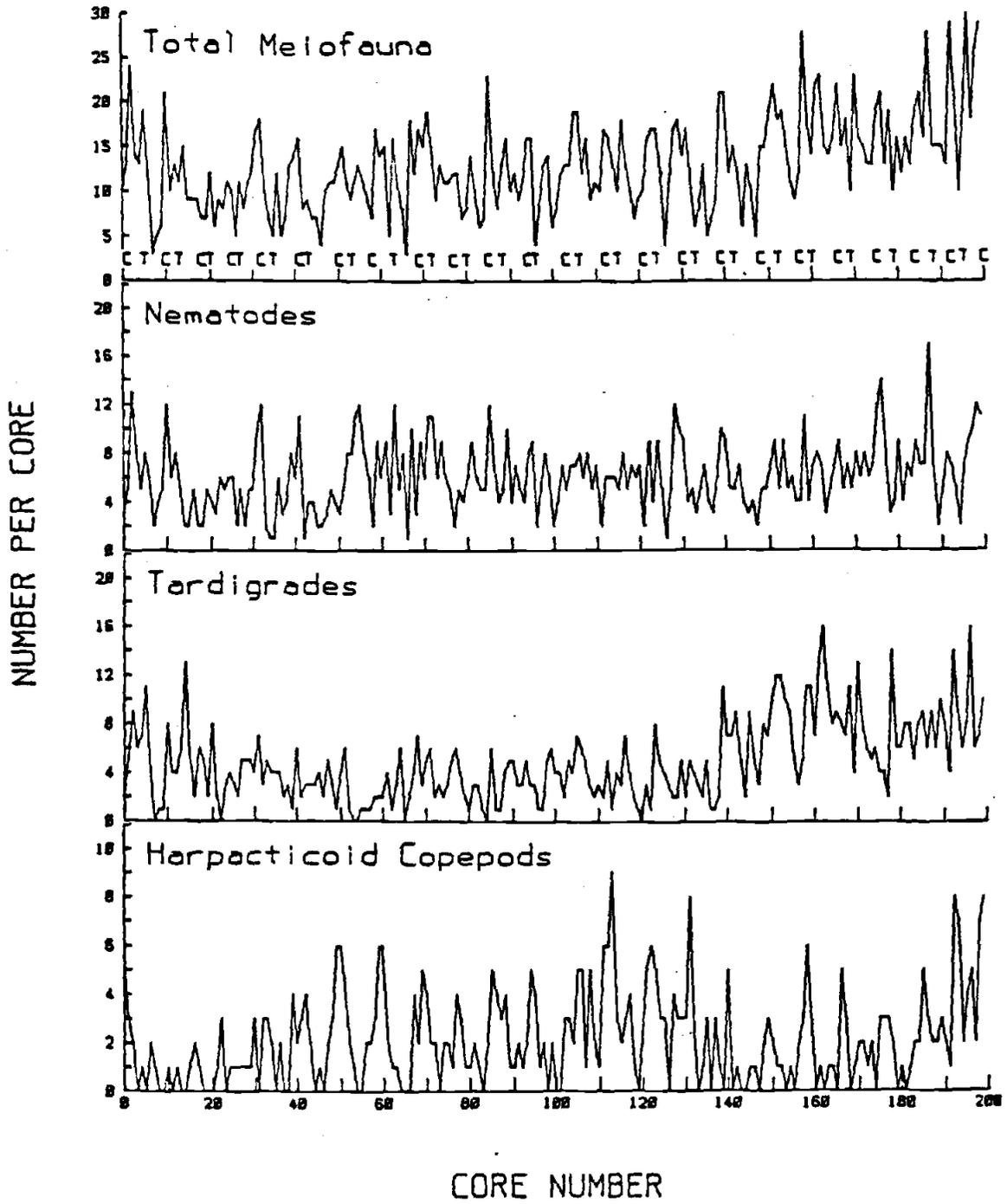
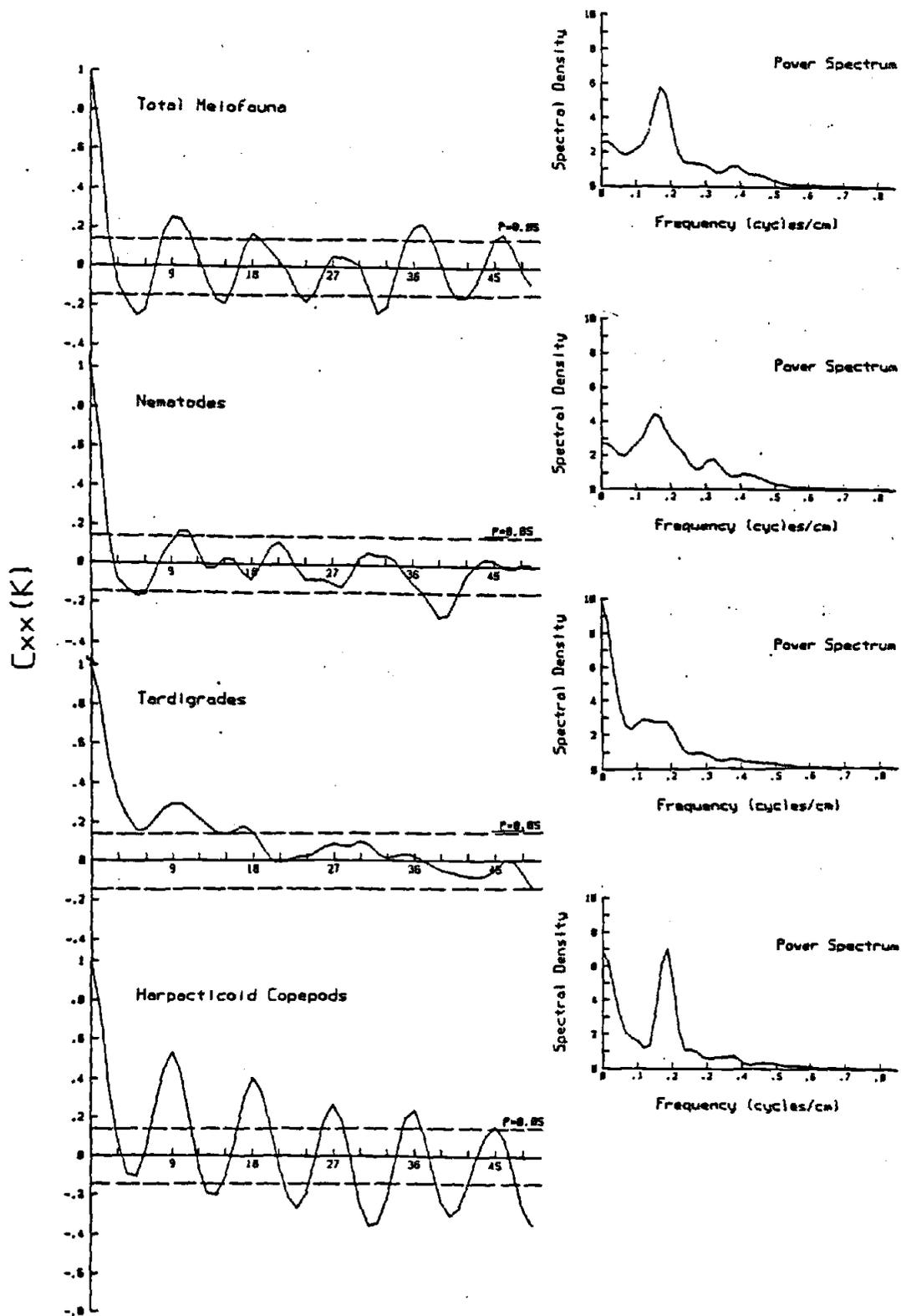


Figure 5: Autocorrelation coefficients for densities of all taxa enumerated on January 12, 1983, plotted from 0 - 50 lags. Insets show corresponding power spectra.

Figure 5



### Manipulation of Sediment Microtopographical Characteristics:

On June 13-14, 1983, poorly defined, but regularly spaced, asymmetrical ripples, of approximately 1 cm height, covered only a small portion of the study site. Short term variation in both ripple wavelength and orientation was common in this section of the beach (direct observations). Much of the sediment surface was covered with burrows of the ghost shrimp, Callinassa californiensis, which were more active or abundant at the study site than in previous months (personal observations).

The wave box created sediment ripples of approximately 10.0 cm wavelength in the experimental enclosure. Sediment ripple wavelengths in the experimental and control areas were similar before the start of the experiment (personal observations). Mean sediment ripple wavelength in the experimental area was 9.9 cm ( $s = 0.9$  cm), and a total of 7 cycles were represented in the straw transect data. In contrast, the control area had a mean ripple wavelength of 6.5 cm ( $s = 0.6$  cm) and a total of 10 cycles were covered by the sampled series. However, ripples in the experimental area were not as regular as natural ripples with respect to trough position or ripple height. Large depressions, due to sediment scour, were observed around the perimeter of the wave box, but no such effects were noted in the center of the enclosure where transects were taken. Time series analysis techniques confirm this marked difference in ripple wavelengths between the experimental and control areas (Fig. 6, Table 3). In the experimental area, a significant ( $P < 0.05$ ) peak in

Figure 6: Autocorrelation coefficients for sediment ripple heights in the manipulation of sediment microtopographical characteristics experiment, June 12-14, 1983, plotted from 0 - 25 lags: experimental treatment (····), control (----). Inset shows corresponding power spectra. Note the difference in dominant sediment ripple wavelengths between treatments.

Figure 6

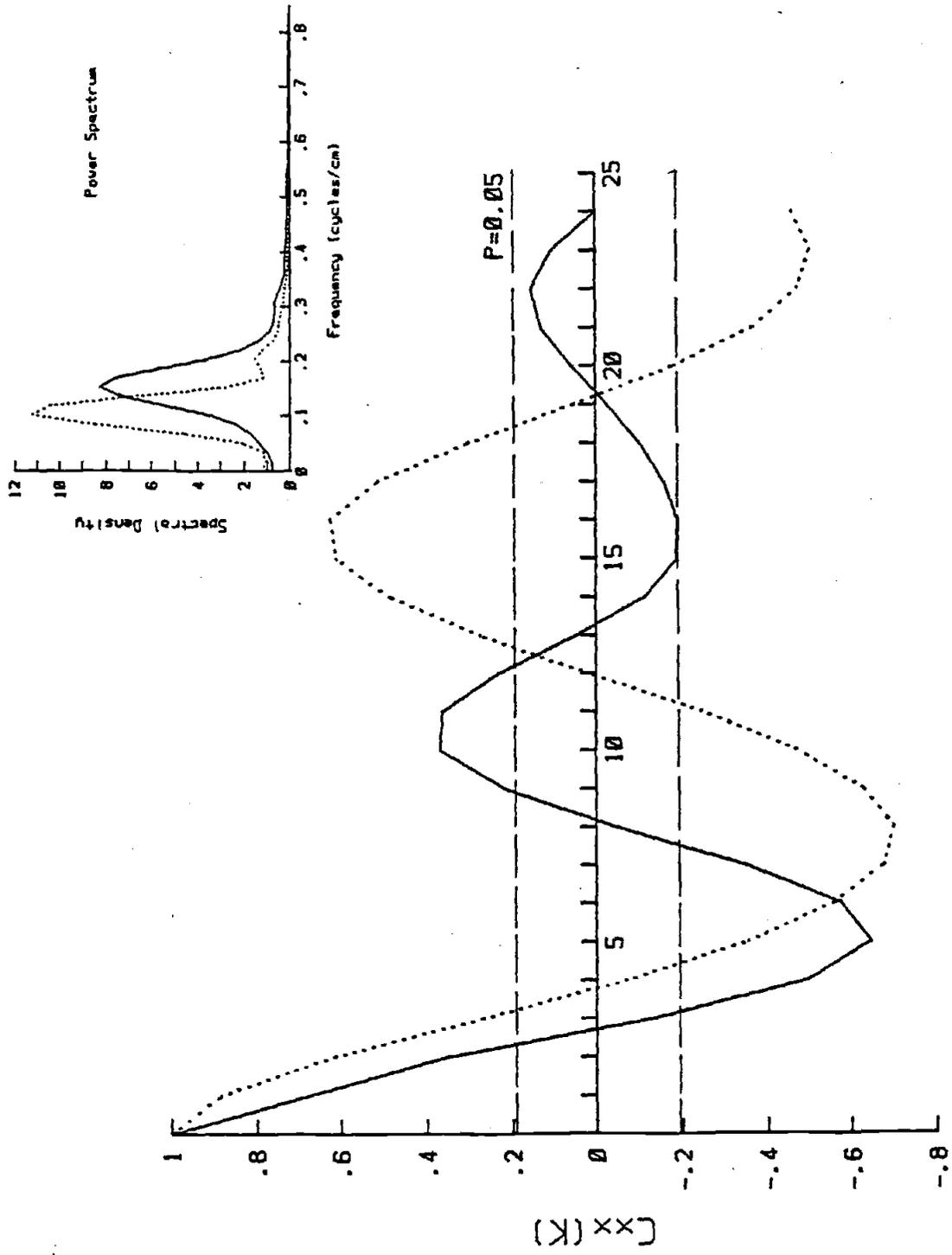


Table 3: Summary of time series analysis results of the manipulation of sediment microtopographical characteristics experiment; June 12-14, 1983.

