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of a Meiobenthic Assemblage on the Open Oregon Coast and Its
Relationship to the Diet of 0-age Flatfishes

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The shallow, wave-swept sea floor off the central Oregon coast
is used by 0-age flatfishes as a nursery ground.  This dissertation
is based on a series of projects designed to:  1) identify the domi-
nant meiobenthic nematodes present in a coastal nursery area; 2)
describe the important temporal and spatial scales of nematode varia-
bility at this site; 3) discuss the role of sediment disturbance in
structuring nematode assemblages; and 4) relate seasonal and spatial
differences in the distributions of meiobenthos to observed changes
in the diet of flatfishes.

The 19 numerically dominant nematode species found at the study
site showed significant fluctuations in density over a 15 month
period, yet their rank order based on abundance did not change.  Four
mechanisms capable of producing seasonal changes in nematode abundance
without altering species proportions are discussed:   winnowing from

sediments, non-selective predation, seasonally variable food resources, and compensatory links between birth and death rates among species.

Significant differences in the abundance of nematodes were found over horizontal distances of kilometers and centimeters. Sediment disturbance contributes to the generation of these spatial patterns. Over broad scales there were two distinct faunal groups associated with different water depths. The division between these assemblages was closely correlated with the threshold depth at which sediments are influenced by passing waves. On small scales ($<0.25$ m$^2$), the distributions of the numerically dominant species varied seasonally. In the winter, frequent storm activity mixes the bottom sediments and randomly distributes the fauna over the sea floor. In the late spring and summer, physical disruption of sediments is minimal and biological factors, e.g., attraction between males and females, lead to aggregation.

Food habits of juvenile English sole were a function of location of capture within the study area, season, and fish length. Diets of fish less than 35 mm SL varied greatly both between seasons in the same year and between years. Diets of English sole captured in trawls obtained at the same depth and different depths were similar in January 1979 but were highly variable in May 1979. These temporal and spatial differences in feeding are thought to be related to seasonal changes in the abundance and spatial distributions of benthic prey.

SEASONAL CHANGE IN THE ABUNDANCE AND SPATIAL DISTRIBUTION

OF A MEIOBENTHIC ASSEMBLAGE ON THE OPEN OREGON COAST

AND ITS RELATIONSHIP TO THE DIET OF 0-AGE FLATFISHES


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## Chapter 1.  Research Goals

Meiobenthic organisms are functionally defined as including all those bottom-dwelling animals which pass through a 0.5 mm sieve and are retained on a 0.064 mm sieve (McIntyre, 1969).  The biology and general ecology of this benthic size fraction has been reviewed elsewhere (Swedmark, 1964; McIntyre, 1969; Gerlach, 1971, 1978; Fenchel, 1978; Coull and Bell, 1979), and only a few basic points need to be emphasized here.  Meiofauna are very abundant, typically reaching densities of $10^6$ $m^{-2}$ in estuarine and coastal waters, and are taxonomically diverse.  Dominant groups which spend their entire life cycle within this size range (permanent meiofauna) include free-living nematodes, harpacticoid copepods, gastrotrichs, turbellarians, kinorhynchs, tardigrades, and rotifers.  Larval stages of some macro-benthic taxa (temporary meiofauna) are occasionally present for brief periods of time.  Nematodes dominate these micrometazoan assemblages, making up 60-95% of all meiobenthic animals in habitats ranging from intertidal sands to deep-sea clays.  Life history characteristics common to most permanent meiobenthos are small clutch size and direct development with no pelagic larval stages.  Generation times range from a few days to 2 years.  Feeding behavior among these small animals is diverse, with herbivore, carnivore, omnivore, and deposit feeders represented.

There are three broad morphological categories of meiobenthic species, each related to a specific sedimentary habitat. Sand-dwelling species are small, vermiform animals adapted for crawling through the interstitial spaces between sand grains. They usually occur in sediments having mean grain sizes greater than approximately 160 μm and a low silt-clay content. Mud inhabitants and epibenthic-epiphytic forms are more robust, with the mud fauna modified for burrowing through sediments and epibenthic-epiphytic species adapted for crawling or swimming at the substrate-water interface.

Until relatively recently most work with meiobenthic animals was strictly taxonomic. Consequently, many questions concerning their ecology remain unanswered. This dissertation is composed of three manuscripts (Chapters 2 through 4) which address several problems in the ecology of continental shelf meiofauna.

The site selected for this work is located on the central Oregon coast in a region which serves four species of flatfishes as a nursery ground (see Fig. 7, p. 104). The sea-floor throughout the study area consists of fine, well-sorted sands, which are frequently mixed and reworked by wave-generated oscillatory currents. My research efforts concentrated on the nematodes of this region, since they are the most abundant meiobenthic group (98% of all meiofauna at the study site), yet the least studied. Specific research goals included: a) evaluation of temporal and spatial variability in the abundance of the dominant nematode and harpacticoid copepod species; b) comparison of this distributional information with measures of environmental parameters to determine the relative importance of physical and biological

factors in structuring shallow-water meiobenthic assemblages; c)

assessment of the trophic importance of nematodes and harpacticoid

copepods as food for juvenile flatfishes; and d) determination of the

relationship between spatial distributions of prey and the diet of 0-

age flatfishes. The following paragraphs describe each of these four

objectives in more detail.

a) Evaluation of temporal and spatial variability

Although quantitative description of meiofaunal assemblages has

been going on for several decades (see Coull and Bell, 1979), there

are significant gaps in this information. Estuaries and protected

bays have been extensively studied, but data from continental shelves

are very limited. Examples of this lack of data include: 1) only

one published report lists the abundances of open coastal nematode

species in the Pacific Ocean (Nichols, 1980), and it was based on

samples from a single box core; 2) studies of seasonal change in

species composition and densities of offshore nematodes have been

limited to the North Sea (Warwick and Buchanan, 1971; Lorenzen, 1974;

Juario, 1975); and 3) detailed description of nematode spatial dis-

tribution on scales less than 1 km has not been attempted. Chapters

2 and 3 address these deficiencies by describing the spatial and

temporal variability of meiobenthic nematodes from the Oregon coast.

This description documents the natural range and scales of variability

present in open-coast meiobenthic populations and establishes a basis

for effective sampling plans and experimental designs which take

these factors into account.

b) <u>Structure of meiobenthic assemblages</u>

Correlations between animal distribution patterns and environmental factors can provide insight into the mechanisms which maintain the relative and absolute abundances of species. A dominant physical feature of the study area is the frequent reworking of sediments by waves. Recent studies of macrofauna distribution patterns in shallow coastal waters (5-20 m) indicate that sediment disturbance generated by waves can profoundly affect the structure of macrobenthic assemblages (e.g., Eagle, 1975; Davis and VanBlaricom, 1978; McCall, 1977, 1978; Rees et al., 1977; Oliver et al., 1980). Sediment resuspension associated with wave activity can produce spatial and temporal variability in species abundance by increasing mortality or redistributing populations. In addition, when the effects of such disturbances are localized in space or time, new habitat patches are created. These are available for colonization by opportunistic species which would otherwise be excluded. Thus, localized disturbance can provide a mechanism by which species coexistence is maintained. The results presented in Chapter 3 were used to indirectly assess the extent to which sediment disturbance influences shallow-water nematode populations in open coastal habitats.

c) <u>Trophic importance of meiofauna</u>

The ecological importance of meiofauna in the marine environment has been frequently debated, with several contrasting points of view expressed. McIntyre (1969), Marshall (1970), McIntyre and Murison (1973), and Giere (1975), among others, concluded that meiobenthic organisms are trophic "dead ends" whose sole function within the

marine ecosystem is the remineralization of nutrients. Alternatively,

Bregnballe (1961), Teal (1962), Feller and Kaczynski (1975), Sibert

et al. (1977), and Sikora (1977) found that meiofaunal species were

important constituents in the diets of larger benthic and epibenthic

predators and hence were important trophic links within marine food

webs. Gerlach (1978) has suggested a third possibility. Based on

estimates of secondary productivity, Gerlach concludes that meiofauna

cannot meet more than 10% of the overall energy requirements of

macrobenthic predators. But he also suggests that meiobenthos can

indirectly increase the food resources of these larger animals by

stimulating bacterial productivity. Support for this contention is

based on work showing that the grazing activity of nematodes on

bacteria and detritus can expedite the breakdown of plant-derived

detritus and increase bacterial biomass (Lee et al., 1976; Tenore et

al., 1977).

Coull and Bell (1979) reviewed much of this often conflicting

literature and noted a correlation between the type of substrate in

which meiobenthic animals live and their relative importance as food

for higher trophic levels. Research which has led to the conclusion

that meiofauna are not fed upon by larger animals has been carried

out entirely in sandy environments. Work leading to the opposite

conclusion has been conducted in muds. This habitat dependent dif-

ference in trophic importance seems to relate to the abundances and

vertical distributions of the fauna within muddy and sandy sediments.

Meiobenthic animals are not only more numerous in muds than in sands,

but they are also restricted to the top few centimeters of sediment.

This is opposed to the situation in sands where the fauna is distributed down to 10 or 15 cm. Predators apparently can better exploit the situation in muds, where potential prey concentrate at the sediment-water interface. Feeding in sands may not be energetically beneficial given the large volumes of sediment which must be processed to extract smaller numbers of prey.

Preliminary examination of 0-age flatfishes from the sandy bottom of the study area indicated that large numbers of harpacticoid copepods and nematodes were being eaten. Such results were contrary to the previously noted association between sediment type and trophic importance. The work outlined in Chapter 4 was carried out to document the food habits of young flatfishes and to investigate the possibility that meiofauna may be important as prey in sandy bottoms.

d) Spatial distributions of prey and food habits of fishes

Ivlev (1961) noted a relationship between the spatial distribution of prey in aquaria and their rate of consumption by small fishes. Increase in aggregation of food had the same effect on the rate of prey ingestion as increase in the overall concentration of food. However, no studies based on field data have demonstrated a relationship between predation rate and aggregation of prey. Preliminary samples from the study site revealed that two harpacticoid species in the genus Halectinosoma were consumed by 0-age English sole. Data obtained on the small-scale spatial distribution of these species were to be compared with their relative abundances in the diet of English sole. A correlation between the proportions of these prey in the guts of fish and their relative degree of spatial aggregation

would suggest that Ivlev's findings may hold in field situations. As will be discussed later, the low densities of harpacticoids at the study site precluded this test.

Chapter 2

SEASONAL FLUCTUATIONS IN THE ABUNDANCE OF SHALLOW-WATER

MEIOBENTHIC NEMATODES ON THE OPEN OREGON COAST

## Abstract

Seasonal changes in the abundance and reproductive status of the nematode fauna located at a sandy site in 25 m of water on the central Oregon coast were monitored between July 1978 and September 1979. Unlike previous reports on offshore nematode assemblages, highly significant fluctuations in total nematode density over time were detected. Abundances ranged from 790 per 10 $cm^2$ in August 1978 to 1617 per 10 $cm^2$ in May 1979, and averaged 1039 per 10 $cm^2$ for the entire period. Both juveniles and gravid females were present in the same relative proportions throughout the year, indicating that reproduction is continuous and asynchronous.

Twenty-three nematode families were identified from this location. The dominant groups were the Desmodoridae, Ceramonematidae, Monhysteridae, Desmoscolecidae, and Comesomatidae. Most species were present in very low numbers throughout the year. Only 19 nematode species averaged 1% or more of the total fauna over time. Abundances of these 19 dominant forms varied among sampling dates, yet their rank order of abundance did not change significantly. Thus, the numerically most common species must respond similarly to environmental changes over time.

Four mechanisms capable of producing seasonal changes in nematode abundance without altering species proportions are discussed: winnowing from sediments, non-selective predation, seasonally variable food resources, and compensatory links between birth and death rates among species. Each of these possibilities, however, fails to explain important features of the data.

Persistence in nematode dominance structure over time resembles that found in plankton communities of the North Pacific central gyre. Although their environments are very different, the nematodes of this study and the plankton of the North Pacific central gyre have several important features in common:  organisms are small, reproduction is continuous, communities are very diverse, and individuals are not space limited.  The key to explaining maintenance of species proportions probably lies in some aspect of these unique features.

## Introduction

Free-living nematodes are numerically the most abundant marine benthic metazoans. They provide food for larger infaunal and epibenthic organisms (e.g., Perkins, 1958; Tietjen, 1969; Sikora, 1977; Oakden, 1980), and may increase benthic productivity by stimulating bacterial growth (Gerlach, 1978; Riemann and Schrage, 1978). Despite this numerical dominance and trophic importance, very little descriptive information has been gathered regarding the species composition of nematode assemblages and the changes in these populations over time, particularly from shallow (<50 m) sediments along high energy coastlines. Evaluations of seasonal fluctuations in the abundances of nematode species inhabiting unprotected waters of continental shelves have been restricted to the North Sea (Warwick and Buchanan, 1971; Lorenzen, 1974; Juario, 1975). Quantitative assessments of species densities in other open coastal regions exposed to continual wave and storm activity have been limited to the waters off Peru (Nichols, 1980) and North Carolina (Tietjen, 1971, 1976).

The goal of this study was to expand upon this earlier work by describing the nematode fauna at a shallow water station on the west coast of North America. Changes in the abundance and reproductive status of the dominant species were monitored over a one year period. Results were used to further define the qualitative and quantitative range of natural variability present in open coastal nematode assemblages.

Materials and Methods

The study site is located off Moolach Beach on the central
Oregon coast, 3.7 km northwest of Yaquina Head at a depth of 25 m
(44°42.4'N, 124°05.7'W, station MB1 of Hogue, 1982). I collected
samples from the well-sorted sands of this station on eight occasions
between July 1978 and September 1979 (see Table 1). During each of
the first six cruises, three replicate samples, spaced 30 m apart,
were obtained using a 0.25 m$^2$ Hessler-Sandia box core. The sediments
within each box were subsampled to a depth of 18 cm with two randomly
placed, clear plastic, core tubes having an internal diameter of 1.9
cm (total 6 cores per date). On both 7 August and 20 September 1979
four replicate samples positioned approximately 10 m apart were
collected using a 0.10 m$^2$ Smith-McIntyre grab. One subsample was
obtained from the center of each of these grabs with the 1.9 cm
diameter corer (total 4 cores per date). Since the Smith-McIntyre
grabs did not penetrate as deeply into the sand as the box cores,
only the top 6 cm of sediment could be collected.

Salinity and temperature of the bottom water were measured
during each cruise by lowering a conductivity-temperature sensor to
1 m off the bottom. Sediment samples were also gathered and were
later wet-sieved to determine the graphic mean grain size ($M_z$),
inclusive graphic standard deviation ($\sigma_I$), and percent silt-clay
(Folk, 1974). Navigational accuracy in returning to the same position
was estimated to be within 50 m. On one date, 23 October 1978,
commercial crabbing operations forced us to sample in deeper water
(28 m), 150 m to the southwest of the usual location.

All samples were preserved immediately in 10% buffered Formalin and stained with rose bengal. Meiofauna were extracted from the sediments by adding water to each sample, shaking, and decanting onto a 38.5 μm sieve. This process was repeated three times, with the fauna then being washed into a petri dish and sorted three times. Extraction efficiency was 98% compared to numbers achieved after 10 rinses and subsequent examination of the tailings. Sorting efficiency was measured by placing the petri dish under a dissecting microscope and instructing independent observers to make 10 passes through the sample. Results indicated that 90% of all nematodes are picked out of the sample after 3 searches through the dish. Nematodes were placed in glycerin mounts and identified to species under a compound microscope for all but two sampling dates, August 1978 and September 1979, for which only the total number of nematodes present was determined. All individuals were tallied into one of four reproductive categories: juveniles, males (spicula present), mature females (ovaries present), and gravid females (eggs present).

Analysis of the data was complicated by uncertainties in comparing results obtained from two sampling devices, box cores and grabs, which did not sample the sediment in the same manner or to the same depth. Likewise, problems existed due to the positioning differences between the October 1978 samples and the rest of the collections. Hogue (1982) found a significant difference between the species composition of the fauna at the 25 m seasonal site (MB1) and that in slightly deeper water only 250 m away. Nematodes from October 1978 belonged to the deeper assemblage. For these reasons, only data

obtained from box cores which were correctly positioned in 25 m of water were used to describe the fauna and to calculate statistical significance of density fluctuations over time. Results from the October 1978 and August and September 1979 collections have been included for comparison only. In the case of total nematode abundances, data from five sampling dates (July and August 1978, January, March, and May, 1979) were log-transformed and a one-way analysis of variance (ANOVA) was used to estimate significance of variations in density over time. I used a one-way multivariate analysis of variance (SPSS program MANOVA; Cohen and Burns, 1977) to test for significant differences in the log-transformed abundances of the dominant species on four dates (July 1978; Jaunary, March and May 1979). Pillia's $\underline{V}$ (Olson, 1976) was selected as the test criterion.

Results

Physical parameters measured on each sampling date are shown in Table 1. Neither temperature nor salinity of the bottom water fluctuated much. Salinities were lowest (32-33°/$_{oo}$) and temperature generally highest (9-14°C) following the periods of southwesterly winds associated with passing storm systems. These winds occurred most frequently between October and March, although they also preceded the August 1978 and September 1979 cruises. The coolest temperatures (7-8°C) and highest salinities (33-34°/$_{oo}$) were usually found during the summer after periodic upwelling events generated by northerly winds. Changes were also noted in the granulometry of the fine, well-sorted sands at the Moolach Beach site. The proportion of silt-clay sized particles varied in response to the seasonally variable hydrodynamic regime, ranging from 0.2 to 0.9% in the winter to over 3.0% in the late summer. Winter storms removed the smaller particles by resuspending and carrying them offshore. Fluctuations in mean grain size and the degree of sorting, however, had no systematic pattern. The sediments were very clean, having an organic content less than 0.1% (see Carey, 1965). Summaries of the physical oceanographic and sedimentary processes occurring on the Oregon continental shelf are available in Komar et al. (1972) and Kulm et al. (1975).

Figure 1 illustrates the changes in total nematode density over the 14 month sampling period. Since data for August and September 1978 were based on cores which penetrated only 6 cm into the sediment, rather than 18 cm as on previous dates, a correction factor was applied to make the densities approximately comparable. Vertical

partitioning of the longer cores showed that 70% of all nematodes living at this site occurred in the uppermost 6 cm of sediment. Values obtained from the shorter corers collected within Smith-McIntyre grabs were therefore adjusted by dividing by 0.7 before being plotted. Numerical abundance of nematodes averaged 1019 per 10 cm$^2$ (SD = 293) over all eight sampling dates and 1039 per 10 cm$^2$ (SD = 350) when October 1978 and August and September 1979 were excluded. Densities were uniformly low during the summer of 1978, but increased twofold between January and May 1979. These changes in total nematode abundance were highly significant (ANOVA, $F_{[4,25]}$ = 7.37, p < 0.001).