| Variable                               | Treatment | Information from autocorrelogram   | Dominant frequencies indicated by the power spectrum  | Dominant periodicity of data |
|--|-----------|--|---|------------------------------|
| Sediment ripples                       | Exp.      | Local maximum at 16 <sup>th</sup> lags<br>(Minimum at 8 <sup>th</sup> and 22 <sup>th</sup> lags)                     | 0.102 cycles/cm<br>0.204 cycles/cm                    | 9.6 - 9.8                    |
|  | Control   | Local maxima at 10 <sup>th</sup> and 22 <sup>th</sup> lags<br>(Minimum at 5 <sup>th</sup> and 16 <sup>th</sup> lags) | 0.153 cycles/cm                                       | 6.0 - 6.5                    |
| Total meiofauna                        | Exp.      | No strong maxima or minima   | A leveling off at<br>0.153 cycles/cm                  | none                         |
|  | Control   | Local maxima at 8 <sup>th</sup> , 14 <sup>th</sup> , and 24 lags   | 0.136 cycles/cm<br>0.204 cycles/cm                    | 4.8 - 4.9                    |
| Nematodes                              | Exp.      | No strong maxima or minima   | none  | none                         |
|  | Control   | Local maxima at 8, 14, and 24 lags<br>Minimum at 19 <sup>th</sup> lags   | 0.119 cycles/cm<br>0.204 cycles/cm                    | 4.8 - 4.9                    |
| Harpacticoid Copepods                  | Exp.      | Local maxima at 8, 12, and 16 lags   | 0.119 cycles/cm<br>0.208 cycles/cm                    | none                         |
|  | Control   | Local maximum at 11 lags   | 0.136 cycles/cm<br>0.270 cycles/cm                    | 6.6                          |
| Total Crustaceans                      | Exp.      | Local maximum at 17 <sup>th</sup> lags<br>(Minimum at 10 lags)   | 0.085 cycles/cm<br>0.187 cycles/cm<br>0.306 cycles/cm | 10.7                         |
|  | Control   | Local maxima at 10 and 23 <sup>th</sup> lags<br>(Minimum at 5 <sup>th</sup> and 17 <sup>th</sup> lags)               | 0.153 cycles/cm<br>0.306 cycles/cm                    | 6.0 - 6.5                    |
| Gastrotrochs &<br><i>Turbellarians</i> | Exp.      | Local maximum at 17 lags   | 0.102 cycles/cm<br>0.187 cycles/cm                    | 9.8 - 10.7                   |
|  | Control   | Local maximum at 10 lags   | 0.153 cycles/cm                                       | 6.0 - 6.5                    |

\*Indicates significance at P<0.05  
 †Indicates significance at P<0.10

autocorrelation coefficients was observed at 16 lags (Fig. 6), or a distance of 9.6 cm. In contrast, autocorrelation coefficients for ripple heights in the control area peaked at 10-11 and 22 lags (Fig. 6), or at approximate multiples of 6.3 cm. The wave box technique was successful in varying the ripple spatial pattern.

Taxa observed in the samples collected on this date included nematodes, harpacticoid copepods (adults and nauplii), tardigrades, gastrotrichs, turbellarians, juvenile brachyurans, ostracods, oligochaetes, polychaetes, mites and rotifers. Total meiofaunal densities represented the combined densities of all of these taxa. Total crustacean densities represented the combined densities of all crustacean taxa listed above. Nematodes were the numerically dominant taxon in all samples; harpacticoid copepod adults ranked second in numerical abundance (Table 4). Only nematodes and harpacticoid copepods were sufficiently abundant for individual taxon analyses. Gastrotrich and turbellarian densities were combined during processing because it was difficult to separate these taxa during the sorting of a preserved sample under a dissecting microscope. Mean densities of all taxa and groupings in the experimental and control transects are given in Table 4. All taxa and meiofaunal groupings were significantly more abundant in samples taken in the experimental enclosure (t-test;  $P < 0.05$ ; Table 4).

Inspection of the raw data revealed two-to four-fold differences in density between areas of high and low densities for all taxa (Fig. 7). Density peaks did not correspond to ripple trough or crest

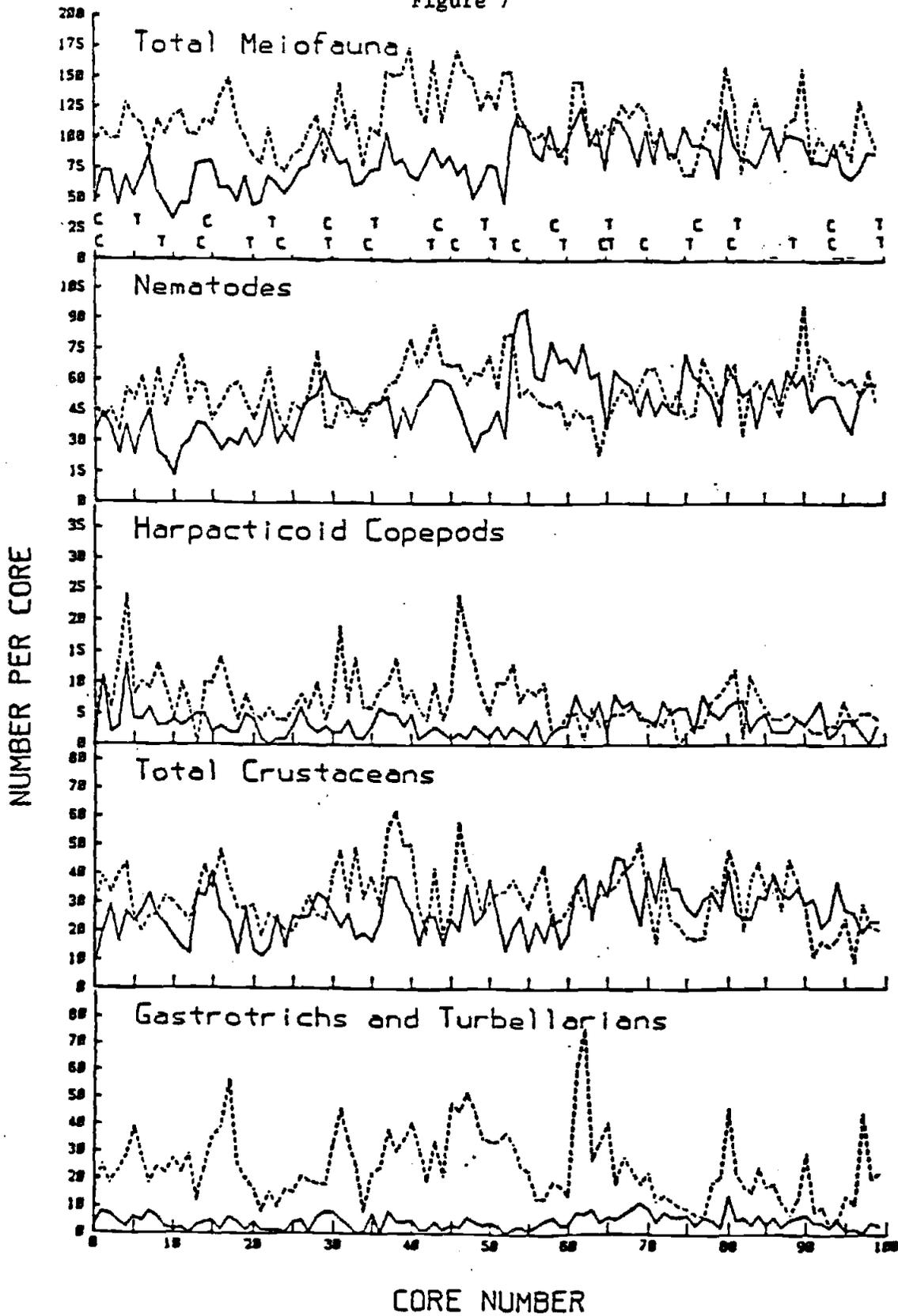
Table 4: Density data for all taxa enumerated in the manipulation of sediment microtopographical characteristics experiment; June 12-14, 1983.

| Taxon                        | Treatment | Mean Density/Core | S. D. |   | Mean Density/10 cm <sup>2</sup> |
|------------------------------|-----------|-------------------|-------|---|---------------------------------|
| Total Meiofauna              | Exp.      | 113.3             | 24.9  | * | 4045.9                          |
|                              | Control   | 80.9              | 20.5  |   | 2888.9                          |
| Nematodes                    | Exp.      | 55.2              | 12.7  | * | 1971.2                          |
|                              | Control   | 48.1              | 15.5  |   | 1717.7                          |
| Harpacticoid Copepods        | Exp.      | 7.1               | 4.4   | * | 253.5                           |
|                              | Control   | 3.6               | 2.3   |   | 128.6                           |
| Total Crustaceans            | Exp.      | 31.6              | 10.6  | * | 1128.4                          |
|                              | Control   | 26.3              | 8.5   |   | 939.2                           |
| Gastrotrichs & Turbellarians | Exp.      | 24.3              | 13.1  | * | 867.8                           |
|                              | Control   | 4.2               | 2.7   |   | 150.0                           |

\*Indicates means were significantly different at  $P < 0.05$

Figure 7: Abundance per core versus distance for each taxon enumerated in the manipulation of sediment microtopographical characteristics experiment, June 12-14, 1983: experimental treatment (····), control (----). Ten cores = 6 cm.

Figure 7



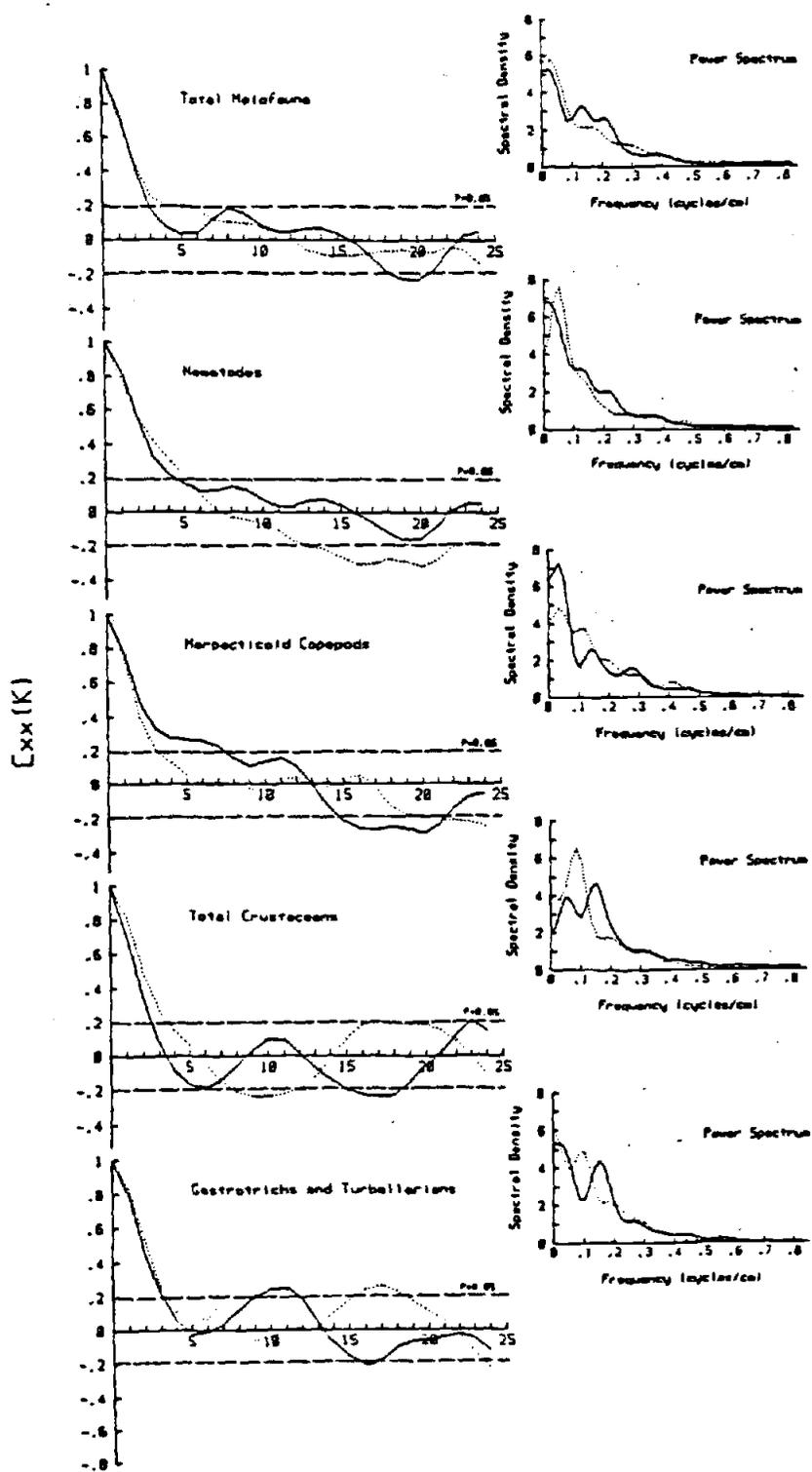
positions in the experimental or control areas for any taxon. In taxa which showed a strong pattern of density fluctuations (e.g. total crustacea in both series, total meiofauna, gastrotrichs/turbellarians, and harpacticoid copepods in the experimental series), peaks in density tended to be offset 2-3 cores (1.2-1.8 cm) towards the leading side of the ripple crest (Fig. 7).