Table 2 lists the 23 nematode families identified during this study along with their overall relative abundances. The Desmodoridae and Ceramonematidae were the most common, each representing slightly less than 19% of the fauna. Also abundant were the Monhysteridae, Desmoscolecidae, Comesomatidae, Oncholaimidae, and Axonolaimidae. A total of 98 species were recognized. Most occurred in low density. Only the 19 forms shown in Table 3 averaged 1% or more of the total assemblage between July 1978 and May 1979. These numerically dominant nematodes combined to make up approximately 50% of the fauna. Abundances of the Microlaiminae are also given in Table 3. Difficulties encountered in consistently identifying members of this subfamily at the species level necessitated grouping them together at this taxonomic level. Several species of Microlaimus and Calomicrolaimus would probably have been included in the list of dominant species had problems with their taxonomy been overcome. It is obvious that this

benthic assemblage is extremely diverse, with the equitability of species composition being quite high.

A MANOVA was used to test the significance of changes in the density of the 19 dominant species listed in Table 3. Seasonal variations were significant (Pillia's $V$ = 2.82, $F_{[57,12]}$ = 3.23, p = 0.01). Even though the absolute abundances of species changed over time, their relative proportions remained quite constant (see Table 3). The density of the most abundant species, Ceremonema sp. A, almost doubled between July 1978 and May 1979, yet its percentage of the total nematode fauna only ranged between 7.4 and 9.7%. The relative abundances of the other dominant nematodes showed similarly limited variations over time. Accordingly, the rank order of species by numerical abundance did not change significantly among sampling dates (Friedman's randomized block ANOVA, $\chi^2_{[18]}$ = 52.5, p < 0.005). Kendall's coefficient of concordance, $W$ (Gibbons, 1971), was used to quantify the magnitude of this agreement in species rankings. This index ranges from 0 for complete independence to 1.0 for complete agreement. In the case of the 19 dominant nematodes, $W$ = 0.71. Although excluded from this analysis, species proportions in August 1979 remained consistent with those found earlier. The relative abundance of the dominant species at Moolach Beach remained constant over a period estimated to include 5 generations (see Gerlach, 1971 for a discussion of meiofauna generation times).

Nematodes species at this site appeared to reproduce both continuously and asynchronously throughout the year. The abundance and relative proportions of juveniles, males, mature females, and gravid

females for the five most abundant species are listed in Table 4.
For these and the other 14 dominant forms, the presence of gravid
females and juveniles on each sampling date suggests that reproduction
was continuous.  The proportions of juveniles and gravid females
generally showed little variation among sampling dates.  Significant
changes in proportions of reproductive catagories were found for only
one species listed in Table 4 (Ticoma sp., 4 x 4 $\chi^2$ contingency test;
Sokal and Rholf, 1969).  The remaining species not shown in Table 4
were too rare for statistical tests of fluctuations in their repro-
ductive category proportions.  Inspection of the raw data, though,
gives no indication that the population structure of these nematodes
was changing either.  Reproduction must, therefore, also be generally
asynchronous, since the pulsed influx of large numbers of juveniles
associated with synchronous reproduction would have altered these
proportions.  Results summarizing the overall abundance of the four
reproductive groupings within the total nematode assemblage are given
at the bottom of Table 4.  Juveniles comprised 57% of all individuals,
while gravid females averaged 10%.

Discussion

Total nematode densities at the Oregon site were comparable to those found in other shallow subtidal habitats. Table 5 lists the water depth, sediment characteristics, and overall nematode abundances previously reported in sandy sediments (mean grain size >64 μm) of both protected and unprotected environments (station depths between 10 and 60 m). The average density at the Moolach Beach site, 1039 per 10 $cm^2$, is at the upper end of the range noted for nematodes inhabiting fine sands. McLachlan et al. (1977) commented that some published estimates of meiofaunal densities in subtidal sands may be low because of failure to sample deep enough into the sediments to collect all of the fauna. This was not a problem in the case of the present study. All cores were vertically partitioned when collected, and only 11% of the fauna was in the 11-18 cm depth increment. Collection of a few cores longer than 18 cm showed that nematodes live in the sands deeper than 18 cm, but their densities are extremely low.

The gross taxonomic composition of the nematodes at this Oregon coastal station also resembles that from other fine sand habitats, though several exceptions were noted. Previous studies indicate that ten families usually predominate in sediments with mean diameters between 125 and 250 μm: Monhysteridae, Comesomatidae, Desmodoridae, Axonolaimidae, Linhomoeidae, Chromidoridae, Oxystominidae, Cyathola-imidae, Oncholaimidae, and Enoplidae [Warwick and Buchanan (1970), station B; Lorenzen (1974), fine-sand stations; Tietjen (1977), stations 25, 103, 105, 126; Tietjen (1980), station 10]. The relative

abundance of the families listed in Table 2 is in agreement with this generalized taxonomic pattern, except that the Ceramonematidae and Desmoscolecidae made up a larger proportion of the fauna than has been reported, 18.6 and 8.3%, respectively, and the Linhomoeidae are much less abundant. Similar abundance trends for the Desmoscolecidae and Linhomoeidae were found in the sands off Peru by Nichols (1980).

Species of Ceramonematidae are not typically among the numerically dominant nematodes (Warwick and Buchanan, 1970; Lorenzen, 1974; Tietjen, 1977; Nichols, 1980), but may occasionally combine to form 5-10% of the total fauna (Tietjen, 1976, 1980). Hogue (1982) sampled five additional sites off Moolach Beach, two in water shallower than the seasonal site (18 and 19 m) and three in deeper water (28, 29, and 32 m). The average distance between these stations was 1.3 km. The proportional composition of the Ceramonematidae was also large at the shallower sites (17.8%), but was significantly less at the deeper locations (9.2%, t = 15.0, p <0.001). Only additional sampling can determine whether the gross taxonomic differences between the Oregon shallow-water sites (≤25 m) and other coastal regions are a result of unique habitat features present at the Moolach Beach location, or instead represent a biogeographic difference between oceans. The former is possible, since the sediments off Moolach Beach are continuously being reworked by wave action (see Hogue, 1982) and have substantially less silt-clay than previously examined fine sand habitats (see Table 5). Considerable taxonomic work remains to be done before comparisons can be made among sites at the species level.

Seasonal changes in nematode densities have not previously been detected in offshore habitats. Neither Warwick and Buchanan (1971), Lorenzen (1974) nor Juario (1975) noted significant variations in densities of nematodes at depths of 25, 35, and 80 m in the North Sea. The cause for the late spring increase in numbers at the Oregon location (Fig. 1) is unknown. The continual, asynchronous reproduction of nematodes off Moolach Beach also occurs in the North Sea populations, and suggests that population increases between January and May are not due to reproduction being limited to this period. Instead, variations in survivorship, growth, or fecundity must be involved.

A remarkable feature of the Moolach Beach nematode assemblage is the consistent numerical ranking of the dominant species, even though densities varied significantly over an interval spanning approximately 5 generations. The concordance in rankings was not only high (0.71), but was equal to that found by Warwick and Buchanan (1971) in a habitat where no significant fluctuations in density were found. Environmental factors which dictate the seasonal variations in abundance of nematodes at Moolach Beach must have the same net effect on all species. A requirement for any explanation of seasonal change in density is that the dominance structure, i.e., species rankings, remain constant. The specific growth rate of each nematode species ($r$) must be approximately the same if this constraint is to be met. This in turn requires that the difference between the instantaneous birth ($b$) and mortality ($m$) rates of each species be equal continuously while both $b$'s and $m$'s are changing. Four mechanisms are

proposed which could meet these requirements, yet each has serious flaws.

a. <u>winnowing from sediments</u>: Storm or wave induced sediment disturbance could winnow a proportion of the nematodes out of the sediments and carry them from the nearshore habitat into deeper water. Silt-clay particles are affected in this way during the winter. It is unlikely, however, that species living 10-18 cm deep in the sand would be removed at the same rate as those 0-1 cm deep. In addition, periods of decreased nematode abundance (see Fig. 1) do not correspond with those of frequent storm activity (October through April). Consequently, I do not feel that winnowing is a dominant process controlling the structure of this assemblage.

b. <u>non-selective predation</u>: If non-selective deposit feeders ingest the same amount of sediment in shallow and deep sand layers, then mortality rates of all nematodes will fluctuate together in accordance with changes in predation pressure. The majority of macrobenthic species at Moolach Beach, however, are surface deposit feeders (A. G. Carey, unpubl.). There is no evidence that the few subsurface deposit feeders present would feed equally on all nematodes.

c. <u>variable food resources</u>: During the late spring and early summer, increased length of the photoperiod coupled with the upwelling of nutrient-rich waters produces intense phytoplankton blooms along the Oregon coast. Examination of sediments collected in January 1979 revealed that few diatoms were present at the study site. By May 1979, however, both centric and pennate forms were approximately three times more abundant. The doubling of nematode densities between

January and May 1979 may be due to these increases in diatom concentrations, but similar changes in estuarine waters have been shown to be associated with shifts in nematode species composition. Epistrate feeders, which use their buccal teeth to either scrape diatoms and bacteria off sand grains or to pierce larger algal cells (see Tietjen and Lee, 1977 and Alongi and Tietjen, 1980), increase in abundance in estuarine habitats during the spring and summer relative to other nematodes (Tietjen, 1969; Levy and Coull, 1977). Similar shifts in species composition at Moolach Beach did not occur; fluctuations in the dominant epistrate feeders (Table 3) paralleled those of other species. Changes in all food resources would have to coincide with those of diatoms to produce this result. Again, this does not seem likely.

d. <u>compensatory adjustments</u>: Increase (decrease) in the exponential rate of population growth, $\underline{r}$, may be accomplished by a continuum of possibilities ranging from elevated (lowered) birth rates accompanied by no change in mortality to decreased (increased) mortality with no change in birth rates. Maintaining equivalent $\underline{r}$'s for all 19 dominant species could occur in one of two ways; either 1) in response to independent events affecting each species differently yet leading by chance to the same $\underline{r}$, or 2) as a result of a complex linkage between the birth and death rates of all nematodes. The former does not seem likely over numerous generations while the latter requires unknown interspecific, compensatory adjustments in demographic parameters. Considerably more information is needed about the life histories of nematodes before a mechanism coupling the

population dynamics of all nematodes can be proposed.

Persistence of dominance structure in this nematode system resembles that found in plankton communities of the North Pacific central gyre. McGowan and Walker (1979) discovered a strong trend for the same copepod species to be numerically dominant over time intervals spanning many copepod generations. Weiler (1980) found similarly that species of the dinoflagelate genus Ceratium had great consistency in the rank order of their abundance over 9 months. One would not predict a priori that two assemblages occurring in such different environments would show the same responses. Shallow, wave-disturbed, coastal habitats seem to have little in common with relatively stable pelagic environments of oceanic gyres. McGowan and Walker (1979) concluded that the North Pacific central gyre has many features of a self-regulating, climax ecosystem. This description generally does not fit shallow-water, benthic assemblages. Coastal macrofauna communities show considerable variation in species propor-tions over time (e.g. Frankenberg and Leiper, 1977; Oliver et al., 1980). Although their environments are very different, the nematodes of Moolach Beach and the plankton of the North Pacific central gyre have several important features in common: organisms are small, reproduction is continuous, communities are diverse, and individuals are not space limited. The key to explaining maintenance of species proportions probably lies in some aspect of these unique features.

Table 1. Summary of type of sampling gear used and number of subsamples collected on each date. Physical characteristics of the bottom water and sediments at the time of sampling are also given. BXC: Box core. SMG: Smith-McIntyre grab.

| Date Sampled | Sampling Gear | No. Cores | Bottom Water | | Sediment Parameters | | |
|---|---|---|---|---|---|---|---|
| | | | Temp (°C) | Salinity (‰) | Mean Size ($M_z$) | Sorting ($\sigma_I$) | % Silt-Clay |
| 27 July 1978 | BXC | 6 | 7.7 | 33.7 | 2.6 ∅ | 0.46 | 2.1 |
| 31 August 1978 | BXC | 6 | 14.0 | 32.1 | 2.6 ∅ | 0.50 | 4.2 |
| 23 October 1978 | BXC | 6 | 9.0 | 33.2 | 2.6 ∅ | 0.36 | 0.2 |
| 23 January 1979 | BXC | 6 | 7.4 | 32.8 | 2.6 ∅ | 0.52 | 0.9 |
| 22 March 1979 | BXC | 6 | 8.6 | 32.9 | 2.6 ∅ | 0.44 | 0.3 |
| 3 May 1979 | BXC | 6 | 8.0 | 33.0 | 2.6 ∅ | 0.46 | 1.1 |
| 7 August 1979 | SMG | 4 | 7.9 | 33.9 | 2.6 ∅ | 0.37 | 3.3 |
| 20 September 1979 | SMG | 4 | 9.9 | 33.3 | 2.5 ∅ | 0.44 | 1.2 |

Table 2.  Average proportions of the 23 nematode families encountered at Moolach Beach.  --: <0.001

| | |
|---|---|
| Desmodoridae | 0.187 |
| Ceramonematidae | 0.186 |
| Monhysteridae | 0.148 |
| Desmoscolecidae | 0.083 |
| Comesomatidae | 0.062 |
| Oncholaimidae | 0.059 |
| Richtersiidae | 0.057 |
| Axonolaimidae | 0.050 |
| Cyatholaimidae | 0.036 |
| Oxystominidae | 0.028 |
| Chromidoridae | 0.026 |
| Monoposthiidae | 0.022 |
| Enoplidae | 0.020 |
| Meyliidae | 0.018 |
| Linhomoeidae | 0.007 |
| Enchelidiidae | 0.004 |
| Siphonolaimidae | 0.002 |
| Anticomidae | 0.002 |
| Scaptrellidae | 0.001 |
| Leptolaimidae | 0.001 |
| Sphaerolaimidae | -- |
| Selachinematidae | -- |
| Choniolaimidae | -- |

Table 3. Changes in density of the total nematode assemblage, the 19 dominant species, and the subfamily Microlaiminae between July 1978 and May 1979. Abundances expressed as no. per 10 $cm^2$, values in parenthesis are percent composition. Feeding type (<u>sensu</u> Wieser, 1959) is also listed, where 1A= selective deposit feeders, 1B = non-selective deposit feeders, 2A = epistrate feeders, and 2B = omnivore-predators.

| Total Assemblage | Feeding Type | July 1978 | January 1979 | March 1979 | May 1979 | Average |
|---|---|---|---|---|---|---|
| | | 807.7 | 853.9 | 1128.0 | 1617.1 | 1039.0[1] |
| <u>Ceramonema</u> sp. A | 1B | 66.7 (8.3) | 82.7 (9.7) | 89.5 (7.9) | 119.0 (7.4) | 89.5 (8.1) |
| <u>Tricoma</u> sp. | 1A | 42.8 (5.3) | 37.6 (4.4) | 69.5 (6.2) | 106.0 (6.6) | 64.0 (5.8) |
| <u>Richtersia</u> sp. | 1B | 58.7 (7.3) | 35.3 (4.1) | 47.9 (4.2) | 53.6 (3.3) | 48.9 (4.4) |
| Ceramonematidae A | 1B | 32.5 (4.0) | 35.3 (4.1) | 22.8 (2.0) | 38.2 (2.4) | 32.2 (2.9) |
| <u>Sabatieria</u> sp. | 1B | 19.4 (2.4) | 42.8 (5.0) | 32.5 (2.9) | 33.6 (2.1) | 32.1 (2.9) |
| <u>Odontophora</u> sp. | 2A | 28.5 (3.5) | 21.1 (2.5) | 20.0 (1.8) | 34.2 (2.1) | 26.0 (2.4) |
| <u>Rynchonema</u> <u>subsetosa</u> | 1A | 9.7 (1.2) | 12.0 (1.4) | 20.0 (1.8) | 56.4 (3.5) | 24.5 (2.2) |
| <u>Marylynnia</u> sp. | 2A | 13.1 (1.6) | 22.2 (2.6) | 16.0 (1.4) | 38.1 (2.4) | 22.4 (2.0) |
| <u>Paramicrolaimus</u> sp. | 2A | 18.2 (2.3) | 18.8 (2.2) | 18.8 (1.7) | 23.9 (1.5) | 19.9 (1.8) |
| <u>Nudora</u> sp. | 2A | 20.5 (2.5) | 12.0 (1.4) | 14.0 (1.2) | 26.8 (1.7) | 18.3 (1.7) |
| <u>Paramesonchium</u> sp. | 2A | 16.0 (2.0) | 15.4 (1.8) | 18.2 (1.6) | 21.7 (1.3) | 17.8 (1.6) |
| Axonolaiminae A | 2A | 9.7 (1.2) | 12.5 (1.5) | 12.5 (1.1) | 30.8 (1.9) | 16.4 (1.5) |
| <u>Meylia</u> sp. | 1A | 6.8 (0.8) | 5.7 (0.7) | 20.5 (1.8) | 29.6 (1.8) | 15.7 (1.4) |
| <u>Xyala</u> sp. | 1B | 6.3 (0.8) | 18.3 (2.1) | 16.5 (1.5) | 17.7 (1.1) | 14.7 (1.3) |
| <u>Ceramonema</u> sp. B | 1B | 9.7 (1.2) | 17.7 (2.1) | 19.4 (1.7) | 10.8 (0.7) | 14.4 (1.3) |
| <u>Halilaimus</u> sp. | 1A | 11.4 (1.4) | 9.7 (1.1) | 14.8 (1.3) | 20.0 (1.2) | 14.0 (1.3) |
| <u>Theristus</u> sp. | 1B | 15.4 (1.9) | 13.1 (1.5) | 10.3 (0.9) | 5.7 (0.4) | 11.1 (1.0) |
| <u>Mononcholaimus</u> sp. | 2B | 1.7 (0.2) | 17.1 (2.0) | 17.1 (1.5) | 8.0 (0.5) | 11.0 (1.0) |
| <u>Cobbia</u> sp. | 2A | 2.9 (0.4) | 4.6 (0.5) | 14.8 (1.3) | 20.5 (1.3) | 10.7 (1.0) |
| Microlaiminae | 2A | 62.7 (7.8) | 75.8 (8.9) | 97.5 (8.6) | 189.2 (11.7) | 106.3 (9.6) |

[1]Includes August 1978 (790.0/ 10 $cm^2$)

Table 4. Temporal changes in the total number of individuals counted and relative proportions of four reproductive categories for the five most abundant species and the total nematode assemblage.

| | Total Counted | Juv. | Males | Mature Females | Gravid Females |
|---|---|---|---|---|---|
| Ceramonema sp. A | | | | | |
| July 1978 | 117 | 0.49 | 0.21 | 0.16 | 0.15 |
| January 1979 | 145 | 0.52 | 0.33 | 0.09 | 0.07 |
| March 1979 | 157 | 0.43 | 0.34 | 0.19 | 0.04 |
| May 1979 | 209 | 0.45 | 0.31 | 0.17 | 0.07 |
| Tricoma sp. | | | | | |
| July 1978 | 75 | 0.32 | 0.36 | 0.26 | 0.06 |
| January 1979 | 66 | 0.39 | 0.23 | 0.17 | 0.21 |
| March 1979 | 122 | 0.31 | 0.41 | 0.11 | 0.17 |
| May 1979 | 186 | 0.22 | 0.27 | 0.20 | 0.32 |
| Richtersia sp. | | | | | |
| July 1978 | 103 | 0.57 | 0.20 | 0.15 | 0.08 |
| January 1979 | 62 | 0.44 | 0.41 | 0.08 | 0.07 |
| March 1979 | 84 | 0.68 | 0.23 | 0.07 | 0.02 |
| May 1979 | 94 | 0.68 | 0.18 | 0.10 | 0.04 |
| Ceramonematidae A | | | | | |
| July 1978 | 57 | 0.45 | 0.23 | 0.09 | 0.23 |
| January 1979 | 62 | 0.40 | 0.32 | 0.09 | 0.19 |
| March 1979 | 40 | 0.50 | 0.14 | 0.16 | 0.20 |
| May 1979 | 67 | 0.49 | 0.24 | 0.14 | 0.13 |
| Sabatieria sp. | | | | | |
| July 1978 | 34 | 0.43 | 0.34 | 0.14 | 0.09 |
| January 1979 | 75 | 0.46 | 0.22 | 0.13 | 0.19 |
| March 1979 | 57 | 0.44 | 0.35 | 0.12 | 0.09 |
| May 1979 | 59 | 0.52 | 0.19 | 0.14 | 0.16 |
| Total Assemblage | | | | | |
| July 1978 | 1417 | 0.56 | 0.21 | 0.11 | 0.12 |
| January 1979 | 1498 | 0.54 | 0.24 | 0.09 | 0.14 |
| March 1979 | 1978 | 0.61 | 0.23 | 0.07 | 0.08 |
| May 1979 | 2837 | 0.57 | 0.23 | 0.12 | 0.09 |

Table 5. Representative values for total nematode densities in subtidal sandy sediments (mean grain size >63 μm). Depth, sediment characteristics, and sieve size used in collecting animals are included. --:either not appropriate or unavailable.

| Location | Depth | Sediment Size | % Silt-Clay | Sieve Size (μm) | Average Density (No./10cm²) | Range (No./10cm²) | Reference |
|---|---|---|---|---|---|---|---|
| **England** | | | | | | | |
| Southwest Coast | 45 m | fine sand | ~25% | -- | -- | 50-116 | Mare (1942) |
| Northumberland | 35 m | very fine sand (103 μm) | 30% | 37 | 185 | -- | Warwick and Buchanan (1970) |
| | 54 m | fine sand (145 μm) | 17% | 37 | 815 | -- | Warwick and Buchanan (1970) |
| German Bight | 25 m | fine sand (~200 μm) | 7% | 50 | 530[1] | 190-1300 | Lorenzen (1974) |
| | 35 m | silty-sand (84-103 μm) | 23-26% | 50 | 3790[1] | 2867-5037 | Juario (1975) |
| South Africa | 5-30 m | fine & medium sand (185-358 μm) | <10% | -- | -- | 570-1722 | McLachlan et al. (1977) |
| **U.S. East Coast** | | | | | | | |
| New England | 40 m | coarse sand (580 μm) | 0 | 74 | 685 | -- | Wigley and McIntyre (1964) |
| | 51 m | fine sand (250 μm) | 15% | 74 | 924 | -- | Wigley and McIntyre (1964) |
| | 58 m | very coarse sand (1470 μm) | <1% | 74 | 50 | -- | Wigley and McIntyre (1964) |
| Buzzards Bay | 18-30 m | fine sand | 12% | -- | 364 | 250-550 | Wieser (1960) Station P |
| Long Island Sound | 5-21 m | fine sand (122-222 μm) | 7-24% | 44 | 743 | 370-1650 | Tietjen (1977) |
| | 5-28 m | muddy sand (58-93 μm) | 32-64% | 44 | 1007 | 560-1450 | Tietjen (1977) |
| | 5-39 m | medium coarse sand (227-492 μm) | 1-12% | 44 | 1352 | 110-5010 | Tietjen (1977) |
| New York Bight | 15 m | coarse sand (651 μm) | 1% | 44 | 938 | -- | Tietjen (1980) |
| | 10-29 m | medium sand (266-438 μm) | 2-4% | 44 | 882 | 221-1319 | Tietjen (1980) |
| | 22 m | fine sand (195 μm) | 13% | 44 | 1098 | -- | Tietjen (1980) |
| | 24-35 m | silty sand (80-82 μm) | 23-24% | 44 | 1056 | 731-1381 | Tietjen (1980) |
| North Carolina | 50 m | medium sand (392-434 μm) | <1% | 44 | 375 | 157-593 | Tietjen (1971) |
| Peru | 40 m | fine sand (250 μm) | -- | 33 | 534 | -- | Nichols (1980) |
| Oregon Coast | 25 m | fine sand (165 μm) | 1% | 38 | 1039[1] | 790-1617 | present study |

[1]Seasonal average

Figure 1.  Average abundance of the total nematode assemblage, ex-

pressed as no./10 cm$^2$, between July 1978 and September 1979.

Vertical bars represent $\pm$1 standard error.  Solid circles:  box

core data.  Solid squares:  Smith-McIntyre grab data.  Solid

triangle:  box core data collected 150 m away from usual sampling

site.
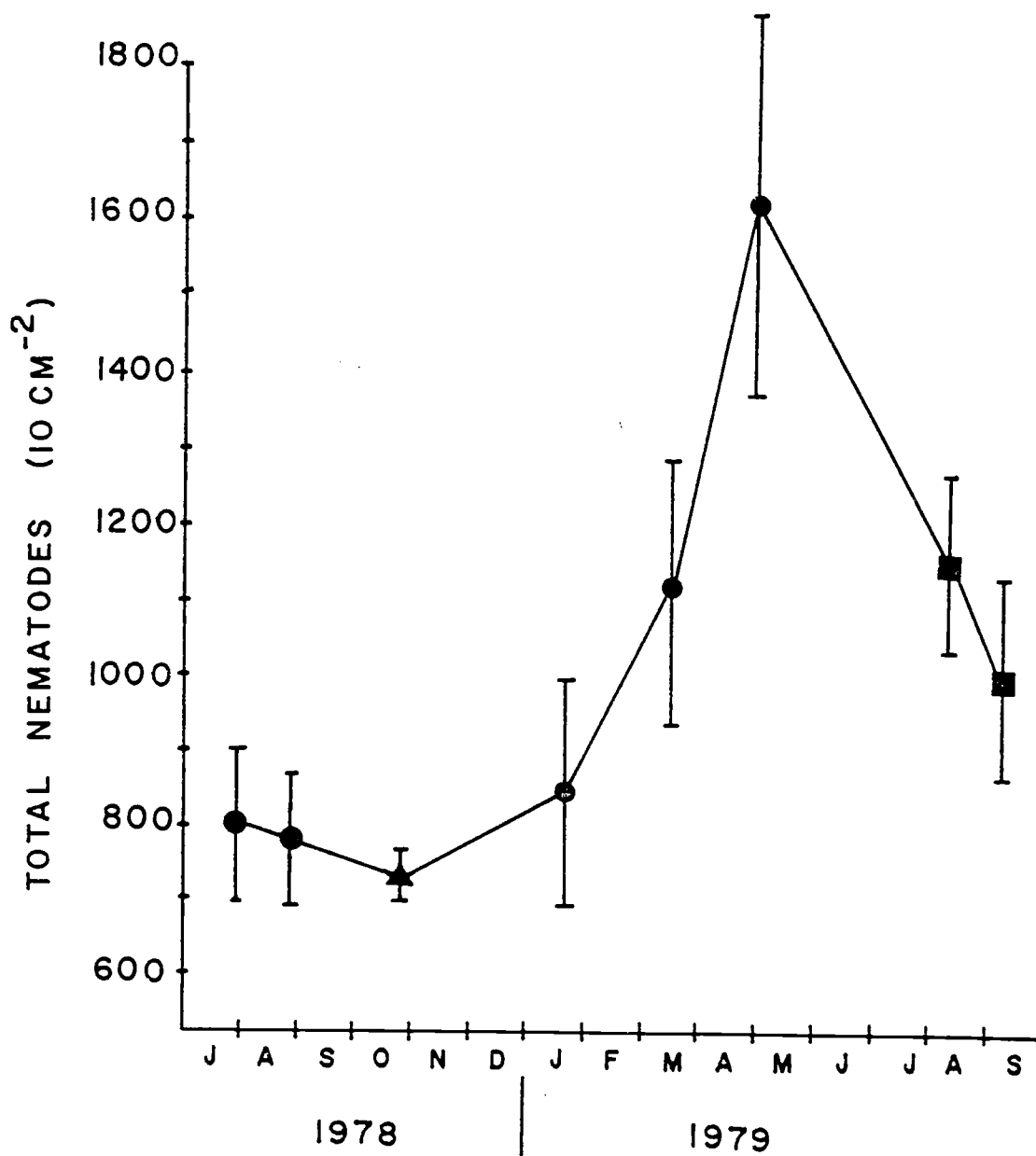
Figure 1.

Chapter 3


SEDIMENT DISTURBANCE AND THE SPATIAL DISTRIBUTIONS

OF SHALLOW WATER MEIOBENTHIC NEMATODES ON THE

OPEN OREGON COAST

Abstract

The relationship between spatial distributions of meiobenthic nematodes and wave generated sediment disturbance was investigated within a 3.3 km$^2$ area on the central Oregon coast. A total of six stations, ranging in depth between 18 and 32 m, were sampled during the summer of 1979. Two distinct faunal groups were associated with different water depths. The division between these assemblages is closely correlated with the threshold depth at which sediments are influenced by passing waves. The fauna from the shallowest stations ($\leq$25 m) is dominated by nematode species which are small (<1.1 mm long) and which have highly modified cuticles (e.g., annulations, spines, ornamentation). Deeper sites (>25 m) are predominantly inhabited by species longer than 1.1 mm with smooth cuticles. Sediment disturbance, or features related to sediment disturbance, are implicated as a determinant of this broad-scale pattern. Other physical parameters, e.g., mean grain size, percent silt-clay, and temperature, do not vary systematically with depth.

Analysis of variance indicates that approximately 50% of the total variance in nematode abundances within the overall study area is due to within-station differences occurring on scales of 0.25 m$^2$ and less. Additional samples were collected to describe these small-scale patterns and their changes over time. The distributions of both the total nematode assemblage and the numerically dominant species were spatially aggregated at the within-station level in May 1979 but were randomly dispersed during January 1979. Two opposing processes are thought to have generated these patterns. In the

winter, frequent storm activity mixes the bottom sediments and randomly distributes the fauna over the sea floor. In the late spring and summer, physical disruption of the sediments is minimal and biological factors, e.g. food or reproduction, lead to aggregation. Stronger intraspecific correlations exist between males and females than between either gravid and non-gravid females or juveniles and adults, indicating that attraction between members of the opposite sex may, in part, explain the non-random distributions of nematodes in May.

The coexistence of many intertidal organisms is maintained when localized disturbances renew limiting resources. Competitively inferior species, which would otherwise be excluded from an assemblage, persist by opportunistically exploiting newly created habitat patches. Coexistence of nematode species within small areas ($<1 \text{ m}^2$) off Moolach Beach does not appear to be similarly controlled. Species were randomly distributed with respect to each other on these small scales. Previous seasonal sampling at the study site also indicated that the relative proportions of the dominant species remained constant over time. If some nematode species were adapted to opportunistically exploit newly generated habitat patches, while others become established in less recently disturbed areas, then significant positive and negative associations between nematode species should have resulted in space or time.

Introduction

Shallow-water, sandy sediments along high energy coastlines are unstable, with wave and storm activity continually mixing and resuspending sediment particles. Benthic organisms living in this hydrodynamically active zone must be adapted to withstand the disturbance caused by shifting sands. Free-living meiobenthic nematodes are successful in this regard; between 70 and 100 nematode species commonly coexist in these environments (e.g., Juario, 1975; Tietjen, 1976; Nichols, 1980; Hogue, 1982). The purpose of this research was to investigate the effects of substrate movement on sediment-dwelling nematodes. Results were used to a) document important spatial scales of faunal variability, b) identify the causes of this variability, and c) discuss the possibility that localized disturbances maintain the coexistence of the dominant nematode species.

a. Document important scales of variability: I collected samples at horizontal separations ranging from millimeters to kilometers within one area near the Oregon coast to assess the spatial scales at which significant faunal changes occur. Data were collected also on seasonal changes in dispersion patterns. The resulting information provides a basis for establishing effective sampling plans and experimental designs in regions of shifting sands. Additionally, analysis of spatial patterns exhibited by benthic invertebrates suggests processes responsible for structuring assemblages of bottom-dwelling organisms (e.g., Jumars, 1975; Tietjen, 1976; Woodin, 1976; Peterson, 1977; Bernstein et al., 1978; Thistle, 1979). Although lacking the power of manipulative experiments to elucidate controlling

mechanisms, this approach is useful in habitats such as wave-swept continental shelves where controlled manipulations are difficult to conduct (see Arntz, 1977).

b. Determine causes of spatial variability: Recent work on the soft-bottom benthos of open coastal habitats (<50 m) reveals that the macrofauna of these wave- and storm-disturbed habitats varies spatially and lacks long-term stability (Eagle, 1975; Davis and VanBlaricom, 1978; Frankenberg and Leiper, 1977; McCall, 1978). The causes of this variability appear to be both physical and biological. Effects of wave-induced sediment motion interact with the reproductive cycles, feeding activities, and overall life histories of the macrobenthic animals living in this zone to produce continual changes in space and time. I examined the association between nematode distributions and sediment stability to evaluate the extent to which meiobenthic communities are similarly affected.

c. Disturbance and species coexistence: Localized habitat disturbances in intertidal environments renew limiting resources and enable opportunistic organisms to coexist with competitively superior species (e.g., Dayton, 1971; Sousa, 1979). The relative distribution of the dominant nematode species with respect to each other was compared at the within-habitat level to ascertain if groups of species were differentially responding to small-scale features of the shallow-water environment. The presence of significant positive or negative correlations among species would be an initial indication that small-scale processes (e.g., sediment or biological disturbance) create microhabitats which serve to ecologically seperate species and

maintain their coexistence.

Materials and Methods

Sample Collection

    The study area is in a region of well-sorted, sandy sediments on

the open Oregon coast between Yaquina Head and Cape Foulweather.  I

studied the broad-scale, spatial distribution of the nematode fauna

within this 3.3 km$^2$ area by analyzing samples collected at six sta-

tions, MB1 through MB6 (Fig. 2), on several dates during the summer

of 1979.  Stations depths, sediment granulometry, and number of

replicate cores obtained are listed in Table 6.  On 30 June and

7 August, samples were gathered at stations MB1 through MB5 from a

commercial fishing vessel using a Smith-McIntyre grab.  At each

station replicate grabs were positioned approximately 10 m apart, and

the center of each was subsampled to a depth of 6 cm with one 1.9 cm

internal diameter plastic core tube.  A reference buoy was used to

establish the distance between replicate grabs.  Station MB6 was

sampled on 30 May from an anchored research vessel with three repli-

cate 0.25 m$^2$ Hessler-Sandia box cores, each positioned 30 m apart.

The distance between successive cores was controlled by veering the

anchor chain.

    Data from station MB6 were used in conjunction with that from

the other sites for the broad scale comparisons and to examine in

detail the within-station spatial distribution of the fauna.  In this

latter regard, each MB6 box core was partitioned into four quadrants

measuring 12 cm on a side, with the distance between the centers of

adjacent quadrants being 25 cm.  Three cf the four quadrants from

each box core were subsampled using three randomly placed core tubes

of 1.9 cm internal diameter (see Fig. 3), resulting in a total of 9
cores per box and 27 cores overall. Three hierarchical scales of
within-station variability were assessed: within-quadrant (12 cm
scale), between-quadrant (25 cm scale), and between-box cores (30 m
scale). Additionally, all MB6 cores were partitioned into six depth
increments (0-1 cm, 1-3 cm, 3-6 cm, 6-11 cm, 11-18 cm, and greater
than 18 cm). Only box cores in which sediments were undisturbed and
which penetrated at least 18 cm into the sediment were used.

Small corers (plastic soda straws, 6 mm internal diameter) were
employed on the May (MB6) cruise to sample a fourth box core for
millimeter scale variability. Two parallel transects, positioned 3
cm apart and each consisting of 73 contiguous small cores, were
placed through the center of this additional box. All straws sampled
the upper 6 cm of sediment.

Seasonal changes in within-station nematode distribution were
investigated by comparing data collected at station MB6 on 30 May
1979 with that obtained 250 m away at MB1 on 23 January 1979.
During this January cruise I also collected three replicate 0.25 $m^2$
box cores (see Table 6), but only one quadrant per box was sampled
using two randomly placed cores (2 cores per box, total 6 cores).
These cores were partitioned into the same depth increments as those
in May. Two straw core transects were also obtained from an addi-
tional box core in the same manner as on the 30 May cruise.

All samples were preserved in 10% buffered Formalin and were
stained with rose bengal. The fauna was extracted from the sediments
in the laboratory by shaking and decanting followed by three rinses.

A 38.5 μm sieve was used to retain the fauna. Nematodes were sorted under a dissecting microscope and placed in glycerin mounts for identification to species and enumeration using a compound microscope. Individuals were categorized by reproductive classes: juveniles, males (spicula present), mature females (ovaries present), or gravid females (eggs present). Extraction efficiency from the sediment was high (98%), while observational efficiency was slightly less (90%).

Sediment samples from each box core and grab were wet-sieved to determine grain size. The graphic mean, $M_z$, and inclusive graphic standard deviation, $\sigma_I$, were used to describe the granulometery (Folk, 1974). Microtopographic sediment features were photographed on 30 May and 20 September using a deep-sea stereoscopic camera system.