Time series analysis for total meiofaunal densities and nematode densities showed no strong periodicities in either the experimental or control series (Fig. 8, Table 3). No pattern in autocorrelation coefficients was observed for either taxonomic grouping in either series. Thus, strong periodic fluctuations were not a dominant feature of the total meiofauna and nematode density data in either the experimental or control series.

In contrast, time series analysis for densities of harpacticoid copepods, total crustaceans, and gastrotrichs/turbellarians revealed periodic fluctuations in the experimental and control series (Fig. 8, Table 3). Total crustaceans and gastrotrich/turbellarians showed an approximate 10.2 cm wavelength in densities in the experimental series. The correlogram for harpacticoid copepods showed density periodicities at 7.2 and 9.6 cm wavelengths in the experimental series. Total crustacean and gastrotrich/turbellarian density data showed a periodicity at a 6.0 cm wavelength in the control series. Harpacticoid copepod density data showed a periodicity at 6.6 cm wavelength in the control series. In these three taxa, autocorrelograms for the control series showed negative

Figure 8: Autocorrelation coefficients for densities of all taxa enumerated in the manipulation of sediment microtopographical characteristics experiment, June 12-14, 1983, plotted from 0 - 25 lags: experimental treatment (····), control (----). Insets show corresponding power spectra.

Figure 8



autocorrelation coefficients at an approximate wavelength of 10.2 cm, the dominant periodicity in the experimental series. Harpacticoid copepod density periodicities observed in the experimental series could be due to a partial response by the organisms to the manipulation of ripple spacing, resulting in the observation of density periodicities in the experimental series at the dominant wavelengths of both the experimental and control sand ripples. Thus, harpacticoid copepods, total crustaceans, and gastrotrichs/turbellarians exhibited a response to the manipulation of ripple spacing (Table 3, compare Fig. 6 and Fig. 8), and, in contrast to the total meiofauna and nematode density data, showed periodicities in the control series which matched periodicities in sediment ripple height (Table 3, compare Fig. 6 and Fig. 8).

This experiment only demonstrated a causal link between sediment ripple spacing and density periodicities for the non-nematode meiofauna. Thus, as in the first experiment, sediment ripple spacing was the dominant influence on the micro-spatial distribution of harpacticoid copepods, total crustaceans, and gastrotrichs/turbellarians. Nematodes (and thus total meiofauna) showed no response to the manipulation of ripple spacing. Nematode and total meiofaunal density periodicities in the control series were weak and not related to the dominant sediment ripple wavelength present at the time of the experiment.

It is possible that the property or properties associated with sediment ripples which influenced the nematode density patterns in the

first experiment did not operate within the duration of this experiment. Alternatively, other factors may have been more important than sediment ripple spacing in influencing the distribution of nematodes at this time. Sediment surface conditions were different during this period than from those of January, 1983. Sediment ripples only covered the small section of beach in which sampling was conducted and within this section, ripple orientation and wavelength varied from one tidal cycle to the next. Callianassa californiensis was also more abundant at the study site during this time. The influence of biogenic microtopography on meiofaunal distribution is well documented (see Introduction). These factors may have affected the micro-spatial distribution of meiofauna.

Addition of Organic Matter to the Ripple System:

During the sampling period November 7-9, 1983, poorly defined, but regularly spaced, asymmetrical sediment ripples of approximately 1 cm height covered most of the study site. Callianassa californiensis burrows were not so prevalent as during the spring and summer months, but they were more abundant than in January, 1983. The spatial pattern of the sediment ripples was not affected by the manipulation: the mean ripple wavelengths were 7.8 cm ( $s = 1.3$  cm) in the experimental transect, 6.8 cm ( $s = 1.5$  cm) in the experimental-control transect, and 7.3 cm ( $s = 2.4$  cm) in the control transect. Autocorrelograms for ripple height in all three transects showed considerable similarity in the location and strength of maxima and minima (Fig. 9, Table 5). The

Figure 9: Autocorrelation coefficients for sediment ripple heights on November 9, 1983, plotted from 0 - 25 lags: experimental treatment (---·---·---), experimental-control treatment (····), and control (----). Inset shows corresponding power spectra. Note similarity of dominant wavelengths between treatments.

Figure 9

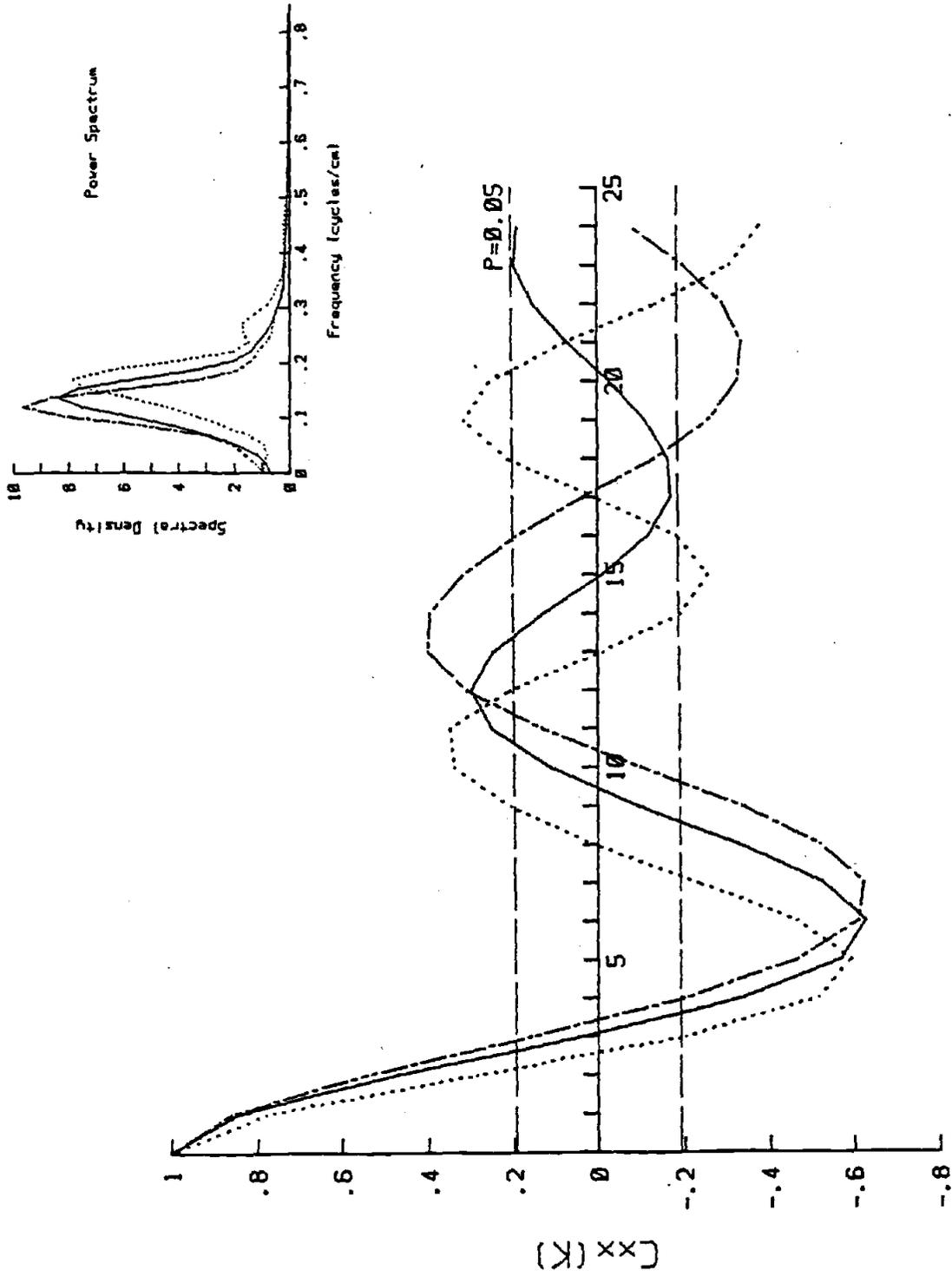


Table 5: Summary of time series analysis results of the addition of organic matter experiment; November 7-9, 1983.

| Variable                   | Treatment    | Information from autocorrelogram   | Dominant frequencies indicated by the power spectrum  | Dominant periodicity of data |
|----------------------------|--------------|--|---|------------------------------|
| Sediment ripples           | Exp.         | Local maximum at 13 <sup>a</sup> lags<br>(Minimum at 7 <sup>a</sup> and 21 <sup>a</sup> lags)  | 0.119 cycles/cm                                       | 3.8 - 8.4                    |
|                            | Exp. Control | Local maxima at 11 <sup>a</sup> and 19 <sup>a</sup> lags<br>(Minimum at 5 <sup>a</sup> , 15 <sup>a</sup> , and 24 <sup>a</sup> lags) | 0.170 cycles/cm<br>0.255 cycles/cm                    | 5.8 - 6.6                    |
|                            | Control      | Local maxima at 12 <sup>a</sup> and 23 <sup>a</sup> lags<br>(Minimum at 6 <sup>a</sup> and 17 <sup>a</sup> lags)                     | 0.136 cycles/cm                                       | 7.0 - 7.4                    |
| Total Meiofauna            | Exp.         | Local maximum at 8 <sup>a</sup> lags<br>(Local maximum at 18 lags <i>β</i> )   | 0.187 cycles/cm                                       | 4.8 - 5.4                    |
|                            | Exp. Control | Local maxima at 5, 9, 16,<br>and 21 lags<br>(Minimum at 18 <sup>a</sup> lags)  | 0.153 cycles/cm<br>0.323 cycles/cm                    | 3.0<br>5.4 - 6.5             |
|                            | Control      | No strong maxima or minima   | none  | none                         |
| Nematodes                  | Exp.         | Local maxima at 8 and 18 <sup>a</sup> lags   | 0.119 cycles/cm<br>0.187 cycles/cm                    | 4.8 - 5.4<br>11.0            |
|                            | Exp. Control | Local maximum at 10 lags<br>(Minimum at 18 lags)   | 0.136 cycles/cm<br>0.306 cycles/cm                    | 6.0 - 7.4                    |
|                            | Control      | No strong maxima or minima   | 0.068 cycles/cm                                       | none                         |
| Total Crustaceans          | Exp.         | Local maximum at 8 <sup>a</sup> lags<br>(Local maximum at 18 lags <i>β</i> )   | 0.187 cycles/cm                                       | 4.8 - 5.4                    |
|                            | Exp. Control | Local maxima at 7, 15 <sup>a</sup> , and 22 lags<br>(Minimum at 18 lags)   | 0.102 cycles/cm<br>0.221 cycles/cm                    | 4.2 - 4.5<br>9.0 - 9.8       |
|                            | Control      | No strong maxima or minima   | 0.068 cycles/cm<br>0.170 cycles/cm<br>0.323 cycles/cm | none                         |
| Gastropods & Turbellarians | Exp.         | Local maxima at 6 <sup>a</sup> and 12 <sup>a</sup> lags  | 0.136 cycles/cm<br>0.255 cycles/cm                    | 3.6 - 3.9<br>7.2 - 7.4       |
|                            | Exp. Control | Local maxima at 17 and 21 lags<br>(Minimum at 18 lags)   | 0.068 cycles/cm<br>0.204 cycles/cm<br>0.306 cycles/cm | none                         |
|                            | Control      | No strong maxima or minima   | 0.102 cycles/cm<br>0.289 cycles/cm                    | none                         |
| Organic Carbon             | Exp.         | Local maximum at 18 <sup>a</sup> lags  | 0.085 cycles/cm<br>0.187 cycles/cm<br>0.289 cycles/cm | 10.8 - 11.7                  |

<sup>a</sup>Indicates significance at  $P < 0.05$   
<sup>b</sup>Indicates significance at  $P < 0.10$   
<sup>β</sup>Indicates local maximum is negative

power spectra reiterate this result (Fig. 9, Table 5).