Statistical Analysis

Emphasis was placed on the most abundant species throughout the statistical treatment of the data, with the rarer forms excluded from the analysis. Without a priori knowledge that a rare species plays a crucial role in structuring an assemblage, restricting atten-tion to dominant species seems an appropriate first step in describing the spatial response of a group of species to the environment. In addition, it is difficult from a statistical standpoint to describe spatial patterns when abundances per sample are very low and many samples contain no individuals (Elliott, 1971).

Between-station (kilometer scale) differences in abundance of the total nematode fauna and each of the numerically dominant species

were tested for significance by one-way analyses of variance (ANOVA).
Data were log-transformed prior to these computations. I estimated
the relative magnitude of the variance components within and between
stations using the mean squares from the ANOVA model (Sokal and
Rohlf, 1969). Faunal similarities between the six stations were
compared using the Bray-Curtis index (Bray and Curtis, 1958).

Several techniques were employed to describe within-station
dispersion patterns at stations MB6 in May and MB1 in January. The
average depth in the sediment was computed for the total nematode
fauna and each of the numerically most abundant species using data
from the vertically partitioned cores following the technique for
determining the mean of a frequency distribution. Between-core
dispersion patterns were tested for significant departures from
randomness using the $\chi^2$ statistic $\underline{I}$, where $\underline{I} = (s^2/\bar{x}) \cdot (n-1)$ and $s^2$ is
the sample variance, $\bar{x}$ is the sample mean, and n is the sample size.
Values of $\underline{I}$ exceeding tabulated 0.05 $\chi^2$ percentage points for n-1
degrees of freedom lead to a rejection of the null hypothesis of
random dispersion. Since differences in means between box cores were
not significant, all of the 1.9 cm cores collected were used for this
test, i.e. for January n=6 and May n=27. In addition, for the May
data, a two-level nested ANOVA was used to measure the percentage of
the total variance over the 27 samples which could be attributed to
within-quadrant, between-quadrant, and between-box core variations in
nematode density.

Direct comparison of the degree of aggregation of nematodes in
May with that in January was made using Green's index of dispersion,

GI, where $GI = [(s^2/\bar{x})-1.]/(\Sigma x-1.)$ (Elliott, 1971). This index

equals 0.0 for random distributions and increases to 1.0 for maximum

aggregation, i.e., when all individuals occur in 1 core. Negative

values indicate evenness. I computed GI for both the total nematode

fauna and the dominant species using all six cores collected in

Janaury. Similar computations were made for May data by reducing the

sample size from 27 to 6 cores. Two cores were selected at random

from the first quadrant of each box core, and the procedure as out-

lined for January was used to compute GI. This was repeated using

cores from the second and then the third quadrants of each box. The

three resulting GI values for May were then averaged to provide an

overall dispersion index suitable for comparison with January results.

Data from the small core transects of January and May, designated

January A and B and May A and B, were analyzed using standard time

series techniques described by Jenkins and Watts (1968). Data were

log-transformed and autocorrelation coefficients, $C_{xx}(k)$, computed

for the four transects up to 18 lags. Cross-correlation coefficients,

$C_{xy}(k)$, were calculated between May-A and May-B transects and between

the January-A and January-B series. Coefficients exceeding $\pm$

$1.96(n)^{-1/2}$ were considered significant (see Chatfield, 1975 on the

significance of auto- and cross-correlation coefficients).

Results

## Between-station Distributions

The data from all six stations were used to analyze broad-scale nematode distributions in the Moolach Beach area, although these sites were not sampled at the same time. While significant temporal changes in nematode density at station MB1 have been detected over a 1-year period (Hogue, 1982), no significant fluctuations occurred at this site during the 9-week interval of this work (unpublished data, t-test between densities on 3 May and 7 August 1979, $p > 0.05$). The relative abundance of species at MB1 remained constant over a 1-year period. Thus, even if changes in density occurred between sampling dates, no shift in dominance would have been expected. Changes in abundance at the other stations have consequently been ignored for the purpose of these broad-scale comparisons.

A total of 110 nematode species was found in the study area, the majority of which were rare. A group of 23 was selected for the analysis of between-site variability by listing the 10 most abundant species at each of the six sampling locations. Although this is an arbitrary reduction of the list to a manageable size, the results illustrate the trends present in the data. Table 7 indicates these dominant nematodes, their abundance (ind./10 $cm^2$), and their proportion of the total nematode fauna at each station. Together, the 23 species averaged 56% of the total nematode fauna at a sampling site. In the case of station MB6, only data from the top 6 cm of each core were used to make the results comparable with the other locations.

The densities of only five of the 23 dominant nematode species did not vary significantly among stations: Sabatiera sp., Rhabdodemaniinae A, Marylynnia sp., Monhysterinae A, and Xyala sp. (ANOVA, $p < 0.05$). The within-station and between-station variance components are shown in Table 7. An average of 60% of the variance in density of single nematode species occurs at the within-station scale. Thus, more variability exists over distances of a few meters (or less) than between stations separated by hundreds of meters; the average distance between stations is 1.3 km. Results for the total nematode fauna were similar, with 62.9% of the total variance in density occurring within-stations.

Pairwise comparison of inter-station faunal similiarity using the Bray-Curtis index revealed that two groups of stations existed, each associated with different water depths. The three stations 25 m and less in depth (MB1, MB2, MB5) were more similar to each other in species composition than to any of the deeper stations (MB3, MB4, MB6). Likewise, the deeper locations were more similar to each other than to any of the shallow sites. Average within-group faunal similarity was 0.65 (SD=0.04, n=6) while the average between-group value was 0.54 (SD=0.06, n=9). These changes in species composition with depth were not detectable using presence-absence data, since the species lists for the six sites were essentially the same. It is only in shifts of numerical abundance that the two groups were detected.

Faunal differences between the shallow and deep water sites were reflected in changes in the size and cuticular structure of the

dominant nematodes. Total length of mature females for each of the dominant species is listed in Table 7, with species arranged in the table from longest to shortest. In general, nematodes 1.1 mm and smaller (lower portion of Table 7) dominated at the three shallowest stations, while larger species reached their peak abundance at the three deeper sites. There are only three exceptions to this size-depth trend: 1) Rhabdodemaniinae A, 2) Monhysterinae A, and 3) Chromadorinae A. These three species are of intermediate length (1.1-1.5 mm). It would be expected that if a few nematodes failed to follow the size-depth relationship, it would be those species which were closest to the transition length (1.1 mm). I constructed a 2 x 6 contingency table to test for independence between nematode body length and water depth and found a highly significant relationship between these two factors (G-test, Sokal and Rholf, 1969; G=324.3, df=5, p<0.001). In addition, all of the species 1.1 mm or smaller with the exception of Axonolaimidae A have cuticles with annulations, spines, or other forms of ornamentation. Larger nematodes differed by having smooth cuticles. Therefore, faunal differences among the Moolach Beach stations are correlated with water depth and involve consistent changes in the morphologies of the dominant nematodes.


Within-station Distributions

a. MB6 box core data. Analyses of summer within-station spatial distributions are based on data collected at station MB6. The 21 species which comprised 1% or more of the total population at this site were selected for analysis of these small-scale patterns;

Table 8 lists each species along with its average abundance per core, proportion of the total fauna, and average depth in the sediment. Taken together, the dominant forms made up 53.5% of the total nematode fauna at this site. Species were split into two groups to allow comparisons of dispersion patterns as a function of sediment depth: those with a mean depth in the sediment of 5 cm or less (14 species total), and those with a mean depth greater than 5 cm (7 species total).

The horizontal distribution of all 21 species, as well as the total nematode fauna at MB6, departed significantly from randomness (dispersion $\chi^2$ test, Table 8). Since distributions were aggregated, I wanted to assess at what spatial scales this variability occurred. A two-level, nested ANOVA revealed that for the total nematode assemblage only 25.8% of the variability in density was accounted for by differences among box cores (Table 8). The remaining 74.2% was within and between quadrants. Average variance components for the dominant species with a mean depth shallower than 5 cm indicated even less variability between boxes, 8.6%. For these species, 67% of the total variation occurred within quadrants (10 cm scale), and 24% occurred between quadrants (25 cm scale). The same basic result was found for the dominant species living deeper in the sediments. There is no indication that nematodes living deeper in the sediments are distributed differently than those living above 5 cm.

In general, there was no statistically significant difference in nematode density among replicate box cores (two-level, nested ANOVA). In the Moolach Beach study area, significant differences in the

abundance of the fauna occur over very small horizontal distances (within 0.25 m$^2$ box cores) and over larger kilometer sized areas (among stations).

b.    <u>MB6 small core data</u>.   The small, soda straw core samples collected in May provide a more detailed description of the smaller scales of variability.   Total nematode abundances from the two parallel transects collected are shown in Fig. 4.   A non-parametric test for runs above and below the median showed fewer runs than expected by chance for both transects, indicating significant aggregation of nematodes within box core-sized areas.   A correlogram based on the autocorrelation coefficients for the total nematodes in transect May-A is shown in Fig. 5.   Values for transect B are similar and have not been presented.   Two points can be made.   First, the coefficients for the first three to five lags are significant (95% confidence interval $\pm 0.23$), confirming the non-random nature of the small core data and indicating that aggregations of nematodes within box cores are approximately 2 to 3 cm in size.   Second, there is no apparent periodicity in density fluctuations over these horizontal distances, i.e. aggregations are not spaced at constant intervals apart.

Figure 6 shows a plot of the cross-correlation coefficients obtained from the May-A and May-B transects.   Significant coefficients occurred from lags 1 through 9.   Since the transects were 3 cm apart and were still correlated with each other, the physical dimensions of aggregations are substantiated to be about 3 cm in size.   Both the auto- and cross-correlations suggest that within a box core the most significant scales of spatial variability are found over distances of

a few centimeters.

c.   Seasonal changes in small-scale distributions.   Data collected

in January 1979 at MBl were used to compare the within-box core

distribution of nematodes in winter with those found in May at MB6.

The total fauna was significantly aggregated in January (dispersion

$\chi^2$ test, Table 8).   Comparison of species dispersion patterns were

made for those species which comprised 1% or more of the total popu-

lation in both January and May.   Fifteen species met this criterion

(Table 8, January).   In contrast to May, when all 15 of these species

were significantly aggregated in the horizontal dimension, dispersion

$\chi^2$ tests showed that a random distribution for 7 of the 15 species

could not be statistically rejected.   Low values of $I$ further indicate

that the intensity of aggregation of those eight species which were

not randomly dispersed may be less than that found in May.

Although useful in testing for departures from randomness, $I$ is

not a good index for comparing relative levels of aggregation (Elliott,

1971).   Green's index, $GI$, was used to compare the intensity of

aggregation in January with that in May for the eight species which

remained non-randomly distributed in the winter (Table 8, January).

Table 9 shows that three of these species and the total nematode

population were more aggregated in May than January.   The opposite

trend was found for three other species while an additional two

showed no change.   Examination of the data from the small core

transects in January (Fig. 4) substantiates this overall tendency for

decreased clumping in winter.   A runs test above and below the median

failed to reject a random spatial arrangement of nematodes within box

cores. The auto- and cross-correlation coefficients for these transects were also not significant (Figs. 5 and 6). Most nematodes were either randomly distributed on these spatial scales during the winter or were less intensely aggregated than during the summer.

d. <u>Vertical distributions</u>. The highest densities of nematodes were found in the uppermost few cm of sediment. In May, 71% of all nematodes occurred in the top 6 cm of sand, while in January this proportion was 68%. Only 10% of the total fauna was found in the 11-18 cm depth interval. A few cores longer than 18 cm revealed that nematodes lived in these deeper layers, but their abundances were greatly reduced. A redox-potential-discontinuity layer (RPD), normally a significant vertical faunal boundary, was never encountered in the cores which were collected.

The mean depth in the sediment of the dominant species encountered in January and May is listed in Table 8. The center of distribution for each species was deeper within the sediment during the winter than in May. Although further down in the sand in January, species maintained the same relative vertical position with respect to each other in January as in May (Friedman's non-parametric randomized block ANOVA, $x^2_{[14]}$ = 27.1, p=0.02). Data from additional cores collected between July 1978 and May 1979 (unpublished) confirm that the species listed in Table 8 are consistently found in the same order with respect to depth. The determinants of these vertical distributions, whatever they may be, must operate similarly over time.

e.  Small-scale interspecific correlations.  Unlike the broad scale
sampling which revealed significant depth related species associa-
tions, the within-station sampling failed to show strong correlations
between the distributions of the dominant species.  I computed the
product-moment correlation coefficients between the 14 dominant
species found in the top 5 cm at MB6 using the log-transformed data
from all 27 cores.  Applying a multivariate test of independence
(Bartlett's test of sphericity, Cooley and Lohnes, 1972; Morrison,
1976) the null hypothesis that variations in species abundances are
uncorrelated was not rejected ($\chi^2$=90.03, df=91, p=0.50).  The average
absolute value of the 91 coefficients was small, 0.19 (SD=0.13),
illustrating this lack of strong spatial correspondence between the
small-scale distributions of species.

f.  Small-scale intraspecific correlations.  At the intraspecific
level the associations between individuals of the four reproductive
groups were far stronger.  I computed the product-moment correlation
between juveniles, males, females, and gravid females for those
species at station MB6 which had a mean depth less than 5 cm and
abundances greater than 3 individuals per core.  Rarer species were
not included because of insufficient densities to produce meaningful
correlations.  Bolbella sp. was also excluded because all individuals
were juveniles except for one gravid female.  Table 10 shows the
average coefficients for the nine species which met these criteria.
The strongest associations were between males and females.  For each
of the nine species examined, males were consistently correlated with
either gravid or mature females more strongly than the two female

categories were correlated with each other. Gravid females would be expected to be more strongly associated with non-gravid individuals in at least one-third of these cases if results were due strictly to chance. The difference between the expected and observed outcomes is statistically significant (Rohlf and Sokal, 1969; p. 208). The weakest intraspecific correlations were between juveniles and the classes of adults. Apparently individuals which have a reproductive need to be associated, i.e. males and females, show the strongest spatial associations among cores.

Discussion

Between-Station Distributions

Faunal differences among the six Moolach Beach stations were associated with an increase in the size of the dominant nematodes as water depth increased.  Before considering this zonation to be caused by depth related factors, two alternative explanations must be rejected.  Differences between shallow water and deep water nematode assemblages may have resulted from the fauna responding to an environmental mosaic rather than depth gradients.  This is not likely, however, since the samples collected within each of the two depth zones were 1-2 km apart.  This should be sufficient to encompass most alongshore variability and eliminate the possibility of mosaic distributions being important.  The second alternative is that the observed affinities were based on chance alone, i.e. stochastic fluctuations in species abundances produced the station groupings. There are 10 possible ways of assigning six sites into two groups of three stations each.  The probability that the observed similarities could be due to chance is, therefore, only 10%.  This is not a likely alternative.  The striking morphological differences in size and cuticular structure of the nematode fauna support the contention that faunal changes involve a common adaptation or response to variations in the habitat with depth.

The division between the large- and small-dominated assemblages was located at a depth between MB1 and MB6, i.e. around 25 to 28 m. Variations in sediment granulometry, which have frequently been found to be significantly correlated with changes in nematode species

(Warwick and Buchanan, 1970; Ward, 1973, 1975; Tietjen, 1976), are probably not responsible for the faunal differences. Sediment parameters are very similar for all stations (Table 6); no systematic differences in mean grain size, percent silt-clay, or sorting could be detected between these two depth zones. There is also essentially no difference in the relative abundance of the four basic nematode feeding types (sensu Wieser, 1959), suggesting that differences in food types are not responsible.

Numerous investigations of macrobenthic populations in shallow water have concluded that wave-induced sediment motion may play a crucial role in explaining observed macrobenthic species patterns (e.g. Field, 1971; Rees et al., 1977; Davis and VanBlaricom, 1978; McCall, 1978; Oliver et al., 1980). I used a relationship developed by Komar and Miller (1973) which expresses the threshold conditions for sediment movement as a function of wave height, wave period, water depth, and mean grain size to determine at what approximate depth at Moolach Beach sediments ceased to be affected by surface waves in the summer. Waves measured off Newport, Oregon between April and September average 1.2 m high with a period of 7.5 s (5 year mean, C. Creech, personal communication). Under these conditions sediments at the two shallowest stations (16 and 18 m) would be constantly disturbed by passing waves while the two deepest stations (32 and 29 m) would be unaffected. The threshold depth for sediment motion is approximately 22 m. Occasional storm activity during the summer will move this point farther offshore, past the 32 m station. It is significant, however, that under "average" summer conditions

the division between the two faunal groupings coincides closely with the approximate depth at which sediments first begin to be disturbed. Sediment stability, or some factor correlated with sediment stability, is probably responsible for the depth zonation of the nematode fauna.

The relationship between the small size of shallow-dwelling nematodes and the sediment disturbance associated with this habitat is opposite that which would be predicted based on most previous work. Gerlach (1953), Wieser (1959), Warwick (1971), and Tietjen (1976) examined nematode species found in a variety of sediment types, and all concluded that in areas of unstable substrates larger forms with long cephalic or somatic setae predominate. Wieser (1959) and Warwick (1971) further suggested that no correlation exists between habitat type and cuticular patterns. Only Ward (1975) has previously noted a positive relationship between cuticular ornamentation and physically dynamic environments.

Several benefits can be hypothesized for small size and modified cuticles in wave disturbed habitats. Annulations and spines may protect the body wall from damage (Swedmark, 1964) and increase mechanical purchase to maintain position within shifting sediments (Ward, 1975). Advantages associated with small size are less obvious. If small nematodes have shorter generation times than larger forms, as is probably the case although Gerlach and Schrage (1972) have noted exceptions, then decreased body size could be related to a reproductive adaptation for maturing and reproducing quickly in a frequently disturbed habitat. Such behavior would parallel that found by McCall (1977) in Long Island Sound where abundance of

opportunistic macrofaunal species greatly increased in waters less than 20 m deep. Comparative life history data for large and small nematodes at Moolach Beach are not available, however, to substantiate this possibility.

Another alternative is that size-selective predation by macro-fauna is responsible for the distributions of nematode species. Oakden (1980) reported that phoxocephalid amphipods from shallow sandy bottoms off the central California coast consume nematodes and other meiofaunal sized prey. Oliver et al. (1980) found that amphipod species belonging to this family were significantly more abundant in shallow, wave disturbed areas of Monterey Bay than in deeper regions. Macrofauna samples collected 1.8 km south of the Moolach Beach site show a similar, dramatic seaward decrease in abundance of amphipods between 25 and 50 m (Carey, 1972). Small nematodes may predominate in the waters less than 25 m deep because the larger species are more susceptible to predation by either phoxocephalid amphipods or other infaunal predators. Similar size-selective feeding behavior has been documented for epibenthic predators within the study area. Juvenile flatfishes occasionally eat nematodes, but only the three largest species (Theristus sp., Mesacanthion sp., and Bolbella sp.) found within the uppermost 1 cm of sediment are ingested (Hogue, 1982).

A third explanation for the dominance of small species in waters less than 25 m deep is associated with potential benefits of small body size in avoiding injury. Larger forms may be more easily damaged when caught in the shearing motion of shifting sands. Only experi-mental work can clarify whether these or other factors are the

determinant(s) of nematode zonation at Moolach Beach.

## Within-Station Distributions

Most of the variability in species abundances did not occur over the broad sampling scale associated with the sediment disturbance gradient, but existed instead within 0.25 $m^2$ areas. Coull et al. (1977) found similar results when examining variations in total meiofauna density along a transect extending from depths of 400 to 4000 m off the North Carolina coast. Many processes are potentially capable of generating these small-scale aggregations, none of which necessarily acts alone. Of the possibilities, several have been suggested to specifically affect meiobenthic animals, including attraction to patchily distributed food (Andrew and Nicholar, 1976; Gerlach, 1977; Lee et al., 1977); association with biogenic sediment structures (Aller and Yingst, 1978; Bell et al., 1978; Thistle, 1979; Riese and Ax, 1980); sediment microtopography (Hogue and Miller, 1981); small-scale variations in sediment fabric (Nichols, 1980); biotic interactions with macrofauna (Thistle, 1979); and intraspecific reproductive processes (Heip, 1975). Several of these possibilities are probably not important in the case of nematodes at Moolach Beach. Biogenic structures such as worm tubes and burrows are not common. The mixed, well-sorted sediments also seem to preclude sediment fabric as a factor. Bottom photographs taken at the time that the May small core transects were collected showed that sediment ripples with a wavelength of 34 cm were present throughout the study area. Data from the May A transect (Fig. 4) indicates that density

fluctuations may have this same periodicity (cores 10 through 65). Sediment microtopography may be important on these scales, but not in determining the predominant within-box core variations which are less than 12 cm in size. Food availability and reproductive processes remain as the two most likely causes of this patchiness.

Correlations between males, non-gravid females, and gravid females (Table 10), implicate behavior for locating mates as a cause for spatial variability. Associations between males and females is stronger than between female categories. Male nematodes may be attracted to females in response to pheromone secretions, as has been suggested by Heip and Engles (1977) for harpacticoid copepods. The distance over which such chemical attractants are effective within interstitial habitats is unknown. The average size of nematode aggregations, 2 cm, may represent the spatial limits of pheromone attraction.

It seems likely that reproductive behavior contributes to the generation of spatial aggregations, yet other factors, e.g. patchy food sources, must also be involved. Reproductive categories which have no known biological need for maintaining close contact, e.g. mature females and gravid females, are still associated more strongly with each other than to different species. Many different factors seem to act concurrently in shaping the distribution pattern of interstital organisms.

Seasonal change in the within-station spatial distribution of nematodes (Table 8; Figs. 4, 5, and 6) probably results from winter storms which vigorously disturb and rework the sediments of the

continental shelf. Komar et al. (1972) noted that average winter storm waves on the Oregon shelf are sufficiently intense to produce sediment ripples out to a depth of 100 m and occasionally to a depth of 200 m. Under these conditions the fauna at the Moolach Beach study site would be extensively disrupted. Bottom photographs taken at 25 m in the study area during the summer showed regularly spaced ripples which were poorly preserved. Animal tracks and occasional worm tubes were clearly visible, indicating that the bottom had not been recently disturbed. This was in marked contrast to photographs taken at the same location in September 1979 immediately following a gale comparable in strength to a winter storm. Sediment ripples were well preserved with no evidence of biological activity. Komar et al. (1972) took a similar series of photographs off Moolach Beach in 28 m of water in February and May 1968 and found the same result. The physical stability of the fine sand in water approximately 25 m deep and greater is seasonally variable. Sediments are continually mixed and reworked in the winter, but only occasionally stirred in the summer.

Small-scale spatial distributions of nematodes reflect this seasonal difference in disturbance. Samples collected in January with both large and small cores indicate that most nematodes were randomly dispersed over the bottom (Table 8; Fig. 4). Waves at the time of sampling in January were sufficiently intense to generate sediment motion on the bottom (wave height = 3 m, period = 10 s). All species were significantly aggregated in May when bottom photographs confirmed that sediments had not recently moved. Two opposing

forces apparently establish the within-station distribution of nematodes at Moolach Beach. Physical mixing from waves tends to disperse the fauna, while biological factors such as reproduction or attraction to food tend to aggregate them.

Though nematodes were randomly dispersed in the horizontal dimension during the winter, their vertical distributions remained the same as in the summer. The environmental cues establishing vertical distributions are either unaffected by frequent sediment mixing or are rapidly re-established. Nematodes evidently respond far more quickly to maintain their vertical position within the sediments than they do to re-aggregate horizontally.

Physical disturbance of sediments, or factors correlated with this disturbance, thus appear to affect the spatial distribution of nematodes at Moolach Beach on both broad (between-station) and small (within-station) scales. In other systems, e.g. rocky intertidal habitats, localized disturbances in space and time renew limiting resources and provided a mechanism for the maintenance of species diversity (e.g. Dayton, 1972; Paine and Levin, 1981; Sousa, 1979). Several lines of evidence suggest that this process may not be important in maintaining the within-station coexistence of the dominant nematode species at Moolach Beach.

If shifting sediments, or any other form of disturbance, generated microhabitats within a station which were important for the coexistence of species, then distinct differences in the temporal or spatial distributions of nematodes should have resulted. Hogue (1982) demonstrated that although the densities of the most abundant

nematode species at station MB1 varied significantly over a one year period, their relative abundances remained constant. Species did not show a differential response over time to environmental changes as would be expected if disturbance were initiating a successional sequence. Likewise, species were essentially randomly distributed spatially with respect to each other at the within-habitat level. If some species were adapted to opportunistically exploit newly generated habitat patches, while others only inhabited less recently disturbed areas, then significant positive and negative spatial associations between species should have resulted. Thistle (1980) has found that only a small proportion of the harpacticoid copepods living in shallow sandy sediments responded to the disturbance generated by enteropneust fecal mounds. Thus far, there is little evidence to suggest that disturbance, either biological or physical, plays a crucial role in promoting the within habitat coexistence of the dominant species in coastal meiobenthic communities.

Conclusions

1. Significant differences in the density of dominant nematode species occur over distances of kilometers (among stations) and centimeters (within box cores). No differences were detected between replicate box cores spaced 30 m apart.

2. Approximately half of the variance associated with fluctuations in nematode abundance within the 3.3 $km^2$ study area is attributable to small-scale differences found within 0.25 $m^2$ box cores.

3. Broad-scale variations in faunal distributions are associated with water depth and the frequency of sediment disturbance. Species found in water deeper than 25 m tend to be over 1.1 mm long and have smooth cuticles. Shallower locations were dominated by smaller species with modified cuticles. Processes capable of generating these patterns include: a) size-selective predation, b) reproductive adaptations to frequently disturbed environments, or c) morphological adaptations which minimize physical damage in shifting sands.

4. Small-scale variability in nematode distributions reflects an equilibrium between sediment disturbance, which tends to randomly disperse the fauna, and biological factors, which tend to aggregate the fauna. Instraspecific attraction between males and females is probably a biological process which contributes to the generation of small-scale aggregations within box cores.

5. Species were randomly distributed with respect to each other at within-station spatial scales. If the coexistence of the dominant nematode species were maintained by localized, small-scale disturbances renewing limiting resources, then distinct groups of species

which were either positively or negatively correlated should have
resulted.  There is no indication that either sediment or biological
disturbances maintain the coexistence of numerically dominant species
on these assayed spatial scales.

Table 6. Depth and sediment characteristics of the six Moolach Beach stations. The type of sampling gear used and number of replicate subsamples collected on each date are also shown. SMG: Smith-McIntyre Grab. BXC: Box core.

| Station | Depth (m) | Date Sampled | Sampling Gear | No. Cores | Mean Size $(M_z)$ | Sorting $(\sigma_I)$ | % Silt-Clay |
|---------|-----------|--------------|---------------|-----------|-------------------|----------------------|-------------|
| | | | | | **Sediment Parameters** | | |
| MB1 | 25 | 8/07/79 | SMG | 4 | 2.6 $\emptyset$ | 0.37 | 3.3 |
| MB1 | 25 | 1/23/79 | BXC | 6 | 2.6 $\emptyset$ | 0.52 | 0.9 |
| MB2 | 18 | 6/30/79 | SMG | 3 | 2.6 $\emptyset$ | 0.53 | 5.0 |
| MB3 | 32 | 8/07/79 | SMG | 4 | 2.7 $\emptyset$ | 0.57 | 2.6 |
| MB4 | 29 | 6/30/79 | SMG | 3 | 2.6 $\emptyset$ | 0.48 | 0.5 |
| MB5 | 16 | 8/07/79 | SMG | 4 | 2.6 $\emptyset$ | 0.45 | 1.2 |
| MB6 | 28 | 5/30/79 | BXC | 27 | 2.7 $\emptyset$ | 0.51 | 2.6 |

Table 7. Broad scale distributions of the dominant nematode species within the Moolach Beach study area. Species are arranged from longest to shortest based on average adult female lenghh. Data includes mean abundance, expressed as No./10 $cm^2$, and percentage of the total nematode population (in parenthesis) at each of the six sites. Mean abundance (No./10 $cm^2$) of the total fauna is shown at bottom. The percentage of the total variation in density attributable to within- and between-fluctuation in abundance is given at left.  SD: standard deviation.

| | AVERAGE LENGTH (mm) | SHALLOW STATIONS | | | DEEPER STATIONS | | | % VARIANCE | |
|---|---|---|---|---|---|---|---|---|---|
| | | MB5 (16 m) | MB2 (18 m) | MB1 (25 m) | MB6 (28 m) | MB4 (29 m) | MB3 (32 m) | Within Station | Between Station |
| Mononcholaimus sp. | 3.2 | 4.3 (0.7) | -- | 13.7 (1.6) | 6.5 (1.3) | -- | 23.9 (2.7) | 68.5 | 31.5 |
| Bolbella sp. | 3.2 | -- | -- | 0.9 (0.1) | 22.2 (4.6) | 18.2 (4.3) | 15.4 (1.8) | 46.1 | 53.9 |
| Sabatiera sp. | 2.0 | 52.2 (9.4) | 52.4 (9.2) | 35.1 (4.2) | 69.8 (14.5) | 43.3 (10.2) | 61.6 (7.0) | 96.6 | 3.4 |
| Anticoma sp. | 1.8 | -- | -- | 3.4 (0.4) | 1.1 (0.2) | -- | 17.1 (2.0) | 35.7 | 64.3 |
| Oncholaiminae A | 1.8 | 10.3 (1.9) | 16.0 (2.8) | 6.8 (0.8) | 4.6 (1.0) | 27.4 (6.4) | 16.3 (1.9) | 58.3 | 41.7 |
| Halalaimus sp. | 1.6 | 5.1 (0.9) | 6.8 (1.2) | 20.5 (2.5) | 15.5 (3.2) | 2.3 (0.5) | 25.7 (2.9) | 64.1 | 35.9 |
| Rhabdodemaniinae A | 1.5 | 11.1 (2.0) | 8.0 (1.4) | 7.7 (0.9) | 3.3 (0.7) | 5.7 (1.3) | 1.7 (0.2) | 92.3 | 7.7 |
| Marylynnia sp. | 1.4 | 20.5 (3.7) | 5.7 (1.0) | 20.5 (2.5) | 19.5 (4.0) | 37.6 (8.8) | 37.6 (4.3) | 84.9 | 15.1 |
| Monhysterinae A | 1.3 | 17.1 (3.1) | 5.7 (1.0) | 13.7 (1.6) | 6.1 (1.3) | 5.7 (1.3) | 10.3 (1.2) | 89.3 | 10.7 |
| Monhysterinae B | 1.2 | 1.7 (0.3) | -- | 2.3 (0.3) | 18.2 (3.8) | 2.3 (0.5) | 4.3 (0.5) | 55.7 | 44.3 |
| Axonolaiminae A | 1.1 | 1.7 (0.3) | 2.3 (0.4) | 35.1 (4.2) | 14.6 (3.0) | 16.0 (3.8) | 9.4 (1.1) | 77.2 | 22.8 |
| Chromadorinae A | 1.1 | 0.9 (---) | 1.1 (0.2) | 4.3 (0.5) | 15.0 (3.1) | 12.5 (2.9) | 61.6 (7.0) | 58.7 | 41.3 |
| Ceramonema sp. B | 1.1 | 2.3 (0.4) | 8.0 (1.4) | 15.4 (1.8) | 6.0 (1.2) | 10.3 (2.4) | 13.7 (1.6) | 27.1 | 72.9 |
| Xyala sp. | 1.1 | 17.1 (3.1) | 16.0 (2.8) | 6.0 (0.7) | 8.7 (1.8) | 5.7 (1.3) | 4.3 (0.5) | 89.7 | 10.3 |
| Ceramonema sp. A | 0.9 | 47.9 (8.7) | 67.3 (11.9) | 109.4 (13.1) | 16.7 (3.5) | 16.0 (3.8) | 37.6 (4.3) | 39.3 | 60.7 |
| Ceramonematidae A | 0.9 | 1.7 (0.3) | 9.1 (1.6) | 33.4 (4.0) | 3.2 (0.7) | 4.6 (1.1) | 9.4 (1.1) | 42.0 | 58.0 |
| Nudora sp. | 0.9 | 6.8 (1.2) | 13.7 (2.4) | 14.5 (1.7) | 1.1 (0.2) | 3.4 (0.8) | 6.0 (0.7) | 43.0 | 57.0 |
| Ceramonema sp. C | 0.8 | 13.7 (2.5) | 19.4 (3.4) | 7.7 (0.9) | 1.3 (0.3) | 4.6 (1.1) | 0.9 (0.1) | 26.7 | 73.3 |
| Chromadorinae B | 0.7 | 18.8 (3.4) | 4.5 (0.8) | -- | -- | -- | -- | 28.6 | 71.4 |
| Tricoma sp. | 0.5 | 6.8 (1.2) | 26.2 (4.6) | 31.6 (3.8) | 9.5 (2.0) | 11.4 (2.7) | 19.7 (2.2) | 70.4 | 29.6 |
| Rynchonema subsetosa | 0.5 | 22.2 (4.0) | 44.5 (7.8) | 22.2 (2.7) | 10.5 (2.2) | 17.1 (4.0) | 3.4 (0.4) | 60.0 | 40.0 |
| Chromadorinae C | 0.4 | 4.3 (0.8) | 23.9 (4.2) | 4.3 (0.5) | 5.1 (1.1) | 9.1 (2.1) | 1.7 (0.2) | 77.5 | 22.5 |
| Richtersia sp. | 0.4 | 41.0 (7.4) | 28.5 (5.0) | 49.6 (6.0) | 6.6 (1.4) | 18.2 (4.3) | 18.0 (2.1) | 48.8 | 51.2 |
| | | | | | | | $\bar{x}$ = | 60.0 | $\bar{x}$ = 40.0 |
| TOTAL NEMATODES SD = | | 553.2 (275.0) | 567.7 (133.4) | 333.6 (170.4) | 482.9 (133.4) | 425.2 (159.0) | 875.5 (87.2) | 62.9 | 37.1 |

Table 8. Small scale distributions of dominant nematode species in May and January 1979. For both sampling dates the average number of individuals sampled per core, percent of the total population, average depth in the sediment, and the dispersion $X^2$ test statistic $\underline{I}$ are listed for each species. The percent of the total variation in density which can be attributed to differences between cores, between quadrants, and between box cores in May is also given. Similar information for the total nematode fauna is shown at bottom.
†: $0.1 < p < 0.05$.  *: $p \leq 0.05$.  **: $p \leq 0.005$.

| | May | | | | % Variance | | | January | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean Depth < 5 cm | No. Core$^{-1}$ | % Total | Mean Depth (cm) | I | Core | Quad | Box | No. Core$^{-1}$ | % Total | Mean Depth (cm) | I |
| Bolbella sp. | 6.5 | 3.3 | 0.8 | 594.4** | 58.8 | 33.6 | 7.6 | ---- | ---- | ---- | ---- |
| Axonolaiminae A | 4.3 | 2.2 | 0.9 | 134.6** | 93.2 | 6.8 | 0 | 3.7 | 1.5 | 1.9 | 8.0 |
| Rynchonema subsetosa | 3.1 | 1.5 | 1.3 | 76.1** | 70.3 | 29.7 | 0 | 3.5 | 1.4 | 2.3 | 14.7* |
| Chromadorinae A | 4.4 | 2.2 | 1.8 | 283.4** | 53.9 | 46.1 | 0 | ---- | ---- | ---- | ---- |
| Mononcholaimus sp. | 1.9 | 1.0 | 2.0 | 44.8* | 75.9 | 22.3 | 1.8 | 5.0 | 2.0 | 3.7 | 12.0* |
| Sabatiera sp. | 20.6 | 10.4 | 2.4 | 174.5** | 55.1 | 0.6 | 44.0 | 12.5 | 5.0 | 3.9 | 14.8* |
| Xyala sp. | 2.5 | 1.3 | 2.7 | 101.2** | 61.1 | 38.9 | 0 | 5.4 | 2.1 | 4.9 | 26.9** |
| Monhysterinae B | 6.1 | 3.1 | 3.1 | 231.5** | 63.6 | 11.4 | 25.0 | ---- | ---- | ---- | ---- |
| Marylynnia sp. | 6.3 | 3.2 | 3.1 | 93.8** | 56.6 | 43.4 | 0 | 6.5 | 3.2 | 6.0 | 4.5 |
| Halalaimus sp. | 5.3 | 2.2 | 3.3 | 39.2* | 91.4 | 6.6 | 2.0 | 2.8 | 1.1 | 5.9 | 8.7 |
| Ceramonema sp. B | 2.3 | 1.1 | 3.5 | 53.6** | 89.8 | 0 | 10.2 | 5.2 | 2.1 | 3.4 | 11.4* |
| Ceramonema sp. A | 5.7 | 2.7 | 3.7 | 84.3** | 40.6 | 56.0 | 3.4 | 24.2 | 9.7 | 4.3 | 9.3† |
| Tricoma sp. | 3.3 | 1.7 | 3.8 | 67.3** | 59.0 | 15.0 | 26.0 | 11.0 | 4.4 | 4.9 | 6.9 |
| Richtersia sp. | 2.9 | 1.5 | 4.9 | 56.3** | 70.1 | 29.9 | 0 | 10.3 | 4.1 | 5.7 | 7.3 |
| | | | | $\bar{X} =$ | 67.1 | 24.3 | 8.6 | | | | |
| Mean Depth > 5 cm | | | | | | | | | | | |
| Monhysterinae C | 2.8 | 1.4 | 5.2 | 81.7** | 97.4 | 1.9 | 0.7 | 2.7 | 1.1 | 6.2 | 2.0 |
| Comesomatidae A | 2.5 | 1.3 | 5.9 | 55.9** | 66.1 | 18.4 | 15.5 | ---- | ---- | ---- | ---- |
| Paramesonchium sp. | 2.4 | 1.2 | 6.3 | 36.4† | 97.9 | 0 | 2.1 | 4.5 | 1.8 | 9.5 | 9.2† |
| Monhysterinae D | 2.7 | 1.4 | 6.5 | 95.3** | 28.0 | 26.9 | 45.1 | ---- | ---- | ---- | ---- |
| Odontophora sp. | 12.5 | 6.3 | 8.2 | 36.1† | 98.3 | 1.7 | 0 | 6.2 | 2.5 | 9.3 | 18.6** |
| Paramicrolaimus sp. | 4.8 | 2.4 | 8.3 | 80.5** | 79.9 | 18.3 | 1.8 | 5.5 | 2.2 | 8.5 | 8.3 |
| Monhysterinae E | 3.0 | 1.5 | 9.2 | 58.7** | 56.3 | 15.5 | 28.2 | ---- | ---- | ---- | ---- |
| | | | | $\bar{X} =$ | 74.8 | 11.8 | 13.3 | | | | |
| TOTAL NEMATODES | 198.0 | ---- | 4.7 | 446.3** | 45.7 | 28.4 | 25.8 | 249.0 | ---- | 5.3 | 109.9** |