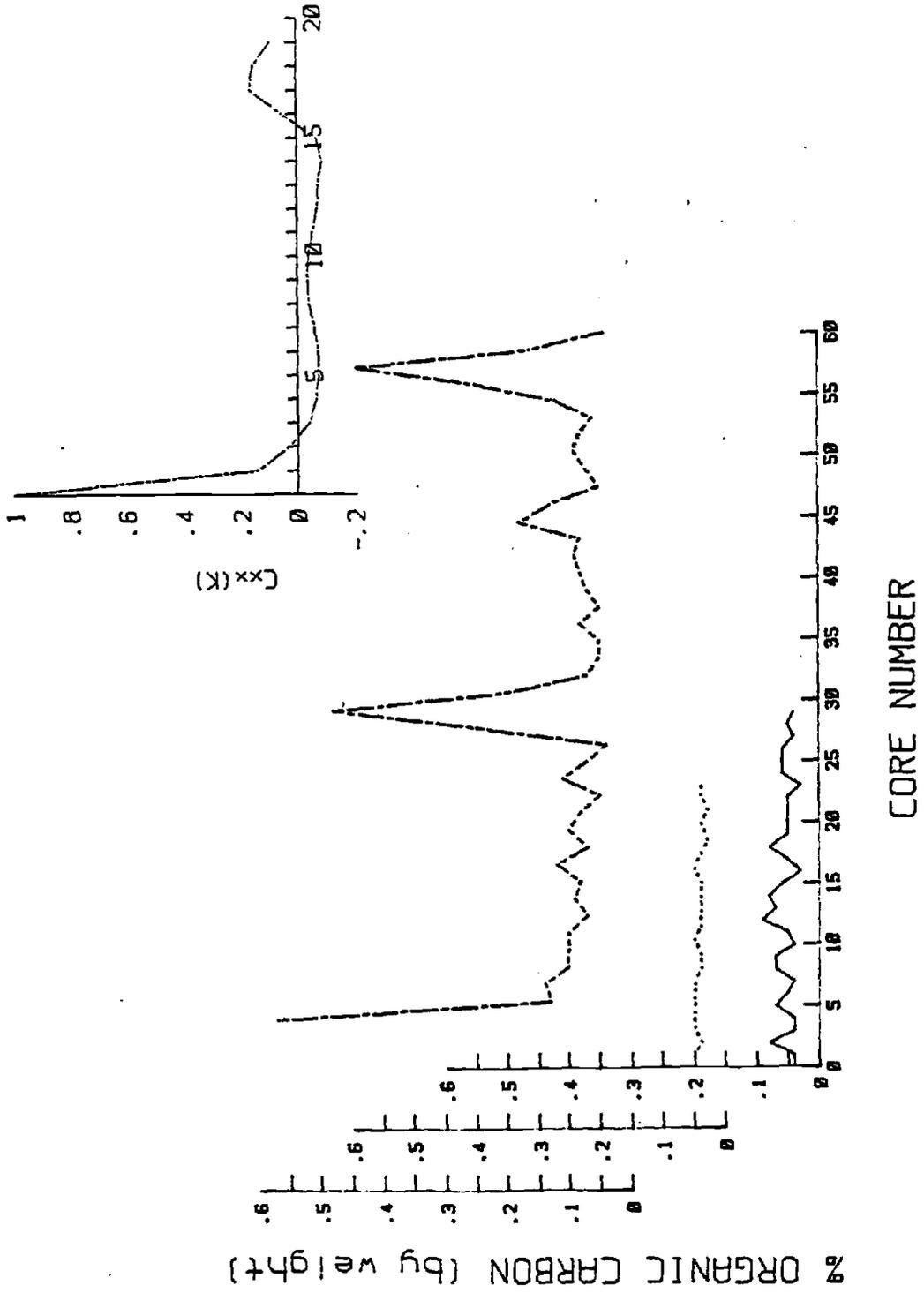
Background levels of sediment organic carbon in November, 1983, were approximately 0.05% by weight ( $s = 0.01\%$ ;  $N = 50$ ). Nitrogen levels were not detectable by the technique used. Although this carbon value is low in comparison with other benthic habitats, it is within the range of values reported in the literature for fine sand beaches. Newell (1965) reported organic carbon values less than 0.5% and nitrogen values less than 0.1% by weight at a mean particle diameter of 0.2 mm, the approximate mean particle diameter at my study site (Hogue and Miller 1981). Hogue (1978) reported an organic content of 0.06% by weight in a subtidal sandflat in South Carolina in which the mean sediment grain size was 0.218 mm.

Analyses for organic content conducted on single fecal pellets of Callianassa californiensis showed them to be significantly enriched in organic carbon and nitrogen relative to the sediment ( $P, 0.05$ ;  $t = 26.40$ ,  $df = 43$ ). Fecal pellets had a mean organic carbon level of 4.41% by weight ( $s = 0.91\%$ ;  $N = 15$ ) and a mean nitrogen level of 0.32% by weight ( $s = 0.10\%$ ;  $N = 15$ ). Frankenberg et al. (1967) measured the composition of fecal pellets of a congeneric species, Callianassa major and found them to be 2.9% organic carbon and 0.3% nitrogen by weight. C:N ratios of the fecal pellets were approximately 14:1. It is generally recognized that C:N ratios less than 17:1 indicate a high quality food source (Russell-Hunter 1970).

The additions of fecal pellets to the ripple system were

Figure 10: Organic carbon levels versus distance for each treatment in the addition of organic matter experiment, November 7-9, 1983: experimental treatment (---·---·---), experimental-control treatment (·····), and control (----). Note peak in organic carbon levels every 18-19 cores (11 cm). Inset shows autocorrelogram for organic carbon levels in the experimental series, note peak at 17-18 lags.

Figure 10



reflected in the organic carbon content data (Fig. 10). Organic carbon values for the experimental transect showed peaks at approximately every 19 samples (Fig. 10, Table 5), or every 11 cm, the frequency at which the additions were made. The autocorrelogram supports this result (Fig. 10, Table 5), although there are not enough cycles in the data for a strong peak to occur at 18 lags. After two days, C:N ratios of the sediment cores were greater than those measured for fecal pellets (Table 5). Some of the increase in C:N ratios is probably due to a volume effect; the entire 4 cm long sediment core was homogenized before analysis, whereas deposits were only made to depth of 2 cm. However, increases in C:N ratios also may have reflected the consumption of the added organic matter by the infauna. During sorting, nematodes were often observed partially within the fecal pellets, as if they had been ingesting portions when sampled (direct observations).

Organic carbon values for the experimental-control and control transects did not show any discernible peaks and showed no pattern in relation to the ripple crest and trough locations (Fig. 10). Sample sizes for the experimental-control and control transects were too small to permit use of time series analysis techniques. It is possible that the sample preparation method diluted any variation that may have been present. Alternatively, local accumulations of organic matter may be so small that it is very difficult analytically to detect them above background levels.

Taxa enumerated included nematodes, harpacticoid copepods (adults

and nauplii), tardigrades, ostracods, juvenile brachyurans, gastrotrichs, turbellarians, oligochaetes, clams, amphipods, rotifers, and polychaetes. Total meiofaunal densities represented the combined densities of these taxa, which include temporary and permanent meiofauna. Total crustacean densities represented the combined densities of all crustacean taxa listed above. Gastrotrich and turbellarian densities were combined during processing to expedite sorting. Only nematodes were sufficiently abundant for individual taxon analysis. Nematodes were the numerically dominant taxon in all samples (Table 6). The mean densities per core for total meiofauna, nematodes, crustaceans, and gastrotrichs/turbellarians can be seen in Table 6.

A total of 7 cycles (ripple crest to ripple crest), 9 cycles, and 8 cycles were represented by the straw transect data in the experimental, experimental-control, and control series, respectively. Inspection of the raw data revealed three- to five-fold differences in densities between regions of maximum and minimum density for all taxa (Fig. 11). Density peaks did not correspond to ripple crest or trough positions for any taxon.

Time series analysis demonstrated periodicities in total meiofauna densities at an approximate 5.4 cm wavelength in the experimental series (Fig. 12, Table 5). A local maximum in autocorrelation coefficients was noted at 10.8 cm (18 lags), the wavelength at which organic matter additions were made. In contrast, the experimental-control series showed a decrease in autocorrelation

Table 6: Density data for all taxa enumerated in the addition of organic matter experiment; November 7-9, 1983. Organic carbon values expressed in % (by weight).

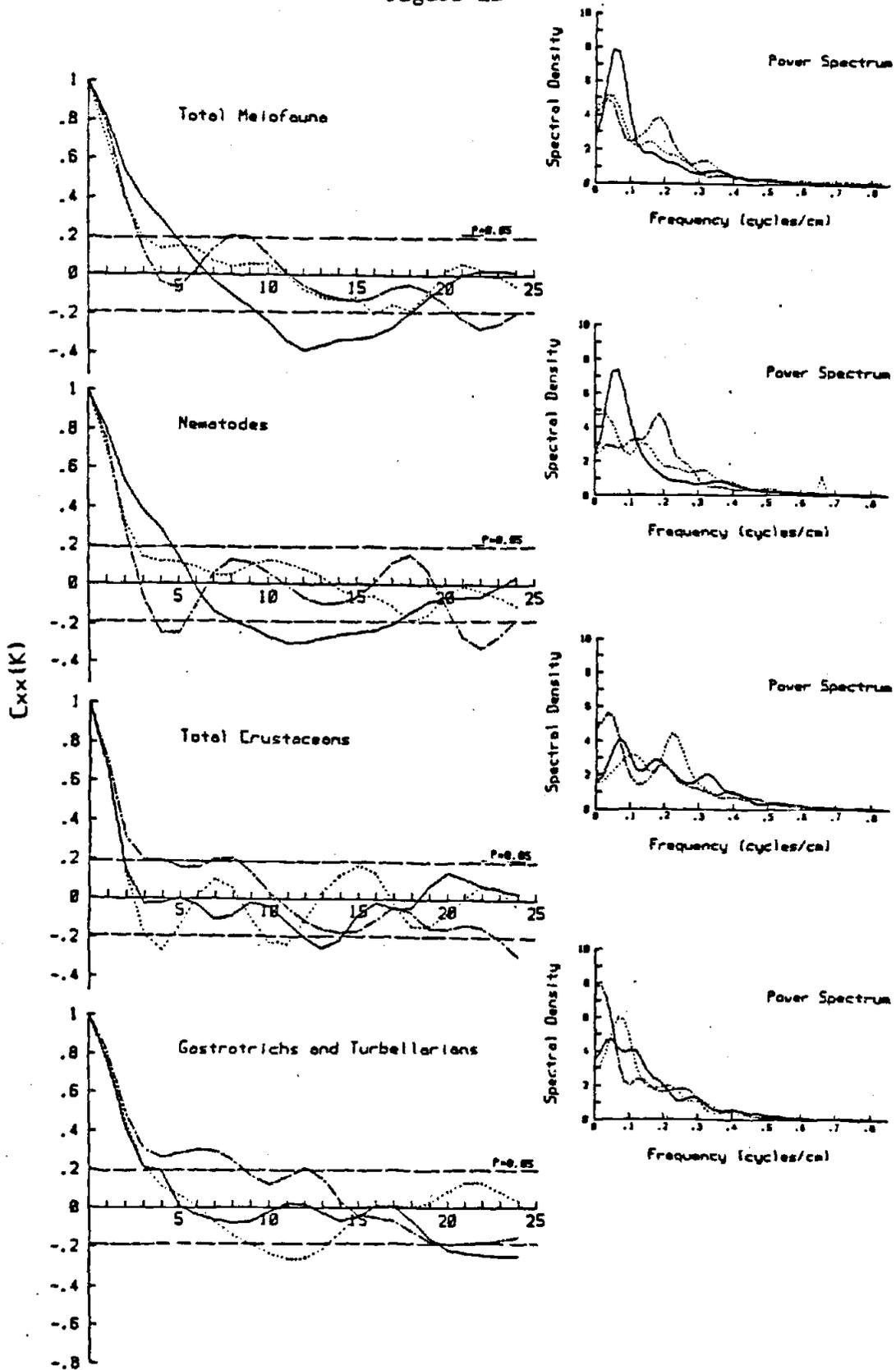
| Taxon/Variable               | Treatment    | Mean Density/Core | S. D.  | Mean Density/10 cm <sup>2</sup> |
|------------------------------|--------------|-------------------|--------|---------------------------------|
| Total Meiofauna              | Exp.         | 28.5              | 11.1   | 1017.7                          |
|                              | Exp. Control | 37.0              | 10.3   | 1321.3                          |
|                              | Control      | 34.3              | 13.6   | 1224.9                          |
| Nematodes                    | Exp.         | 19.4              | 9.0    | 692.8                           |
|                              | Exp. Control | 23.1              | 6.8    | 824.9                           |
|                              | Control      | 21.8              | 11.3   | 778.5                           |
| Total Crustaceans            | Exp.         | 3.1               | 1.9    | 110.7                           |
|                              | Exp. Control | 4.8               | 2.7    | 171.4                           |
|                              | Control      | 3.7               | 2.4    | 132.1                           |
| Gastrotricha & Turbellarians | Exp.         | 4.8               | 3.7    | 171.4                           |
|                              | Exp. Control | 7.3               | 5.2    | 260.7                           |
|                              | Control      | 4.4               | 2.6    | 157.1                           |
| Organic Carbon               | Exp.         | 0.1065            | 0.1076 | --                              |
|                              | Exp. Control | 0.0425            | 0.0063 | --                              |
|                              | Control      | 0.0543            | 0.0159 | --                              |

Figure 11: Abundance per core versus distance for each taxon enumerated in the addition of organic matter experiment, November 7-9, 1983: experimental treatment (upper ----), experimental-control treatment (····), and control (lower ----). Ten cores = 6 cm.



Figure 12: Autocorrelation coefficients for densities of all taxa enumerated in the addition of organic matter experiment, November 7-9, 1983, plotted from 0 - 25 lags: experimental treatment (---'---'---), experimental-control treatment (····), and control (----). Insets show corresponding power spectra.

Figure 12



coefficients at 10.8 cm. Density fluctuations of total meiofauna did not exhibit any pattern in the control series (Fig. 12).

Nematode densities in the experimental series exhibited a significant peak ( $P < 0.10$ ) in autocorrelation coefficients at a 10.8 cm wavelength. In contrast, nematode densities in the experimental-control series showed a negative peak in autocorrelation coefficients at 10.8 cm. Nematode density fluctuations in the control series again showed no pattern (Fig. 12). Thus, nematodes showed a response to the addition of organic matter (Fig. 12, Table 5). This response was also reflected in the total meiofauna density data (Fig. 12, Table 5). Microscopic inspection of a number of fecal pellets showed few nematodes (personal observation), so I do not believe the results were due to the addition of nematodes with the fecal pellets. Other density periodicities in nematodes and total meiofauna were similar among transects and between taxa but did not appear to be related to ripple spatial pattern (Table 5, compare Fig. 9 and Fig. 12), indicating that sediment ripple spacing was not the dominant influence on the micro-spatial distribution of nematodes during this experiment.

Crustaceans responded weakly but discernibly to the organic matter additions showing a weak periodicity at a 4.8 cm wavelength and local maxima at 10.8 and 12.6 cm, even though autocorrelation coefficients remained negative in the latter two cases (Fig. 12, Table 5). The experimental-control and control series showed similar periodicities in crustacean density, and both exhibited negative

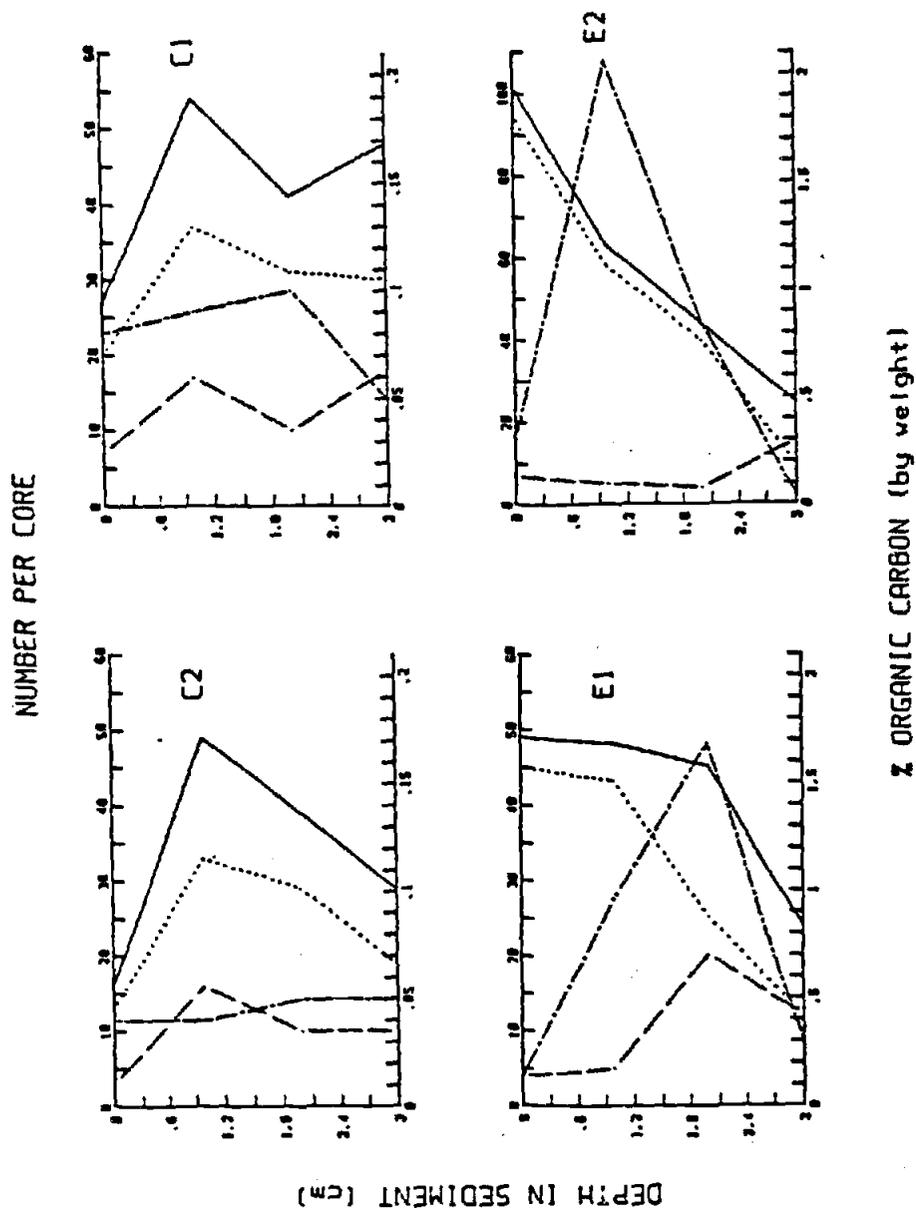
autocorrelation coefficients at 10.8 cm. Density periodicities at the 4.8 cm wavelength were not related to ripple spatial pattern (Table 5, compare Fig. 9 and Fig. 12), indicating that sediment ripple spacing was not the dominant factor affecting the micro-spatial distribution of crustaceans.

Gastrotrich/turbellarian densities showed no indication of a response to the additions of organic matter. Weak periodicities in gastrotrich/turbellarian densities in the experimental transect were observed at a 7.2 cm wavelength (Fig. 12, Table 5). Autocorrelation coefficients were negative and decreasing at 10.8 cm. The experimental-control series showed weak density periodicities at a 12.6 cm wavelength. The control series showed weak density periodicities at 6.6 and 9.6-10.2 cm wavelengths. Thus, gastrotrichs and turbellarians showed no response to the additions of organic matter. In contrast to the results for other taxa, density periodicities at a wavelength of 6.6-7.2 cm corresponded to the ripple spacing, (Table 5, compare Fig. 9 and Fig. 12), indicating that sediment ripples influenced their small scale distribution.

Densities of total meiofauna, nematodes, and total meiofauna minus nematodes in the vertical transects taken in the experimental series can be seen in Figure 13. Vertical transects demonstrated contrasting patterns in the distribution of meiofauna in the organically enriched versus the non-enriched area. In the transects sampled from organically enriched areas, maximum densities of nematodes (and therefore total meiofauna) occurred in the surface

Figure 13: Vertical distribution in the sediment of total meiofauna (---), nematodes (····), remaining meiofauna (-----), and organic carbon (-·-·-·-) in experimental and control areas on November 9, 1983.

Figure 13



cores (Fig. 13). Densities of nematodes declined gradually with increasing depth in the sediment. No pattern was observed for the remaining meiofaunal taxa. Transects from areas with no organic matter additions showed maximum densities of all taxa at an approximate depth of 1.2 cm (Fig. 13). Densities of all taxa generally decreased with increasing sediment depth. Thus, the vertical distribution pattern of nematodes, but not other meiofaunal taxa, was affected by the organic matter additions. Mean densities of total meiofauna and nematodes were not significantly different ( $t$ -test;  $P > 0.05$ ) between transects taken in experimentally enriched areas and those taken in control areas.

Organic carbon values for corresponding vertical transects are shown in Figure 13. Mean organic carbon values were significantly ( $P < 0.05$ ;  $t = 2.56$ ,  $df = 8$ ) greater in vertical transect samples taken in experimentally enriched areas. Maximum organic carbon concentrations were observed at a depth of 2-3 cores (1.2-1.8 cm; Fig. 13) in areas of organic enrichment; sharp declines in organic content were noted with increasing depth in the sediment (Fig. 13). Organic carbon values showed little variation with depth in transects taken in areas with no organic matter additions (Fig. 13). The absence of variation was unexpected as many authors have noted that sediment organic content decreases with sediment depth (Johnson 1974, 1977, Sanders and Hessler 1969). However, most studies have been conducted on more extensive sediment profiles and in habitats with higher levels of organic carbon. It is possible that the differences are too small to be

detectable by the technique used.

## Discussion

### Confirmation of Meiofaunal Distributional Patterns:

The first experiment in this study revealed significant periodicities in the density of all meiofaunal taxa at the wavelength of the sediment ripples. Sediment ripples were important in influencing the distribution of meiofauna in January, 1983. This confirms the result of Hogue and Miller (1981) for nematodes and extends it to other meiofauna, specifically tardigrades and harpacticoid copepods. Although both studies were conducted at the same site, sediment ripple wavelengths were significantly different. Hogue and Miller (1981) found that the dominant ripple wavelength was 8.0 cm in May, 1980, whereas in January, 1983 (this study), the dominant ripple wavelength was 5.4 cm. In addition, the mean densities of nematodes per core in the transects sampled by Hogue and Miller (1981) were 3 and 10 times greater than in the transect sampled in January, 1983. I conclude that sediment ripples can exert a strong influence on the small scale spatial distribution of meiofauna.

### Manipulation of Sediment Microtopographical Characteristics:

The experiment involving the manipulation of sediment ripple spacing revealed a causal link between sediment ripple spacing and density periodicities for the non-nematode meiofauna. Experimentally

changing the ripple spacing suggested that sediment ripples were the dominant influence on the small scale spatial distribution of harpacticoid copepods, crustaceans, and gastrotrichs and turbellarians. Nematodes (and thus total meiofauna) showed no response to the altered ripple spacing. In addition, nematode and total meiofaunal density periodicities in the control series were weak and were not close to the dominant sediment ripple wavelength at the time of the experiment. It appears that other factors were more important than sediment ripples in influencing the distribution of nematodes during this time.

Sediment surface conditions at my study site were much different in June than in January. Sediment ripples were less regular than in January and only covered a small portion of the study area. In addition, within this area, ripple orientation and wavelength varied frequently, often every tidal cycle. Thus, frequent changes in ripple wavelength and orientation may have precluded the establishment of strong density periodicities. However, Callianassa californiensis appeared to more active or abundant at the study site in the summer months. The effect of Callianassa californiensis and its burrows on the small-scale distribution of meiofauna is unknown. The burrow formed by this organism extends approximately 45 cm into the sediment and forms a conspicuous mound on the sediment surface about 7 cm in diameter and 5 cm in elevation (personal observation). Preliminary evidence (small core sampling to a depth of 4 cm) regarding the effect of burrows on the horizontal distribution of meiofauna suggests that

this organism causes a reduction in densities of all meiofaunal taxa, an effect which extends to the diameter of the mound (unpublished data). Thus, the activities of this organism may have influenced the observed pattern of nematode density fluctuations.