Table 9.  Green's index of dispersion for the dominant species which were not randomly distributed in January.

|  | Green's Index (GI) | |
|---|---|---|
|  | January | May |
| Mononcholaimus sp. | 0.05 | 0.05 |
| Sabatiera sp. | 0.03 | 0.03 |
| Xyala sp. | 0.14 | 0.16 |
| Ceramonema sp. B | 0.04 | 0.17 |
| Ceramonema sp. A | 0.01 | 0.06 |
| Rynchonema subsetosa | 0.10 | 0.04 |
| Paramesonchium sp. | 0.03 | 0.01 |
| Odontophora sp. | 0.08 | 0.01 |

Table 10. Averaged intraspecific correlations between reproductive categories of nine nematode species (Chromadorinae A, Tricoma sp., Halalaimus sp., Sabatiera sp., Marylynnia sp., Monhysterinae B, Ceramonema sp. A, Axonolaiminae A, and Rynchonema subsetosa). Values in parenthesis are standard deviations. The number of significant coefficients (Sig.) in each category is also listed.

| | Female | Gravid Female | Juvenile |
|---|---|---|---|
| Male | 0.33 (0.18) sig.=6 | 0.45 (0.24) sig.=7 | 0.27 (0.14) sig.=4 |
| Female | | 0.31 (0.21) sig.=5 | 0.28 (0.29) sig.=6 |
| Gravid Female | | | 0.16 (0.29) sig.=2 |

Figure 2.  Chart of Moolach Beach study area, including positions of stations MB1 through MB6.
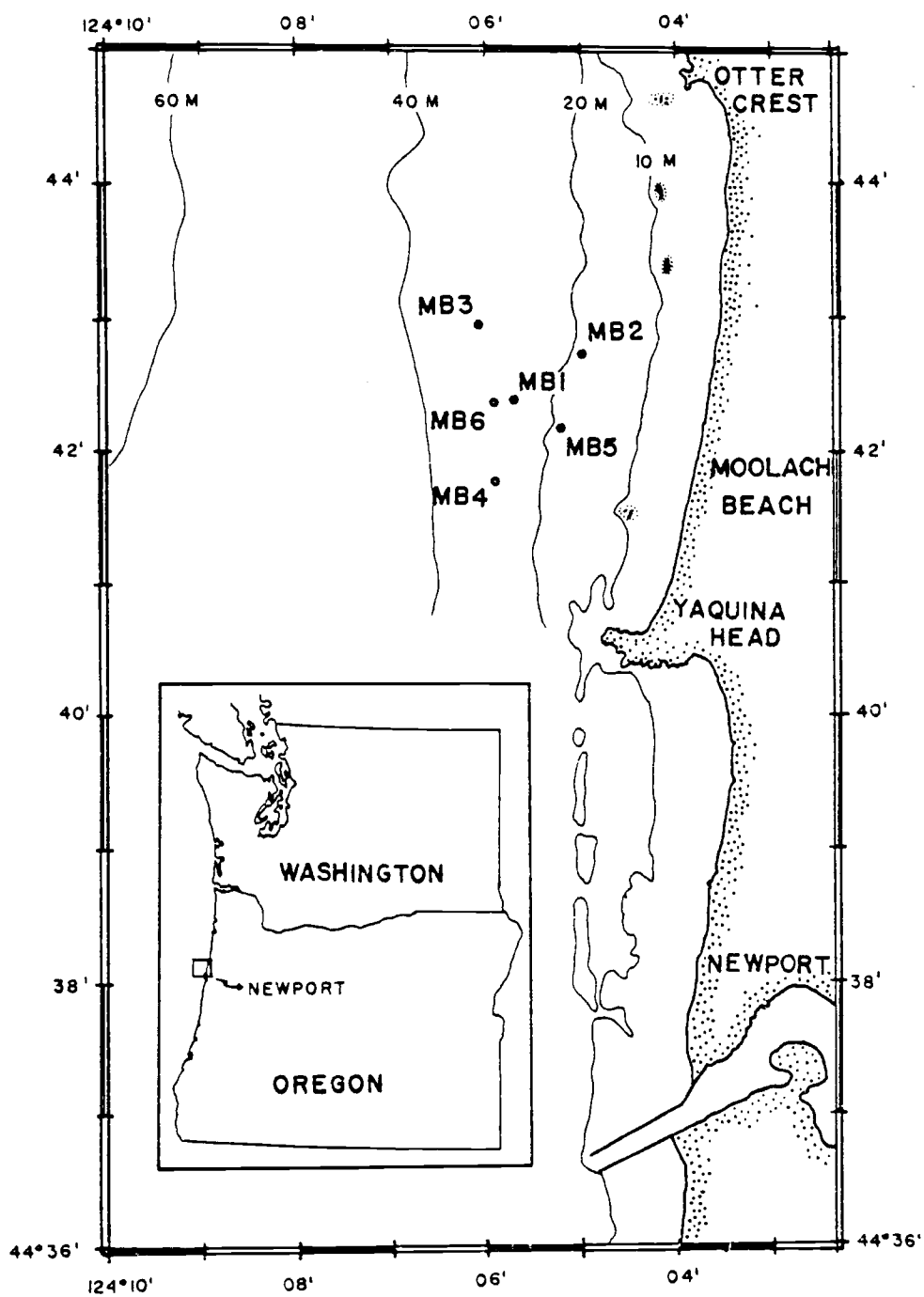
Figure 2.

Figure 3.  Diagram illustrating positions of subsamples collected

from three 0.25 m$^2$ box cores on 30 May 1979.  Plastic corers

with a 1.9 cm internal diameter were used to obtain nine samples

from each box.
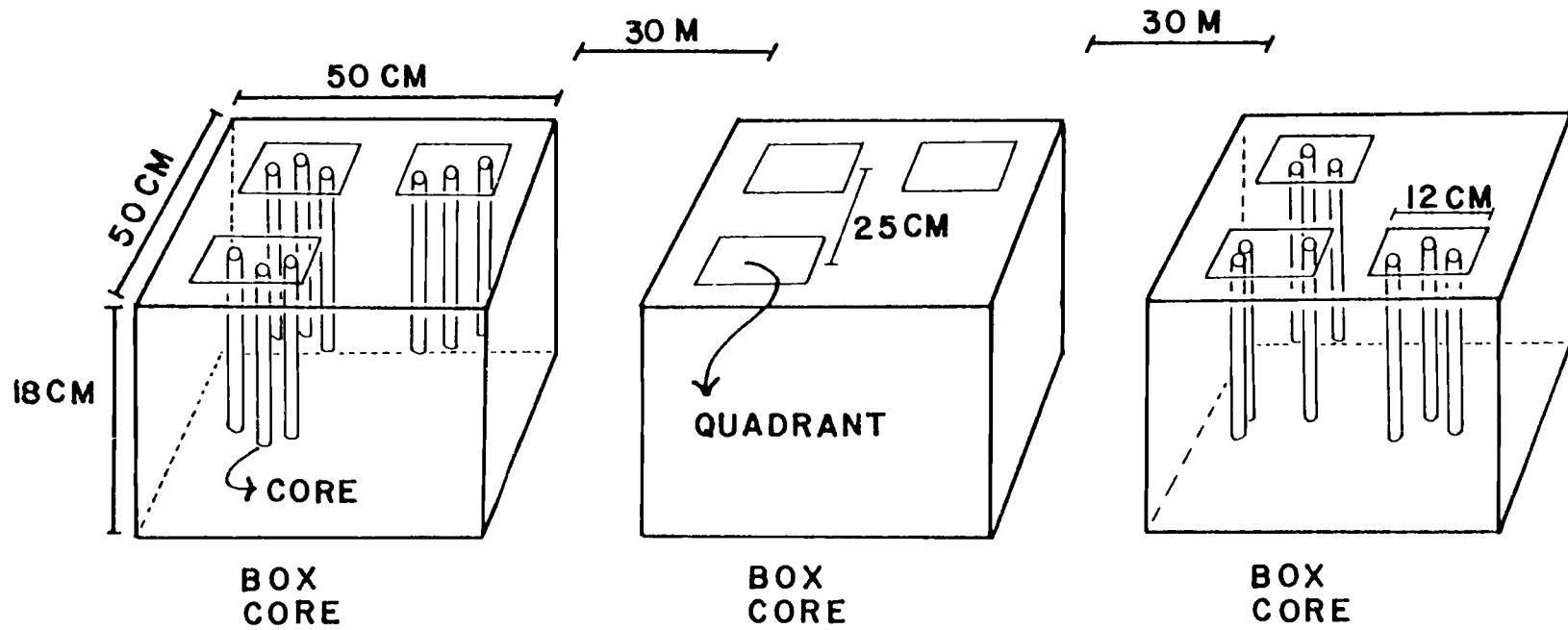
Figure 3.

Figure 4.  Total number of nematodes sampled by paired transects of

contiguous small (6 mm diameter) cores in both May and January.

Paired transects, designated "A" and "B", were positioned paral-

lel to each other, 3 cm apart.  Ten cores equals 6 cm.
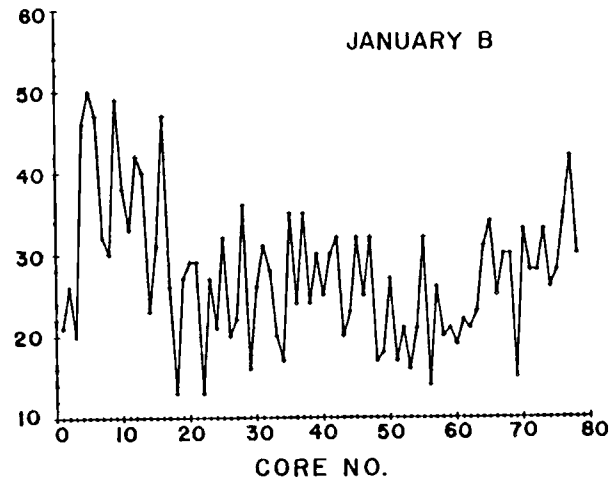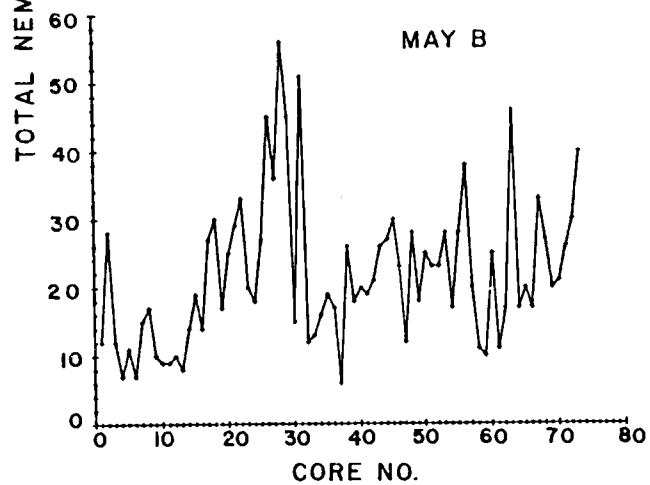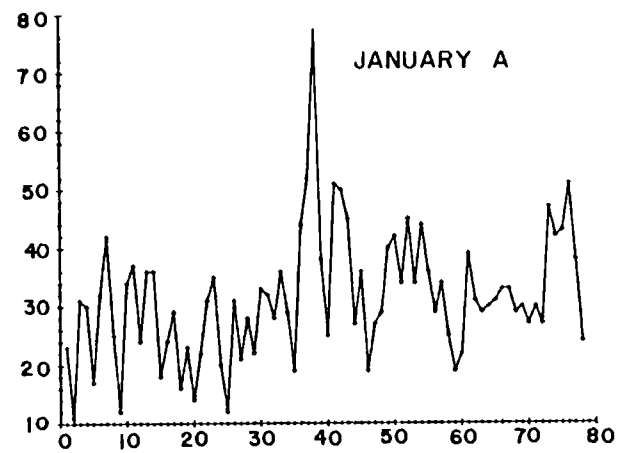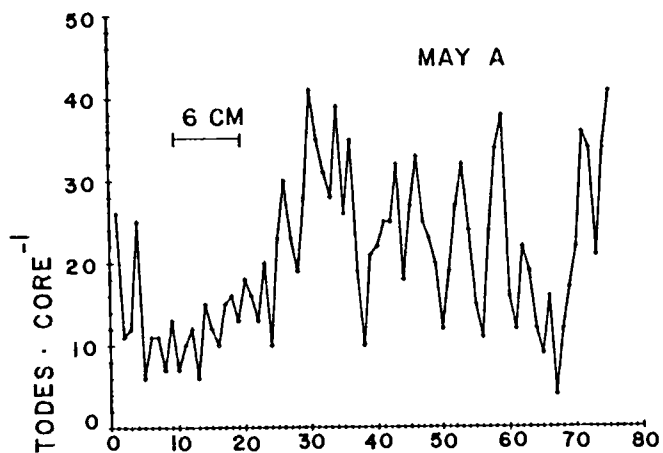
Figure 4.

Figure 5. Autocorrelation coefficients, $C_{xx}(k)$, plotted from 1 to 18 lags for the total nematodes per core in transects May "A" and January "A." Three lags equals 1.8 cm.
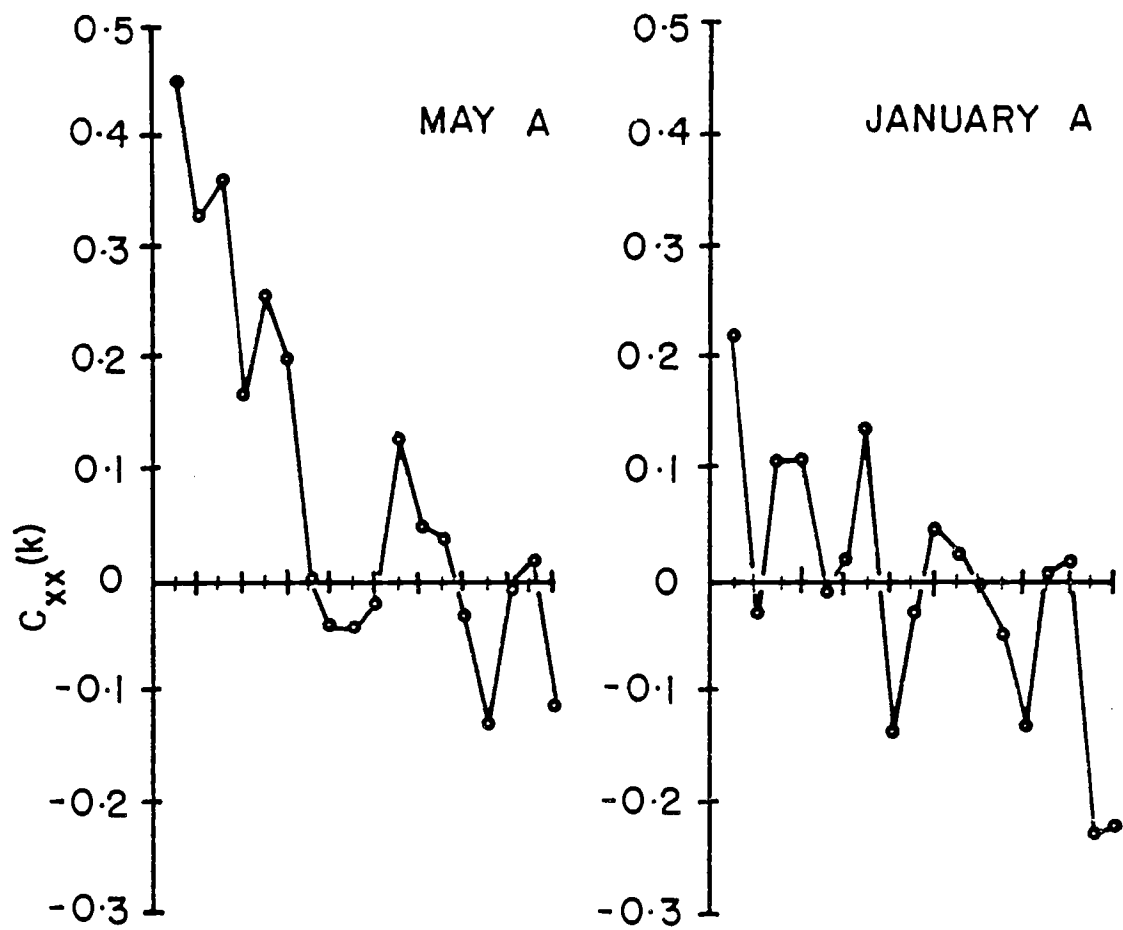
Figure 5.