It is also possible that the mechanism by which sediment ripples affect the distribution of nematodes was not operative within the time scale of the experiment. The hypothesis of Hogue and Miller (1981) is that the observed distribution of nematodes is due to the distribution of their food source, particulate organic matter. Following this hypothesis, nematode response to the altered ripple spacing was not detected because of the time scale of the experiment; no response to the manipulation would have been observed after only one tidal cycle, because food resources would not yet have been regularly distributed with a periodicity matching that of the new ripple spacing. Frequent changes in ripple spacing, as discussed above, would have resulted in the observation of weak density periodicities at wavelengths unrelated to ripple wavelengths present on the day of sampling.

#### Addition of Organic Matter to the Ripple System:

The results of the organic enrichment experiment demonstrated a response by the nematodes to the fecal pellet deposits. However, other meiofauna, with the possible exception of the crustaceans, showed no response to the additions of organic matter. These results supported the hypothesis of Hogue and Miller (1981) that a sequence of

events extending over several tidal cycles results in nematode density periodicities at the wavelength of the sediment ripples. As the ripples migrate under the influence of tidal currents, a portion of the organic matter (primarily fecal pellets) located in the ripple trough is buried, rather than being resuspended and transported elsewhere. As this process is repeated over several tidal cycles, additional localized lines of organic material are laid down, but with a phase difference from previous series equal to the migration distance of the ripples. Nematodes would be attracted to this buried organic matter and its associated microbial flora resulting in periodic nematode density peaks. In this study, the nematodes had adequate time after two days, to detect and migrate toward the fecal pellet deposits, thus producing the observed periodicity at 11 cm. Other fauna showed no density periodicities at this wavelength, possibly because they were not attracted to the buried fecal pellets.

A corollary of the hypothesis of Hogue and Miller (1981) is that food resources are regularly distributed in the sediment; that is parallel strips of organic material are deposited with a frequency matching that of the sediment ripple wavelength. Organic carbon analyses conducted on samples from the experimental control and control series did not show any variation in organic carbon levels with respect to ripple spatial pattern. It is probable that the sample preparation method diluted any variation that was present. Localized areas of organic material may have been present in the upper 1 cm, as predicted by the hypothesis, but their detection may have

been prevented by homogenization of the entire 4 cm sediment sample. Local accumulations of organic matter may also be too small to detect above background levels.

#### Implications:

Data presented here suggest that the small-scale distribution of meiofauna is influenced by many processes. In addition, different meiofaunal taxa appear to be responding to different features of the environment. The spatial distribution of nematodes appears to be influenced by the micro-spatial distribution of their food resource, particulate organic matter. The spatial distribution of the other meiofaunal components at my study site, however, appears to be influenced to a greater extent by a physical property or properties associated with the sediment ripples. I believe this property may be the micro-flow regime associated with a rippled sediment surface. The deposition of organic matter and the micro-flow regime may be controlled, directly or indirectly, by sediment ripples. In the former case, sediment ripples determine the pattern of organic matter deposition and in the latter case, determine flow patterns directly over the sediment surface.

Studies of meiofaunal migration and dispersal have revealed important differences between nematodes and meiofaunal copepods. These differences parallel the responses of these groups to the manipulations I have applied. Bell and Sherman (1980) observed 13-44%

of the meiobenthic community in overlying water and suspended sediment fractions. Despite the numerical dominance of the meiofaunal community by nematodes, only a small fraction of this percentage were nematodes. Chandler and Fleeger (1983) investigated mechanisms of meiofaunal dispersal using two azoic sediment chambers, one of which allowed entry only by crawling through open sides under the sediment surface and another which permitted entry via suspended movement through an open top. After 48 h, mean harpacticoid copepod and naupliar densities in the sediment chambers open to colonization via suspended movement were not significantly different from background sediment densities, but sediment chambers open to colonization only by infaunal crawling showed densities significantly less than background levels. Nematode densities in both suspension and infaunally colonized chambers were significantly less than background sediment densities even after 29 days, but densities were not significantly different between chambers. Alldredge and King (1980) observed harpacticoid and epibenthic cyclopoid copepods in samples taken from water overlying a subtidal sand flat but found few nematodes. Eckman (1983) found that nematodes required a longer period of time to reestablish ambient densities than did harpacticoid copepods following defaunation. Sherman and Coull (1980), however, observed complete colonization of a  $9 \text{ m}^2$  area of an intertidal mud flat by copepods and nematodes after 12 hr and suggested that suspended transport may have been the mechanism for colonization. Hagerman and Rieger (1981) found that not only harpacticoids, but nematodes, kinorhynchs, polychaetes, turbellarians, gastrotrichs, rotifers, and halicarid mites occurred

regularly in the water column 1-1.5 m above the sediment-water interface; however, comparative densities were not given. Meiofaunal taxa may exhibit different behavioral patterns which would affect their relative ability to become suspended in the water column. Such behavioral patterns have been demonstrated for macrofaunal taxa (Cubit 1969, Trueman 1971).

Thus, migration and dispersal studies, and comparative vertical distribution information on meiofaunal organisms have indicated contrasting colonizing modes among nematodes and harpacticoid copepods. Nematodes primarily colonize new habitats by subsurface crawling and harpacticoid copepods primarily colonize new habitats via suspended transport in the water column. These generalizations have not been substantiated for other meiofaunal taxa. In my study, the small scale distribution of nematodes appeared to be influenced by a feature of the sedimentary environment whereas the distribution of the other taxa appeared to be controlled by a property of the environment at the sediment-water interface.

Experimental studies have demonstrated that flow patterns and velocities vary in a complex manner over different points on a rippled sediment surface (Raudkivi 1976, Yalin 1972, Du Toit and Sleath 1981). Passive or active response by the meiofauna to these micro-flow regimes may result in the observation of density periodicities associated with the wavelength of the sediment ripples. The meiofauna suspended in the water column may act as particles in a manner analogous to that described in the hypothesis by Hogue and Miller

(1981) for the organic matter. Reduced boundary shear stresses in ripple troughs would result in deposition in this area. Over time, local accumulations of organisms would be formed with periodicities matching that of the sediment ripples. Crenshaw (1980) has combined field studies and theoretical models of flow to show that regions of the beach only a few millimeters apart have different sediment properties which cause local variations in the flow regime. Crenshaw (1980) has also demonstrated that the turbellarian Tetranchroderma papii seeks interstitial spaces which provide reduced shear stresses. The water-borne component of the meiofauna at my study site may be behaving similarly.

It is also known sediment grain sorting occurs when sediment ripples are formed (Shepard 1963). Smaller grains are deposited in the ripple troughs, leaving larger grains to be concentrated on the ripple crests. This process may result in more pore space, or living space, in the vicinity of ripple crests than in ripple troughs. Ripple crest regions also may experience greater exchange of water and associated factors, such as oxygen and food. The non-nematode component of the meiofauna may actively seek out ripple crest regions for any of these reasons. Jumars and Nowell (1984) have reviewed the impact of hydrodynamic processes on microbial population growth, faunal recruitment, and particle feeding; three biological processes which potentially impact on the small-scale spatial distribution of meiofauna. How these processes vary over a rippled sediment surface is not known.

The results of my study also indicate that sediment ripples are not always the major determinant of the distribution of meiofauna. Biogenic microtopography, in the form of Callianassa burrows, may have played a large role in influencing the distribution of meiofauna during the spring and summer months. Myers (1977) studied bioturbation and sediment processing by the macrofaunal community at West Basin in a Rhode Island coastal lagoon. He concluded that, in general, microtopographical features of the sediment surface were dominated by the sediment reworking activity of the holothurian Leptosynapta tenuis when sediment temperatures (measured at a depth of 5 cm) exceeded 10<sup>o</sup> C, but were dominated by wave activity when temperatures were less than 10<sup>o</sup> C. Both processes produced topographical relief of the same scale, 2-4 cm. A similar situation may occur at my study site. Data from January demonstrate clear periodicities in meiofaunal density fluctuations. This may indicate the overriding importance of physically-generated sediment microtopography in influencing the distribution of meiofauna at that time. Periodicities in the meiofaunal density data from June were not as strong nor as clear as those in January. This could reflect an increase in the importance of biogenic microtopography in controlling the distribution of meiofauna.

Although not investigated in this study, biotic interactions may also affect the small scale distribution of meiofauna. Density fluctuations may result in variations in the importance of biotic interactions over time. Density fluctuations of meiofaunal taxa did

occur in this study. Mean densities in January were low for all taxa (see Results), whereas mean densities in June were much greater (Table 4). Although species data is not yet available, fluctuations in the relative importance of taxa also occurred (Tables 4, 6). For example, tardigrades comprised a greater proportion of the meiofaunal assemblage in January than in June or November. Jansson (1968) observed seasonal fluctuations in meiofaunal abundance and composition in the Baltic. Meiofaunal densities peaked in August and were at a minimum in November; however, density fluctuations were most pronounced among the turbellarians, gastrotrichs, oligochaetes, halacarid mites, and harpacticoid copepods, while nematode densities remained high all year. Perkins (1958) noted that, although nematodes were the numerically dominant taxon all year, other meiofaunal taxa reached density maxima only when nematode abundance was at its lowest. Seasonal changes in nematode faunal composition in the absence of large density fluctuations have also been documented (Wieser and Kanwisher 1961). The importance of biotic interactions and the variation of their importance over time remains to be investigated.

A number of important factors that organize meiofaunal community structure have been proposed in the literature (see reviews by Bell et al. 1978, Coull and Bell 1979). These include the partitioning of space and food resources, predation, disturbance, competition, stochastic processes, and small-scale spatial heterogeneity created by biogenic microtopography. The results of this study suggest that

small-scale spatial heterogeneity created by physically-generated microtopography also affects the organization of meiofaunal communities. The presence of sediment ripples affects the small-scale distribution of food resources, and probably affects the hydrodynamic regime. Alterations in the hydrodynamic regime may affect the distribution of those organisms which undergo water-column mediated transport for dispersal, migration, recruitment, and for foraging activities or those forms which are easily suspended from surficial sediments.

At my study site, the distribution of the meiofaunal assemblage in the upper layer of sediment at any given time is a dynamic product of hydrodynamic processes, small-scale distribution of food resources, relative mobility of meiofauna taxa, temporal variabilities in population abundance, vertical migrations, and the effects of biogenic microtopography. The relative importance of physical and biotic factors affecting this community may change over a tidal cycle, vary seasonally, or exhibit longer-term changes.

Recently, it has been pointed out that current ecological theory does not reflect the complexity of real systems (Pielou 1981). For many years ecological studies have focused on demonstrating the importance of a one dimensional type of interaction in structuring communities. Cody and Diamond (1975) stated that "It is natural selection, operating through competition, that makes the strategic decisions on how sets of species allocate their time and energy". The assumed ubiquitous role of competition in nature has increasingly come

under attack (Dayton 1971, Connell 1975, Menge and Sutherland 1976, Wiens 1977). Recently, ecologists have demonstrated that several types of interactions and processes are important in structuring the community. Previously unfashionable abiotic factors, generally assumed to be causal only in determining species' upper limits, to be "modifying" factors in biotic interactions, or to be inversely correlated in intensity with biotic interactions have been found to play important roles in determining structure of some communities (Strong 1983). Community patterns may be influenced by spatial and temporal changes in the environment, or by competition, or by predators and parasites, or by stochastic events, or by the complex interplay of all of these elements.

I believe that my results argue for the inclusion of more processes and factors in our explanations of the establishment and change of community structure. It is natural that studies which first suggest strong roles for single factors are based on very strong data. It is also natural that later researchers on the same or similar ecosystems are working in a situation different, however slightly, from the first. Changes over time in many factors may have modified the physical and biological character of the system. New data, thus, will not lead to the same conclusions as reached in previous studies.

I believe this has happened here. Hogue and Miller (1981) show strong data establishing a relationship between the spacing of sediment ripples and density oscillations of nematodes on two dates.

In returning to this site, I have encountered a modified situation. Overall densities of meiofauna were different between their study and mine. A large population of Callianassa californiensis had developed at the site. Ripple spacings were different and at times more variable. Thus, it is not surprising that I have found less strength in the relation of density oscillations than they did, and that I have found apparent effects of interfering factors which were not operating at the time of their study.

It is time to adopt a pluralistic approach to determining the important elements structuring various communities. Future ecological studies concerning community dynamics need to concentrate on revealing patterns in the relative importance of specific processes critical to determining community structure.