Figure 6. Cross-correlation coefficients, $C_{xy}(k)$, computed between

the total nematode abundance in paired small core transects

plotted from -15 to +15 lags.
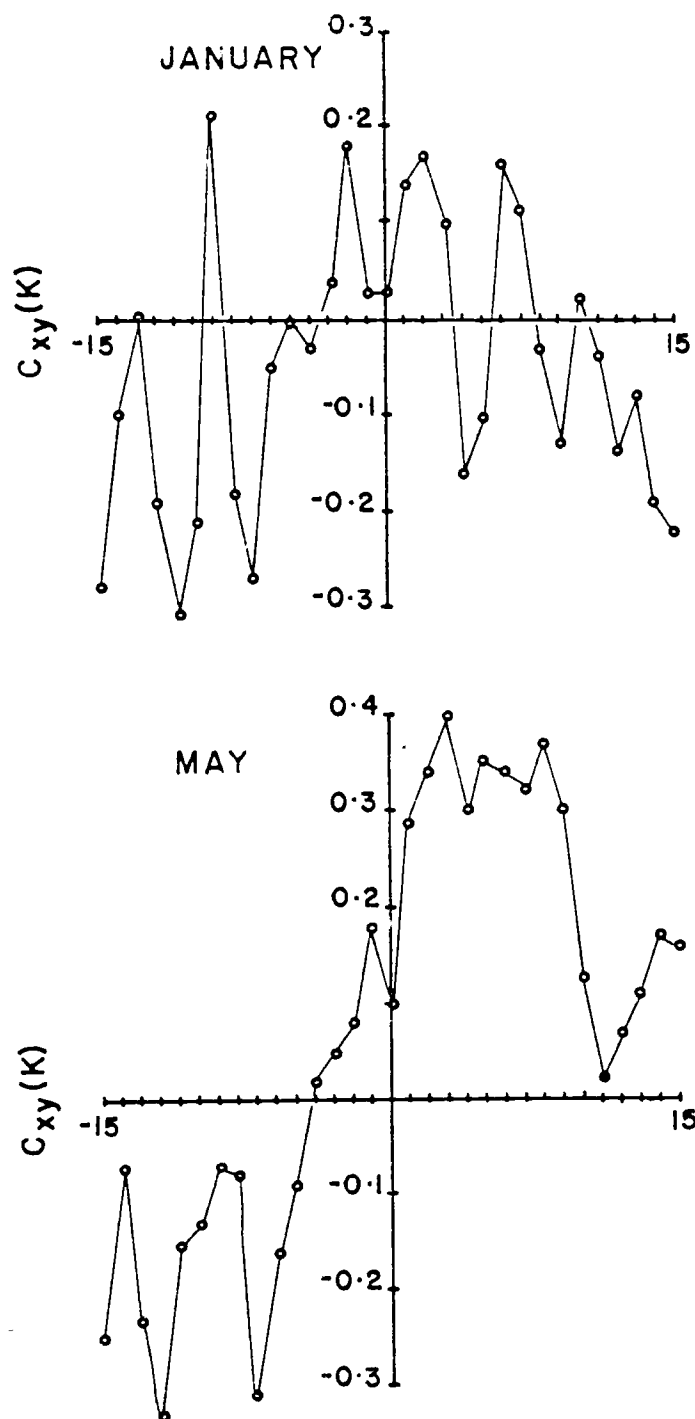
Figure 6.

Chapter 4

FEEDING ECOLOGY OF 0-AGE FLATFISHES (BOTHIDAE, PLEURONECTIDAE)

AT A NURSERY GROUND ON THE OPEN OREGON (USA) COAST

Abstract

The food habits of 0-age English sole (Parophrys vetulus),

butter sole (Isopsetta isolepis), speckled sanddab (Citharichthys

stigmaeus), and sand sole (Psettichthys melanostictus) were investi-

gated over a 2-1/2 year period at a shallow nursery area (9-30 m) off

the central Oregon coast. A total of 422 guts from recently meta-

morphosed fish (17-88 mm SL) were examined; only 16 were empty (4%).

The greatest similarity in diets was between English and butter

soles. Both species were benthophagous, feeding on a wide variety of

prey, including palps of the polychaete Magelona sacculata, juvenile

bivalves, siphons from tellinid clams, harpacticoid copepods, amphi-

pods, cumaceans, and juvenile decapods. Speckled sanddabs fed equally

on benthic prey (amphipods, cumaceans, decapods) and mysids, while

sand sole almost exclusively ate mysids. The guts of all four

species tended to be less than 25% full in the morning before 0900;

stomach fullness gradually increased during the late morning and

afternoon.

Food habits of English sole were a function of location of

capture within the study area, season, and fish length. Juveniles

less than 35 mm SL fed on small prey, e.g. polychaete palps, juvenile

bivalves, tellinid clams, and harpacticoids, while larger individuals

fed on larger prey, e.g. amphipods, cumaceans and decapods. Diets of

English sole less than 35 mm SL varied greatly both between seasons

in the same year and between years. Spatially, the diets of English

sole captured in trawls at the same depth and different depths were

similar in January 1979 but highly variable in May 1979. These

caused by seasonal changes in the abundance and spatial distributions

of benthic prey.

## Introduction

Many juvenile flatfishes recruit to the sea floor in well
defined nursery areas following metamorphosis from pelagic larvae.
The types and densities of food items present in such benthic regions
potentially can affect growth and mortality of recently settled
flatfish species (Paloheimo and Dickie 1966; Steele et al. 1970;
Cushing and Harris 1973). In addition, whenever the nursery grounds
of several species coincide or overlap, interspecific interactions
originating from similarities in diet may also be a factor regulating
growth and survival (e.g. Edwards and Steele 1968). Four species of
pleuronectiform fishes, English sole (Parophrys vetulus), butter sole
(Isopsetta isolepis), speckled sanddab (Citharichthys stigmaeus), and
sand sole (Psettichthys melanostictus), utilize the shallow water of
the open Oregon coast as a site of benthic recruitment and early
growth. All but C. stigmaeus are important to the Oregon trawl
fishery. English sole ranks among the top three commercial species
based on annual landings. In conjunction with a long-term research
program designed to improve management of Oregon's multi-species
demersal fishery (Pearcy et al. 1977; Richardson and Pearcy 1977;
Pearcy and Hancock 1978; Laroche and Richardson 1979; Hayman and
Tyler 1980), we examined the prey selected by recently settled indi-
viduals of these four species at one site over a 2-1/2 year period.
Our specific goals were to describe the food habits of these fishes,
to relate the temporal and spatial variability of the English sole
diet to changes in prey abundance and distributions, and finally to
compare the dietary and habitat overlap of English and butter soles.

Materials and Methods

The area selected for this work was located off Moolach Beach on the open Oregon coast (Figure 7). Situated between Yaquina Head and Cape Foulweather 10 km north of the nearest estuary, this site has been the focus of recent work on the recruitment and growth of juvenile pleuronectids (Laroche and Holton 1979; Rosenberg 1981; Krygier and Pearcy unpubl.) and the food habits of adult flatfishes (Wakefield, unpubl.). Trawl samples collected from this area between May 1977 and September 1979 were utilized for our work. A 1.5 m beam trawl fitted with a recording odometer wheel and a 7 mm stretch mesh liner was employed for all but one of these collections. On one occasion, 22 March 1979, we obtained samples using a small otter trawl which also had a 7 mm stretch mesh liner. On each sampling date, 10 min. tows covering approximately 750 m$^2$ surface area were made at several depths between the 9 and 30 m isobaths (0.9 and 2.7 km offshore, respectively). Fish were preserved in 10% buffered Formalin immediately upon collection. No regurgitation of gut contents was observed. The daily time of sampling varied between 0830 and 1800.

From the 35 trawl collections obtained during this 29 month period, we selected 31 for examination. Several criteria were used in choosing these samples. In keeping with an overall goal of the Pleuronectid Project to obtain detailed information on the most important commercial species, emphasis was placed on those trawls which contained English sole. Priority was also given to using samples which were collected between July 1978 and September 1979,

since quantitative meiobenthic samples were also gathered from the study area during that period. We used selected trawl collections from 1977 and 1978 to investigate the between-year repeatability of trends noted in the 1979 data. Finally, only hauls containing specimens 70 mm standard length (SL) and less were used.

In the laboratory a size range of juvenile flatfish was selected from each of the trawls chosen for study. Standard length of each specimen was recorded prior to removal of the gut. Both the stomach and intestinal tract were removed and opened under a dissecting microscope; gut contents were identified to the lowest possible taxon and counted. We used a subjective scale ranging between 0 and 4 to quantify the degree of gut fullness (0 = less than 5% full, 1 = 5 - 25% full, 2 = 25 - 50% full, 3 = 50 - 75% full, 4 = 75 - 100% full).

Quantitative data for each prey category were summarized in two ways. The frequency of prey occurrence, expressing the proportion of all fish sampled which had a given food item in their gut, was computed for each flatfish species within a trawl. The mean percent composition, based on numerical abundance, was determined also by averaging the percent composition of each individual fish gut for a given species within a trawl. When more than one trawl was examined from a sampling date, the frequency of occurrence and percent composition from the separate trawls were averaged to give an overall mean. Diversity (H') of prey consumed was computed using natural logarithms (Pielou 1969).

On two sampling dates, 29 May and 30 June 1979, English sole were captured at the study site and returned live to the laboratory

along with sand collected from the same area using a 0.25 m$^2$ box core. Fish were placed in aquaria with the sediments, and their behavior was monitored over several days while they fed on naturally occurring prey in the sediments. Fresh seawater (12°C) was circulating continually through each aquarium. A photoperiod matching that experienced by the fish in the field was maintained using room lighting.

Quantitative meiobenthic samples were obtained from the study area at one site in 25 m of water (Figure 7). Three replicate 0.25 m$^2$ box cores, positioned 30 m apart, were collected on each of six cruises between July 1978 and May 1979. Box cores were subsampled with at least three randomly placed clear plastic cores (1.9 cm internal diameter) which were in turn vertically partitioned into six depth increments (0-1 cm, 1-3 cm, 3-6 cm, 6-11 cm, 11-18 cm, and greater than 18 cm). These plastic corers were also used to subsample Smith-McIntyre grabs collected on two cruises in July and September 1979 at the same site. Samples were preserved in 10% buffered Formalin and stained with rose bengal. The fauna was extracted from the sediments (well sorted fine sand) by shaking and decanting followed by three rinses. A 38.5 µm sieve was used to retain the fauna. Harpacticoid copepods and nematodes were identified to species and enumerated.

Results

The data for all four flatfish species are summarized in Table 11. A total of 422 guts from recently settled fish (17-88 mm SL) were examined, only 16 of which were empty (4%). The guts of an additional 40 late stage IV and early Stage V P. vetulus larvae (sensu Shelbourne 1957) were also examined. These metamorphosing individuals, ranging in size from 16-18 mm SL, all had empty stomachs and intestinal tracts.

The 13 prey categories identified (Table 11, top) were placed into three broad groupings based on the size of individual food items and their typical location within the habitat. Small benthic prey were composed of palps from the surface deposit feeding polychaete Magelona sacculata, juvenile bivalves (predominantly Tellina modesta and occasionally Siliqua patula), siphon tips cropped from tellinid clams, harpacticoid copepods (mainly Halectinosoma spp. and a few Thompsonula hyaenae and Rhizothrix curvata), free-living nematodes (Theristus sp. and Mesacanthion sp.), and tube feet from the sand dollar Dendraster excentricus. These food items were on the order of 0.5 to 1.5 mm in length. Larger benthic prey were amphipods (predominantly Ampelisca spp. and Eohaustoris sp.), cumaceans, decapods (juvenile Cancer magister, pinnotherid crabs, and Callianassa californiensis), and polychaetes (Nephtys sp., Glycinde armigera, Magelona sacculata, Thalenessa spinosa, and Spiophanes bombyx). These prey were usually juveniles measuring 1.5 to 4 mm in their largest dimension. Species identifications were difficult for this latter group because of their immature status and tendency to fragment after being

eaten. Examination of the meiofaunal cores revealed that all the organisms classified as "benthic" occurred in the upper 1 cm of sediment. Prey items which were never found in benthic samples were defined as "pelagic" and consisted of mysids (mainly _Neomysis kadiakensis_), calanoid copepods (_Pseudocalanus_ sp.), and veliger larvae. This distinction between benthic and pelagic organisms is somewhat arbitrary, since some of these species are mobile epibenthic forms which are probably capable of occurring both in the sediments and the overlying water.

Adequacy of the sample sizes used in determining food habits of the flatfish species was assessed using several techniques. The guts of 16 _P_. _vetulus_ (19 to 48 mm SL) and 16 _I_. _isolepis_ (19 to 33 mm SL) were examined from each of two tows. These two species were selected because they fed on a much broader spectrum of prey than _C_. _stigmaeus_ or _P_. _melanostictus_ and hence are subject to greater sampling error. The cumulative number of prey categories encountered, expressed as a function of sample size, is shown in Figure 8. For both English sole and butter sole, after 7-8 fish have been examined no new food categories were found. After examining only 4 fish, 75% of all food items have been collected. This qualitative consistency among guts is also reflected in the high frequency of occurrence (Table 11) for most prey. Quantitatively, the composition of gut contents varies little among individuals of a species within a trawl. For each species studied, food items from fish caught in the same trawl tend to have the same rank order of numerical abundance. This consistency of results was statistically significant; the null hypothesis of

independnece among prey rankings was rejected (Friedman's nonparametric randomized block ANOVA, p<0.005; Gibbons, 1971).  On several sampling dates the number of fishes available for study was small, e.g. P. vetulus on 5 September 1978 (3 fish), I. isolepis on 30 May 1979 (4 fish).  The small within-sample variability of these species, however, indicates that such small sample sizes will not unduly bias determination of the major food items consumed.

As is apparent from Table 11, P. vetulus feeds on a wide variety of benthic animals.  Juvenile bivalves, harpacticoid copepods, Magelona palps, and amphipods are particularly abundant in English sole guts.  On most sampling dates, the frequency of occurrence of these four prey in the diet of English sole was high, although typically only one or two items dominated the diet numerically.  Occasionally a food item which was usually rare became a major component in the guts of English sole, such as free-living nematodes on 25 July 1978 or echinoid tube feet on 30 June 1979.  The diet of I. isolepis was very similar to P. vetulus with the exception that butter sole fed to a greater extent on mysids and decapods.  Citharichthys stigmaeus fed equally on large epibenthic crustaceans (amphipods, decapods, cumaceans) and pelagic prey.  Polychaetes were totally lacking in the diet. Psettichthys melanostictus consumed mysids almost exclusively; only on 8 August 1979 were other pelagic prey found in the guts of this species.  Average H' diversity of food consumed per sampling date in 1979 was 1.38 for English sole, 1.47 for butter sole, 0.81 for speckled sanddabs, and 0.14 for sand sole.  The similarity in diets of these four species was compared by computing the percent similarity

index (PSI: Whittaker 1960) based on the average 1979 proportions of prey consumed by each species (Table 12). Two of these paired comparisons, P. vetulus-I. isolepis and C. stigmaeus-P. melanostictus, indicate similarities exceeding 50%. In the case of the speckled sanddab and the sand sole, this dietary overlap is based on their common utilization of one food category, mysids. English and butter soles share a wide variety of prey which were consumed in very similar proportions, e.g. 29 May 1979.

Observations of 20-25 mm P. vetulus feeding in laboratory aquaria revealed two basic types of foraging behavior. In the first, fish remained motionless on the bottom and then periodically lunged forward 1-2 cm, striking at objects located on the surface of the sediment. In the second, fish slowly raised their heads above the bottom then rapidly thrust forward, causing the upper few millimeters of sediment to billow into suspension. Parophrys vetulus would then strike in rapid succession at small objects presumably temporarily displaced from the bottom. Neither type of behavior predominated; both were detected in all of the individuals observed. After monitoring these responses for several hours, fish were sacrificed and the guts examined. Harpacticoid copepods dominated the diet of these fish.

Shifts in prey preference as a function of fish size (age) were observed in English sole. The average diets of all P. vetulus less than and greater than 35 mm SL were computed using the 1979 data and compared (Table 13). The dramatic difference in prey of these two size classes is apparent. Smaller fish (17 to 35 mm SL) consumed small prey almost exclusively while larger fish (35 to 82 mm SL) only

occasionally ingested these small items, choosing instead amphipods and cumaceans. Isopsetta isolepis showed a similar shift in the preferred size of prey as standard length increased from 30 to 40 mm. Fourteen butter sole (17-35 mm SL) caught on 29 May 1979 fed predominantly on small food items while the gut contents of four larger fish (49-60 mm SL) caught one day later were composed of amphipods, cumaceans, and decapods (Table 11). A similar distinction was found in fish collected on 19 July 1979. Neither C. stigmaeus nor P. melanostictus altered the taxonomic composition of their diet within the size ranges of fish we examined, although as with English and butter soles larger fish eat larger prey.

The guts of all four species were generally less than 25% full in the morning before 0900. Stomach fullness gradually increased during the late morning and afternoon. The correlation between the time of capture (ranging between 0830 and 1800 h) and average gut fullness for English sole was significant; $r = 0.49$, $p = 0.05$. On 22 March 1979 two otter trawl hauls were made, one at 1000 and another at 1800. Guts of 10 English sole ranging in size between 19 and 35 mm SL were examined from both trawls. The diets of both groups of fish were the same, but the fish collected at 1800 had an order of magnitude more food items in their guts than the earlier collection: 90% full, $198 \pm 56$ (standard deviation, SD) items, versus 10% full, $18 \pm 17$ (SD) items. Isopsetta isolepis, C. stigmaeus, and P. melanostictus showed similar daily trends.

Sufficient numbers of English sole of the same size were collected on 23 January and 29 May 1979 to compare the similarity of

diets within and between replicate trawls. The percent similarity

index (PSI) was used to quantify the proportion of food items found

in common for each possible pair of fish collected on a sampling

date. Mean similarity values were then obtained by averaging the PSI

values for the fish within the same trawl and for fish collected in

different trawls. Comparing replicate samples obtained at the same

depth (Table 14, top), the average PSI for fish guts within the same

trawl in both January and May as well as the mean PSI between fish in

different trawls in January were approximately the same, 50%. The

similarity between two trawls at the same depth in May, though, is

very low (3%). Table 14 (bottom) also shows a comparison of within-

trawl and between-trawl similarity, where trawls were collected at

different depths (20 m and 30 m). Again the within-trawl affinities

are high in both January and May as is the between-tow similarity in

January. The average PSI in May for fish from different depths is

low. The increased between-trawl variability in food habits noted on

29 May was a general feature observed in all late spring and early

summer replicate collections of P. vetulus. For example, on 13 July

1978 trawls were made at 15 m and 20 m. Magelona palps numerically

comprised 72% of the English sole diet at 15 m but only 19% at 20 m,

while juvenile bivalves and harpacticoid copepods combined to form

19% of the prey consumed at 15 m and 63% at 20 m.