### Conclusions

1. Physically generated sediment microtopography in the form of sand ripples affects the micro-spatial distribution of meiofauna.
2. On the basis of my results and reports in the literature I conclude that the mechanism by which sediment ripples affect meiofaunal distribution is different for different taxa.
3. The small scale distribution of nematodes is primarily influenced by the micro-spatial distribution of particulate organic matter, their presumed food resource. Sediment ripples control the depositional pattern of organic matter, thus indirectly influencing nematode distribution.
4. The distribution of the non-nematode component of the meiofauna appears to be directly influenced by a property or properties of the sediment ripples. I believe this property may be the micro-flow regime over the sediment surface.
5. The importance of sediment ripples in determining the micro-spatial distribution of meiofauna appears to vary over time. Biogenic microtopography may have affected the distribution of meiofauna at my study site during the spring and summer months. Additionally, seasonal and aseasonal fluctuations in densities and taxonomic composition may have

resulted in changes in the distribution of meiofauna.

6. My data suggests that the distribution of the meiofaunal assemblage in the upper layer of sediment is, at any given time, a dynamic product of hydrodynamic processes, micro-spatial distribution of food resources, relative mobility of meiofaunal taxa, temporal variabilities in population abundance, vertical migrations, and the effects of biogenic microtopography. The relative importance of these factors may change over many temporal scales.

## Literature Cited

- Allredge, A.L. and J.M. King. 1980. Effects of moonlight on the vertical migration pattern of demersal zooplankton. *J. Exp. Mar. Biol. Ecol.* 44:13-156.
- Aller, R. C. 1980. Relationships of tube-dwelling benthos with sediment and overlying water chemistry, *In* Marine Benthic Dynamics. K.R. Tenore and B.C. Coull, eds., Columbia, Univ. South Carolina Press, 451 pp.
- Aller, R.C. and J.Y. Yingst. 1978. Biogeochemistry of tube-dwelling: A study of the sedentary polychaete Amphitrite ornata (Leidy). *J. Mar. Res.* 36:201-254.
- Andrews, P.A. and W.L. Nichols. 1976. Effect of bacteria on dispersal of Caenorhabditis elegans (Rahbdtidae). *Nematologica* 22:451-461.
- Barnett, P.R.O. 1968. Distribution and ecology of harpacticoid copepods of an intertidal mudflat. *Int. Revue ges Hydriobiol.* 53:177-209.
- Bell, S.S. 1979. Short- and long-term variation in a high marsh meiofauna community. *Est. Coastal Mar. Sci.* 9:331-350.
- Bell, S.S. 1983. An experimental study of the relationship between below-ground structure and meiofaunal taxa. *Mar. Biol.* 76:33-39.
- Bell, S.S. and K.M. Sherman. 1980. A field investigation of meiofaunal dispersal: tidal resuspension and its implications. *Mar. Ecol. Prog. Ser.* 3:245-249.
- Bell, S.S. and L.D. Coen 1982a. Investigations on epibenthic meiofauna. I. Abundances on, and repopulation of, the tube-caps of Diopatra cuprea (Polychaeta: Onuphidae) in a subtropical system. *Mar. Biol.* 67:303-309.
- Bell, S.S. and L.D. Coen. 1982b. Investigations on epibenthic meiofauna. I. Influence of microhabitat and macroalgae on abundance of small invertebrates on Diopatra cuprea (Bosc) (Polychaete: Onuphidae) tube-caps in Virginia. *J. Exp. Mar. Biol. Ecol.* 61:175-188.
- Bell, S.S., M.C. Watzin, and B.C. Coull. 1978. Biogenic structure and its effect on the spatial heterogeneity of meiofauna in a salt marsh. *J. Exp. Mar. Biol. Ecol.* 35:99-107.

- Boaden, P.J.S. 1968. Water movement—a dominant factor in interstitial ecology. *Sarsia* 34:125-136.
- Boaden, P.J.S. and D.F. Erwin. 1971. Turbanella hyalina versus Protodriloides symbioticus: A study in interstitial ecology. *Vie Milieu* 22:479-492.
- Boaden, P.J.S. and H.M. Platt. 1971. Daily migration patterns in an intertidal meiobenthic community. *Thalassia Jugosl.* 7:1-12.
- Bradley, W.H. and R. Cooke. 1959. Living and ancient populations of the clam Gemma gemma in a Maine coast tidal flat. *U.S. Fish. Wildl. Ser. Fish. Bull.* 137:304-334.
- Bush, L.F. 1966. Distribution of sand fauna in beaches at Miami, Florida. *Bull. Mar. Sci.* 16:58-75.
- Byers, S.C., E.L. Mills and P.L. Stewart. 1978. A comparison of methods of determining organic carbon in marine sediments, with suggestions for a standard method. *Hydrobiologia* 58:43-47.
- Capstick, C.K. 1959. The distribution of free-living nematodes in relation to salinity in the middle and upper reaches of the River Blyth estuary. *J. Anim. Ecol.* 28:189-210.
- Chandler, G.T. and J.W. Fleeger. 1983. Meiofaunal colonization of azoic estuarine sediment in Louisiana: Mechanisms of dispersal. *J. Exp. Mar. Biol. Ecol.* 69:175-188.
- Chatfield, C. 1980. *The Analysis of Time Series: An Introduction*. Second edition. New York, Chapman and Hall, 268 pp.
- Cody, M.L. and J.M. Diamond. 1975. Introduction. *In Ecology and Evolution of Communities*. M.L. Cody and J.M. Diamond, eds., Cambridge, Mass., Belknap Press, 545 pp.
- Connell, J.H. 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. *In Ecology and Evolution of Communities*. M.L. Cody and J.M. Diamond, eds., Cambridge, Mass., Belknap Press, 545 pp.
- Conrad, J.C. 1976. Sand grain angularity as a factor affecting colonization by marine meiofauna. *Vie Milieu* 26:181-198.
- Coull, B.C. 1970. Shallow water meiobenthos of the Bermuda Platform. *Oecologia (Berlin)* 4:325-357.
- Coull, B.C. 1973. Estuarine meiofauna: A review: Trophic relationships and microbial interactions, *In Estuarine Microbial Ecology*. L.H. Stevenson and R.R. Colwell, eds., Columbia, Univ. South Carolina Press, 536 pp.

- Coull, B.C. and S.S. Bell. 1979. Perspectives in marine meiofaunal ecology. In Ecological Processes in Coastal and Marine Ecosystems. R.J. Livingston ed., New York, Plenum Press, 548 pp.
- Coull, B.C., S.S. Bell, A.M. Savory, and B.W. Dudley. 1979. Zonation of meiobenthic copepods in a Southeast U.S. salt marsh. Est. Coast. Mar. Sci. 9:181-188.
- Crenshaw, D.G. 1980. How interstitial animals respond to viscous flows. Dissertation Abst. #8112290.
- Cubit, J. 1969. Behavior and physical factors causing migration and aggregation of the sand crab *Emerita analoga* (Stimpson). Ecology 50:118-123.
- Dayton, P.K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41:351-389.
- Du Toit, C.G. and J.F.A. Sleath. 1981. Velocity measurements close to rippled beds in oscillatory flow. J. Fluid Mech. 112:71-96.
- Dye, A.H. and J.F. Furstenburg. 1977. An ecophysiological study of the benthic meiofauna of the Swartkops estuary. II. The meiofauna: Composition, distribution, seasonal fluctuations, and biomass. Zool. Afr. 13:19-32.
- Dye, A.H. and J.F. Furstenburg. 1981. Estuarine meiofauna with particular reference to southern Africa, In Estuarine Ecology. J.H. Day, ed., Rotterdam, A.A. Balkema, 411 pp.
- Eckman, J.E. 1979. Small-scale patterns and processes in a soft-substratum, intertidal community. J. Mar. Res. 37:437-457.
- Eckman, J.E. 1983. Hydrodynamic processes affecting benthic recruitment. Limnol. Oceanogr. 28:241-257.
- Eckman, J.E., A.R. Nowell, and P.A. Jumars. 1981. Sediment destabilization by animal tubes. J. Mar. Res. 39:361-374.
- Feller, R.J. 1980. Quantitative cohort analysis of a sand-dwelling meiobenthic harpacticoid copepod. Est. Coastal Mar. Sci. 11:459-476.
- Fenchel, T. 1970. Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudineum*. Limnol. Oceanogr. 15:14-20.
- Fenchel, T. 1978. The ecology of micro- and meiobenthos. Ann. Rev. Ecol. Syst. 9:99-121.

- Fenchel, T. and B.O. Jansson. 1966. On the vertical distribution of the microfauna in the sediments of a brackish-water beach. *Ophelia* 4:227-243.
- Fenchel, T. and R.J. Riedl. 1970. The sulphide system: A new biotic community underneath the oxidized layer of marine sand bottoms. *Mar. Biol.* 7:255-268.
- Fenchel, T., B.O. Jansson, and W.J. Thun. 1967. Vertical and horizontal distribution of the metazoan microfauna and of some physical factors in a sandy beach in the northern part of the Oresund. *Ophelia* 4:227-243.
- Frankenberg, D., S.L. Coles, and R.E. Johannes. 1967. The potential significance of Callianassa major fecal pellets. *Limnol. Oceanog.* 12:113-120.
- Gerlach, S.A. 1977. Attraction to decaying organisms as a possible cause for patchy distribution of nematodes in a Bermuda beach. *Ophelia* 16:151-165.
- Gerlach, S.A. 1978. Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. *Oecologia (Berlin)* 33:55-69.
- Giere, O. 1975. Population structure, food relations and ecological of marine oligochaetes, with special reference to meiobenthic species. *Mar. Biol.* 31:139-156.
- Gray, J.S. 1965. The behavior of Protodrilus symbioticus Giard in temperature gradients. *J. Anim. Ecol.* 34:455-61.
- Gray, J.S. 1966. The attractive factor of intertidal sands to Protodrilus symbioticus. *J. Mar. Biol. Ass. U.K.* 46:627-645.
- Gray, J.S. 1967a. Substrate selection by the archiannelid Protodrilus rubropharyngeus. *Helgol. Wiss. Meeresunters* 15:253-269.
- Gray, J.S. 1967b. Substrate selection by the archiannelid Protodrilus hypoleucus (Armenante). *J. Exp. Mar. Biol. Ecol.* 1:47-54.
- Gray, J.S. 1968. An experimental approach to the ecology of the harpacticoid Leptastacus constrictus Lang. *J. Exp. Mar. Biol. Ecol.* 2:278-292.
- Gray, J.S. 1974. Animal-sediment relationships. *Oceanog. Mar. Biol. Ann. Rev.* 12:223-261.
- Gray, J.S. and R.M. Johnson. 1970. The bacteria of a sandy beach as an ecological factor affecting the interstitial gastrotrich Turbanella hyalina Schultze. *J. Exp. Mar. Biol. Ecol.* 4:119-133.

- Gray, J.S. and R.M. Rieger. 1971. A quantitative study of the meiofauna of an exposed beach at Robin Hood's Bay, Yorkshire. *J. Mar. Biol. Ass. U.K.* 51:1-19.
- Hagerman, G.M. and R.M. Rieger. 1981. Dispersal of benthic meiofauna by wave and current action in Bogue Sound, N.C. USA. *Mar. Ecol.* 2:245-270.
- Harrison, B. 1977. The effect of sand ripples on the small-scale distribution of the intertidal benthos with particular reference to the harpacticoid copepods. *Abst. Third Intn. Conf. Meiofauna, Hamburg, FRG.*
- Heip, C. 1975. On the significance of aggregation in some benthic marine invertebrates, *In Proc. 9th Europ. Mar. Biol. Symp.* H. Barnes, ed. Aberdeen University Press, 760 pp.
- Heip, C. and P. Engels. 1977. Spatial segregation of copepod species from a brackish water habitat. *J. Exp. Mar. Biol. Ecol.* 26:77-96.
- Hogue, E.W. 1978. Spatial and temporal dynamics of a subtidal estuarine gastrotrich assemblage. *Mar. Biol.* 49:211-222.
- Hogue, E.W. 1982. Sediment disturbance and the spatial distributions of shallow water meiobenthic nematodes on the open Oregon coast. *J. Mar. Res.* 40:551-573.
- Hogue, E.W. and C.B. Miller. 1981. Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. *J. Exp. Mar. Biol. Ecol.* 53:181-191.
- Hulberg, L.W. and J.S. Oliver. 1980. Caging manipulations in marine soft-bottom communities: Importance of animal interactions or sedimentary habitat modifications. *Can. J. Fish. Aqu. Sci.* 37:1130-1139.
- Hulings, N.C. and J.S. Gray. 1976. Physical factors controlling the abundance of meiofauna on tidal and atidal beaches. *Mar. Biol.* 34:77-83.
- Hummon, W.D., J.W. Fleeger and M.R. Hummon. 1976. Meiofauna-macrofauna interactions: I Sand beach meiofauna affected by maturing Limulus eggs. *Chesapeake Sci.* 17:297-299.
- Jansson, B.P. 1968. Quantitative and experimental studies of the interstitial fauna of four Swedish beaches. *Ophelia* 5:1-71.
- Jenkins, G.M. and D.G. Watts. 1968. *Spectral Analysis and its applications.* San Francisco, Holden-Day, 525 pp.
- Johnson, R.G. 1974. Particulate matter at the sediment-water interface

- in coastal environments. *J. Mar. Res.* 33:313-330.
- Johnson, R.G. 1977. Vertical variation in particulate matter in the upper 20 cm of marine sediments. *J. Mar. Res.* 35:273-282.
- Joint, I.R., J.M. Gee, and R.M. Warwick. 1982. Determination of fine-scale vertical distribution of microbes and meiofauna in an intertidal sediment. *Mar. Biol.* 72:157-164.
- Jumars, P.A. and A.M. Nowell. 1984. Fluid and sediment dynamic effects on marine benthic community structure. *Amer. Zool.* 24:45-55.
- Komar, P.D. 1974. Oscillatory ripple marks and the evaluation of ancient wave conditions and environments. *J. Sed. Petrol.* 44:169-180.
- Komar, P.D., R.H. Neudeck, and L.D. Kulm. 1972. Observation and significance of deep-water oscillatory ripple marks on the Oregon continental shelf. *In Shelf Sediment Transport: Process and Pattern.* D. Swift, D. Duane, and O. Pilkey, eds., Stroudsburg, Pa., Dowden, Hutchinson, and Ross, Inc., 656 pp.
- Kulm, L.D. and J. Bryne. 1966. Sediment response to hydrography in an Oregon estuary. *Mar. Geol.* 4:85-118.
- Lee, J.J., K. Tenore, J.H. Tietjen, and C. Mastropaola. 1974. An experimental approach towards understanding the role of meiofauna in a detritus-based marine food web. *Biol. Bull.* 147:488-489.
- Lee, J.J., J.H. Tietjen, C. Mastropaola and H. Rubin. 1977. Food quality and the heterogenous distribution of meiofauna. *Helgol. wiss. Meeres.* 30:272-282.
- Levinton, J.S. 1982. *Marine Ecology.* New Jersey, Prentice-Hall, 526 pp.
- McCall, P.L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J. Mar. Res.* 35:221-266.
- McIntyre, A.D. 1961. Quantitative differences in the fauna of boreal mud associations. *J. Mar. Biol. Ass. U.K.* 41:599-616.
- McIntyre, A.D. 1968. The meiofauna and macrofauna of some tropical beaches. *J. Zool. Lond.* 156:377-392.
- McIntyre, A.D. 1969. Ecology of marine meiobenthos. *Biol. Rev.* 44:245-290.
- McIntyre, A.D. and D.J. Murison. 1973. The meiofauna of a flatfish nursery ground. *J. mar. biol. Ass. U.K.* 53:93-118.
- McLachlan, A., D. Winter, and L. Botha. 1977. Vertical and horizontal

- distribution of sub-littoral meiofauna in Algoa Bay, South Africa. *Mar. Biol.* 40:355-364.
- Mare, M.F. 1942. A study of a marine benthic community with special reference to the micro-organisms. *J. Mar. Biol. Ass. U.K.* 25:517-554.
- Menge, B.A. and J.P. Sutherland. 1976. Species diversity gradients: Synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Nat.* 110:351-369.
- Moore, H.B. 1931. The muds of the Clyde Sea area. *J. Mar. Biol. Ass. U.K.* 17:325-358.
- Myers, A.C. 1977. Sediment processing in a marine subtidal sandy bottom community: I Physical aspects. *J. Mar. Res.* 35:609-632.
- Newell, R.C. 1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch Hydrobia ulvae and the bivalve Macoma balthica. *Proc. Zool. Soc. London* 144:25-43.
- Newton, R.S. 1968. Internal structure of wave formed ripple marks in the near-shore zone. *Sedimentology* 11:275-292.
- Nicholas, W.L. 1975. *The Biology of Free-Living Nematodes*. Oxford, Clarendon Press, 219 pp.
- Oakden, J.M. 1980. Feeding and habitat selection in phoxocephalid amphipods. *Amer. Zool.* 20:754.
- Oliver, J.S., J.M. Oakden, and P.N. Slattery. 1982. Phoxocephalid amphipod crustaceans as predators on larvae and juveniles in marine soft bottom communities. *Mar. Ecol. Prog. Ser.* 7:179-184.
- Osenga, G.A. and B.C. Coull. 1983. Spartina alterniflora (Loisel) root structure and meiofaunal abundance. *J. Exp. Mar. Biol. Ecol.* 67:221-225.
- Paine, R.T. 1977. Controlled manipulations in the marine intertidal zone, and their contribution to ecological theory. *In* *The changing scenes in natural sciences, 1776-1976*. Acad. Nat. Sci. Phil. Sp. Publ. 12.
- Perkins, E.J. 1958. The food relationships of the microbenthos, with particular reference to that found at Whitstable, Kent. *Ann. Mag. Nat. Hist.* 13:64-77.
- Peterson, C.H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons, *In* *Ecological Processes in Coastal and Marine Systems*. R.J. Livingston, ed., New York, Plenum Press, 548 pp.

- Peterson, C.H. 1980. Approaches to the study of competition in benthic communities in soft sediments, In Estuarine Perspectives. V.S. Kennedy, ed., New York, Academic Press, 533 pp.
- Pielou, E.C. 1969. An Introduction to Mathematical Ecology. New York, Wiley-InterScience. 286 pp.
- Pielou, E.C. 1981. The usefulness of ecological models: A stock taking. *Quarterly Rev. Biol.* 1:17-33.
- Platt, H.M. 1977. Vertical and horizontal distribution of free-living marine nematodes from Strangford Lough, Ireland. *Cahiers de Biologie Mar.* 18:261-273.
- Platt, H.M. and R.M. Warwick. 1980. The significance of free-living nematodes to the littoral ecosystem, In The Shore Environment, vol. 2: Ecosystems. J.H. Price, D.E.G. Irvine, and W.F. Farnham, eds., New York, Academic Press, 945 pp.
- Platt, T. and K.L. Denman. 1975. Spectral Analysis in Ecology. *Ann. Rev. Ecol. Syst.* 6:189-210.
- Powell, E.N. , T.J. Bright, A. Woods, and S. Gittings. 1983. Meiofauna and the thibios in the East Flower Garden Brine Seep. *Mar. Biol.* 73:269-283.
- Raudkivi, A.J. 1976. Loose Boundary Hydraulics. 2nd. ed. New York, Pergamon Press, 397 pp.
- Rees, C.B. 1940. A preliminary study of the ecology of a mudflat. *J. Mar. Biol. Ass. U.K.* 21:185-199.
- Reise, K. 1981a. Gnathostomulida abundant alongside polychaete burrows. *Mar. Ecol. Prog. Ser.* 6:329-333.
- Reise, K. 1981b. A high abundance of small zoobenthos around biogenic structures in tidal sediments of the Wadden Sea. *Helgol. wiss Meeres.* 34:413-425.
- Reise, K. and P. Ax. 1979. A meiofaunal 'thibios' limited to the anaerobic sulfide system of marine sand does not exist. *Mar. Biol.* 54:225-237.
- Remane, A. 1933. Verteilung und Organisation der benthonischen Mikrofauna der Kieler Bucht. *Wiss. Meeresuntersuch N.F.* 21:161-221.
- Russell-Hunter, W.D. 1970. Aquatic productivity: An introduction to some basic aspects of biological oceanography and limnology. New York, Macmillan Pub. Co., Inc., 306 pp.
- Sanders, H.L. and R.R. Hessler. 1969. Ecology of deep-sea benthos.

Science 163:1419-1424.

- Sanders, H.L., E.M. Goudsmit, E.L. Mills, and G.E. Hampson. 1962. A study of the intertidal fauna of Barnstable Harbor, Mass. *Limnol. Oceanog.* 7:63-79.
- Schafer, C.T. 1971. Sampling and spatial distribution of benthonic foraminifera. *Limnol. Oceanog.* 16:944-951.
- Sharma, J. and J.M. Webster. 1983. The abundance and distribution of free-living nematodes from two Canadian Pacific beaches. *Est. Coastal and Shelf Sci.* 16:217-227.
- Sharma, J., B.E. Hopper, and J.M. Webster. 1978. Benthic nematodes from the Pacific coast with special reference to the Cyatholaimids. *Annales Soc. r. Zool. Belg. T.* 108:47-56.
- Shepard, F.P. 1954. Nomenclature based on sand-silt-clay ratios. *J. Sed. Petrol.* 24:151-158.
- Shepard, F.P. 1963. *Submarine Geology*. 2nd. ed. New York, Harper and Row, Pub., 557 pp.
- Sherman, K.M. and B.C. Coull. 1980. The response of meiofauna to sediment disturbance. *J. Exp. Mar. Biol. Ecol.* 46:59-71.
- Sibert, J.R. 1981. Intertidal hyperbenthic populations in the Nanaimo Estuary. *Mar. Biol.* 46:259-265.
- Sikora, J.P., W.B. Sikora, C.W. Erkenbrecher, and B.C. Coull. 1977. Significance of ATP, carbon, and caloric content of meiobenthic nematodes in partitioning benthic biomass. *Mar. Biol.* 44:7-14.
- Smidt, E.L.B. 1951. Animal production in the Danish Waddensea. *Medd. Komm. Dan. Fisk. Havunders* 11:151.
- Strong, D.R., Jr. 1983. Natural variability and the manifold mechanisms of ecological communities. *Am. Nat.* 122:636-660.
- Swedmark, B. 1964. The interstitial fauna of marine sand. *Biol. Rev.* 37:1-42.
- Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43:614-624.
- Teal, J.M. and W. Wieser. 1966. The distribution and ecology of nematodes in a Georgia salt marsh. *Limnol. Oceanog.* 11:217-222.
- Tenore, K.R., J.H. Tietjen and J.J. Lee. 1977. Effect of meiofauna on the incorporation of aged eelgrass, *Zostera marina*, detritus by the polychaete *Nephtys incisa*. *J. Fish. Res. Bd. Can.* 34:563-567.

- Thistle, D. 1978. Harpacticoid dispersion patterns: implications for deep-sea diversity maintenance. *J. Mar. Res.* 36:377-397.
- Tietjen, J.H. 1969. The ecology of shallow-water meiofauna in two New England estuaries. *Oecologia* (Berlin) 2:251-291.
- Trueman, E.R. 1971. The control of burrowing and the migratory behavior of Donax denticulatus (Bivalvia: Tellinacea). *J. Zool.* 165:453-469.
- van Blaricom, G.R. 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. *Ecol. Monogr.* 52:283-305.
- Virnstein, R.W. 1977. The importance of predation by crabs and fishes on benthic infauna in the Chesapeake Bay. *Ecology* 58:1199-1217.
- Virnstein, R.W. 1978. Predator caging experiments in soft sediments: caution advised, *In* *Estuarine Interactions*. M.L. Wiley, ed., New York, Academic Press, 603 pp.
- Ward, A.R. 1975. Studies on the sublittoral free-living nematodes of Liverpool Bay. II. Influence of sediment composition on the distribution of marine nematodes. *Mar. Biol.* 30:217-225.
- Wiens, J.A. 1977. On competition and variable environments. *Amer Sci.* 65:590-597.
- Wieser, W. 1959. The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. *Limnol. Oceanog.* 4:181-194.
- Wieser, W. 1960. Benthic studies in Buzzards Bay II The meiofauna. *Limnol. Oceanog.* 5:121-137.
- Wieser, W. and J. Kanwisher. 1961. Ecological and physiological studies on marine nematodes from a small salt marsh near Woods Hole, Mass. *Limnol. Oceanog.* 6:262-270.
- Woodin, S.A. 1976. Adult-larval interactions in dense infaunal assemblages: Patterns of abundance. *J. Mar. Res.* 34:25-41.
- Woodin, S.A. 1978. Refuges, disturbance, and community structure: A marine soft-bottom example. *Ecology* 59:274-284.
- Woodin, S.A. 1981. Disturbance and community structure in a shallow water sandflat. *Ecology*, 62:1052-1066.
- Yalin, M.S. 1972. *Mechanics of Sediment Transport*. New York, Pergamon Press, 290 pp.