The diet of recently settled English sole changed continually

among sampling months. Comparing similar sized fish (17-35 mm SL)

caught in 1979 (Figure 9) reveals that dominant food items on a

numerical basis varied from Magelona palps (November 1978, January

1979), juvenile bivalves (March 1979), bivalve siphons (April and May 1979), to juvenile bivalves and harpacticoid copepods (July 1979). Examination of samples collected in 1977 and 1978 shows that the sequence of changes noted in 1979 does not repeat each year. Magelona palps, which in 1979 were never a dominant item in the diet of P. vetulus after January, were numerically the most abundant food on two sampling dates in the summer of 1978. Other between-year differences exist, e.g. 5 September 1978 and 24 September 1979, but it is impossible to determine whether these differences are real or are a result of spatial variability in diet combined with insufficient sampling.

The apparent increased equitability of prey items shown in Figure 9 for April and May relative to January and March does not indicate that spring and summer diets of individual fish are more diverse than in winter. Instead, the difference is an artifact of the spatial variability previously noted, being generated by averaging the data for all fish caught in different tows. The average dietary diversity (H') of an individual fish on 23 January 1979 ($0.43 \pm 0.35$ SD, n=24) was not significantly different from that on 29 May 1979 ($0.37 \pm 0.41$ SD, n=32).

The only seasonal data currently available on the abundance of benthic organisms at Moolach Beach are for nematodes and harpacticoid copepods. Nematodes are very abundant ($\overline{X} = 1050 \cdot 10 \text{ cm}^{-2}$) but quantitatively, with the exception of one sampling date, are not significant in the diet of the fish species we studied. Harpacticoids are important in the diets of English and butter soles, yet are not abundant at the study site. Their average density for the eight

sampling dates between July 1978 and September 1979 was $12.2 \pm 4.0$ (Standard error, SE) $\cdot$ 10 cm$^{-2}$. Only the larger species found in the 0-1 cm depth increment were present in fish guts. <u>Halectinosoma</u> spp. comprised more than 80% of all harpacticoid prey. Seasonally, <u>Halectinosoma</u> ranged in abundance from a mean of $6.8 \cdot 10$ cm$^{-2}$ between May and September (n=5) to zero from October to March (n=3). Their period of maximum density coincides with their maximum occurrence in the diet of 17-35 mm SL English sole (Figure 9).

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Discussion

The diet of recently settled English sole is a function of size,
location of capture, and season (Tables 11, 13 and 14). Both the
within-year and between-year differences in diet noted for P. vetulus
are similar to changes documented for other pleuronectid species
(Macer 1967; Edwards and Steele 1968) and are probably related to
temporal changes in density of prey organisms. Steele et al. (1970)
concluded that variations in predation on Tellina siphons and poly-
chaetes by young plaice, Pleuronectes platessa, were a result of
changes in both the absolute and relative abundances of these prey
over time. The observed relationship between seasonal changes in
harpacticoid copepod abundance and the utilization of these prey as
food by English sole is the only direct evidence we have to support
this contention. However, the juvenile bivalves (Tellina and Siliqua)
consumed by P. vetulus were all young of the year which are known to
have temporally variable recruitment (H. R. Jones, personal communi-
cation), suggesting that seasonal availability of this food item is
also not constant. Moreover, Oliver et al. (1980) seasonally sampled
the nearshore macrobenthos in a region of Monterey Bay, California,
which was very similar to Moolach Beach in terms of physical environ-
ment and fauna present. Their results indicate that the abundance of
amphipods and such polychaetes as Magelona sacculata vary both within
and between years. English sole at Moolach Beach probably alter
their diet over time in accordance with similar temporal changes in
the density of these larger prey species, but additional benthic data
obtained concurrently with fish collections are necessary to

substantiate this conclusion.

The marked differences between summer and winter spatial varia-
bility in English sole diets (Table 14) are thought to be related to
changes in both the abundance and spatial distribution of prey.
During the winter, intense storm activity along the Oregon coast
produces large waves which continually disturb and mix the sediments
of the inner continental shelf (Komar et al. 1972). The meiobenthos
has been shown to become randomly distributed during these periods
within small areas (1 m$^2$) and only slightly aggregated on larger
scales (Hogue 1982). Small benthic prey fed upon by 0-age English
sole would most likely be affected by this vigorous physical mixing
in much the same way as the meiofauna. As a result, English sole
feeding at either the same depth or different depths may consume
similar prey in the winter (Table 14, January) because prey organisms
are more evenly distributed within the study area compared to other
times of the year. Such a distribution, when coupled with the
numerical dominance of one food item, would increase the similarity
of food items available for consumption throughout the region.
During the late spring and summer the physical disruption of sediment
is minimized and the spatial distribution of the meiofauna becomes
increasingly aggregated (Hogue 1982). Distinct differences in the
species composition and abundance of nematodes and harpacticoids have
been found at locations only 250 m apart. During this period there
is little similarity in diets of English sole from replicate trawls
(Table 14, May). In the spring and summer, P. vetulus may be oppor-
tunistically exploiting different prey which are densely aggregated

in different sectors of the Moolach Beach site.

Seasonal changes in the spatial distribution of prey items may also alter the rate at which prey are consumed. Experiments with fish feeding in aquaria (Ivlev 1961) have shown that an increase in the degree of aggregation of food sources has the same effect on the rate of food consumption as an increase in the concentration of food. Results of Tinbergen et al. (1967) suggest similar relationships between the spatial distribution of prey and predation. Fish commencing their benthic feeding in the late spring and summer at Moolach Beach may benefit energetically from the increased aggregation of benthic organisms during this period relative to that found during the winter.

The consumption of parts of macrobenthic organisms, e.g. _Magelona_ palps and tellinid clam siphons, rather than whole individuals by English sole less than 35 mm in length is probably related to the maximum size of food items capable of being captured and ingested by these fish. We measured the mouth size of 30 mm _P. vetulus_ and found that prey greater than approximately 2 mm in their largest dimension are too large to be consumed by such small fish. Siphons and palps are apparently the only portion of larger prey which are available for ingestion by fish less than 35 mm SL. As fish grow larger than 35 mm, small food items are neglected in favor of polychaetes, amphipods, and cumaceans which yield far more energy per individual item. Two fortuitous consequences of this size dependent predation may be important. First, the dietary overlap between small juveniles and larger fish is minimized, thus conserving food stocks for recently

settled individuals. Second, both siphons and palps are capable of being regenerated. By consuming only parts of benthic organisms, food sources are not destroyed and may be cropped again in later months by other individuals following regeneration. This may be particularly important in the case of English sole because juveniles are continuously recruited to the bottom over a 9 month period (Krygier and Pearcy, unpubl.).

The four pleuronectiform fishes we studied form a trophic continuum, ranging from generalists feeding upon numerous benthic prey (P. vetulus) to specialists relying on a few pelagic food items (P. melanostictus). Isopsetta isolepis and C. stigmaeus are intermediate in their position on the continuum. Few published results exist with which to compare ours. Cailliet et al. (1979) investigated the food habits of P. vetulus, C. stigmaeus, and P. melanostictus at an ocean station in Monterey Bay. The fish they examined were all larger than the ones for which we have data, but the same basic trends emerge. They found that English sole was a generalist, eating a wide variety of benthic food items, sand sole relied almost totally on mobile crustaceans for food, and speckled sanddab fed on pelagic and epibenthic crustacea and occasional infaunal worms and molluscs. Wakefield (unpubl.) has studied the adult food habits of these three species as well as those of I. isolepis collected at the Moolach Beach site. Although the specific food items ingested differ for recently settled juveniles and adults at this site, the basic modes of feeding, e.g. infaunal generalist or pelagic specialist, remained unchanged at Moolach Beach as the youngest juveniles mature to adults.

The greatest similarity among diets is between those of P. vetulus and I. isolepis. Both of these benthophagous species have similar mouths with small, asymmetrical jaws and small incisor teeth. Both complete metamorphosis and commence benthic feeding at the same size (18-20 mm SL). Qualitatively there is no difference in their diet, although quantitatively butter sole occasionally feed more heavily on mysids. Comparing fish of the same size (17-35 mm SL) on 29 May 1979, P. vetulus and I. isolepis fed on the same prey items in the same proportions. If food should be limiting for these two species, then in the absence of subsequent shifts in food preference the potential exists for competitive interaction. While observing the feeding behavior of P. vetulus in the laboratory, several butter sole were placed in the aquaria along with the English sole. Isopsetta isolepis were observed to bite the fins of P. vetulus and pursue them around the tank. These were casual observations which were only replicated over a 2 day period. Should this aggressive behavior be substantiated by further work, then interference competition between P. vetulus and I. isolepis in the Moolach Beach area seems likely. On the whole, however, English and butter soles do not settle at the same time or place. Parophrys vetulus has a protracted benthic recruitment period, settling to the bottom between November and July in estuarine and coastal waters less than 30 m deep (Krygier and Pearcy, unpubl.). Isopsetta isolepis, on the other hand, has a restricted settling period (May-August) yet occurs over a broader depth range (9-60 m) (Krygier and Pearcy, unpubl.). If interspecific interactions were occurring between English and butter soles, it is

likely that they would be limited to regions of overlap like Moolach

Beach in the summer months.

Table 11. Summary of data collected for English sole (Parophrys vetulus), butter sole (Isopsetta isolepis), speckled sanddab (Citharichthys stigmaeus), and sand sole (Psettichthys melanostictus). Numbers in parenthesis under the heading "No. Fish Examined" are the number of fish out of the total examined which had empty guts. The two values listed for each prey category are average numerical percent composition (on left) and average frequency of occurrence (on right, in parenthesis). "--" indicates prey item <0.01.

| | No. Tows Examined | No. Fish Examined | Length Range -mm | SMALL BENTHIC PREY | | | | | | LARGER BENTHIC PREY | | | | PELAGIC PREY | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Magelona Palps | Juvenile Bivalvea | Tellinid Siphons | Harpacticoid Copepoda | Nematodes | Dendraster Tube Feet | Amphipods | Cumacea | Decapods | Polychaetes | Mysids | Calanoid Copepod | Veliger Larvae |
| **ENGLISH SOLE** | | | | | | | | | | | | | | | | |
| 12 May 1977 | 1 | 12 (1) | 18-29 | .08 (.64) | .42 (.91) | .22 (.73) | .22 (.82) | --- (.18) | | .03 (.27) | | --- (.09) | | .01 (.18) | | |
| 23 June 1977 | 1 | 16 (0) | 19-48 | .01 (.19) | --- (.19) | .18 (.56) | .42 (.69) | --- (.06) | | .15 (.63) | | .24 (.44) | | | | |
| 12 June 1978 | 1 | 3 (0) | 22-24 | .04 (.33) | .88 (1.0) | | .04 (.66) | .02 (.33) | | .01 (.33) | | | .01 (.33) | | | |
| 15 June 1978 | 1 | 5 (0) | 20-25 | .59 (1.0) | .17 (.80) | | .14 (1.0) | .05 (.40) | | .02 (.40) | | | .04 (.60) | | | |
| 13 July 1978 | 2 | 14 (0) | 19-46 | .46 (.89) | .24 (.83) | .08 (.33) | .18 (.70) | --- (.06) | | .02 (.40) | .01 (.36) | .02 (.42) | | | | |
| 25 July 1978 | 1 | 12 (0) | 24-84 | .09 (.75) | .01 (.08) | | .17 (.42) | .40 (.67) | | .18 (.25) | .04 (.25) | . | .03 (.10) | .04 (.08) | | |
| 5 Sept. 1978 | 1 | 3 (0) | 45-58 | | 1.0 (1.0) | | | | | | | | | | | |
| 14 Nov. 1978 | 1 | 5 (0) | 18-21 | .99 (1.0) | | | | | | | | | | .01 (.20) | | |
| 23 Jan. 1979 | 4 | 24 (2) | 17-34 | .72 (.94) | .05 (.25) | --- (.06) | .13 (.52) | | | .08 (.52) | .02 (.14) | | | --- (.06) | | |
| 22 Mar. 1979 | 2 | 20 (0) | 19-35 | .02 (.50) | .80 (1.0) | .02 (.36) | .14 (.90) | | | .03 (.60) | --- (.30) | | | --- (.10) | | |
| 18 Apr. 1979 | 2 | 27 (1) | 19-38 | .10 (.50) | .20 (.73) | .17 (.61) | .23 (.67) | --- (.22) | | .25 (.62) | .04 (.35) | --- (.03) | | --- (.09) | | |
| 29 May 1979 | 4 | 37 (5) | 18-42 | .07 (.24) | .20 (.25) | .24 (.38) | .20 (.41) | .05 (.19) | | .03 (.19) | .03 (.05) | .17 (.17) | .02 (.16) | --- (.13) | | |
| 30 June 1979 | 2 | 23 (1) | 18-61 | | .01 (.09) | --- (.09) | .14 (.75) | | .61 (.75) | .18 (.50) | | --- (.09) | --- (.09) | | | |
| 19 July 1979 | 3 | 10 (0) | 27-62 | | .20 (.25) | | .30 (.79) | | | .33 (.70) | .15 (.50) | .01 (.08) | | | | |
| 8 Aug. 1979 | 2 | 11 (0) | 30-87 | | .26 (.19) | .03 (.06) | .03 (.19) | | | .45 (.86) | .21 (.81) | .01 (.13) | --- (.33) | .01 (.06) | | |
| 24 Sept. 1979 | 2 | 13 (0) | 46-82 | | .02 (.07) | | .10 (.35) | | | .29 (.90) | .41 (.84) | | .18 (.57) | --- (.09) | | |
| SUM | | 235 (10) | | | | | | | | | | | | | | |
| x̄ 1979 | | | | .11 (.27) | .22 (.41) | .06 (.20) | .16 (.57) | .01 (.05) | .08 (.09) | .21 (.62) | .11 (.41) | .02 (.06) | .03 (.14) | --- (.07) | | |
| **BUTTER SOLE** | | | | | | | | | | | | | | | | |
| 23 June 1977 | 1 | 6 (1) | 18-23 | .01 (.20) | | .25 (.80) | .47 (.80) | | | .07 (.80) | | | | .20 (.20) | | |
| 15 June 1978 | 1 | 16 (0) | 19-30 | .62 (.87) | .13 (.60) | .01 (.13) | .01 (.27) | .05 (.47) | | .02 (.33) | .01 (.20) | | .16 (.87) | | | |
| 25 July 1978 | 1 | 16 (0) | 22-31 | .44 (.75) | .06 (.12) | | .24 (.82) | .13 (.57) | | .03 (.25) | .05 (.38) | | .05 (.38) | --- (.06) | | |
| 29 May 1979 | 3 | 14 (2) | 17-35 | .04 (.10) | | .25 (.62) | .17 (.63) | .11 (.25) | | .04 (.21) | .03 (.16) | | .05 (.16) | .05 (.33) | | |
| 30 May 1979 | 1 | 4 (0) | 49-60 | | .03 (.25) | | .03 (.25) | | | .32 (1.0) | .26 (1.0) | .29 (1.0) | .07 (.25) | | | |
| 19 July 1979 | 3 | 7 (0) | 21-88 | --- (.08) | .38 (.58) | | .11 (.33) | | | .21 (.58) | .04 (.17) | .18 (.33) | | .08 (.08) | | |
| 8 Aug. 1979 | 4 | 9 (1) | 24-34 | .02 (.38) | .43 (.50) | --- (.13) | .47 (.58) | | | .07 (.54) | .01 (.63) | | | --- (.13) | | |
| SUM | | 72 (4) | | | | | | | | | | | | | | |
| x̄ 1979 | | | | .02 (.12) | .25 (.46) | .06 (.19) | .20 (.45) | .03 (.06) | | .16 (.58) | .09 (.49) | .12 (.33) | .03 (.10) | .03 (.14) | | |
| **SPECKLED SANDDAB** | | | | | | | | | | | | | | | | |
| 23 June 1977 | 1 | 4 (0) | 34-44 | | | .41 (.75) | .13 (.25) | | | .20 (.50) | .13 (.25) | .11 (.25) | | .03 (.25) | | |
| 25 July 1978 | 1 | 5 (0) | 41-65 | | | | | | | | | | | 1.0 (1.0) | | |
| 22 Mar. 1979 | 1 | 10 (0) | 29-39 | | .08 (.10) | .01 (.10) | .10 (.10) | | | .08 (.30) | .01 (.10) | | | .72 (.80) | | |
| 18 Apr. 1979 | 1 | 10 (0) | 29-38 | | | | | | | .20 (.20) | .52 (.60) | .03 (.10) | | .25 (.30) | | |
| 29 May 1979 | 2 | 14 (0) | 33-50 | .13 (.13) | | | | | | .25 (.43) | | .30 (.53) | | .32 (.53) | | |
| 30 June 1979 | 1 | 7 (0) | 30-52 | | | | | | | .03 (.57) | --- (.05) | .01 (.29) | | .96 (1.0) | | |
| 19 July 1979 | 2 | 11 (1) | 35-70 | | | | | | | .04 (.20) | | | | .96 (1.0) | | |
| 24 Sept. 1979 | 3 | 15 (0) | 38-70 | | | | | | | .14 (.52) | .08 (.25) | .20 (.52) | | .59 (.86) | | |
| SUM | | 76 (1) | | | | | | | | | | | | | | |
| x̄ 1979 | | | | .02 (.02) | .01 (.02) | --- (.02) | .02 (.02) | | | .12 (.37) | .10 (.17) | .09 (.24) | | .63 (.75) | | |
| **SAND SOLE** | | | | | | | | | | | | | | | | |
| 22 Jan. 1979 | 2 | 6 (0) | 30-38 | | | | | | | | | | | 1.0 (1.0) | | |
| 18 Apr. 1979 | 1 | 3 (0) | 29-55 | | | | | | | | | | | 1.0 (1.0) | | |
| 19 July 1979 | 2 | 6 (0) | 29-50 | | | | | | | | | | | 1.0 (1.0) | | |
| 8 Aug. 1979 | 2 | 13 (0) | 31-52 | | | | | | | | | .03 (.17) | | --- (.13) | .69 (.80) | .28 (.40) |
| 24 Sept. 1979 | 2 | 11 (1) | 30-48 | | | | | | | | | | | 1.0 (1.0) | | |
| SUM | | 39 (1) | | | | | | | | | | | | | | |
| x̄ 1979 | | | | | | | | | | | | .01 (.03) | | .80 (.83) | .14 (.13) | .06 (.08) |

Table 12. Percent similarity of prey consumed by English sole

(Parophrys vetulus), butter sole (Isopsetta isolepis), speckled

sanddab (Citharichthys stigmaeus), and sand sole (Psettichthys

melanostictus) based on the average 1979 diets shown in Table 1.

| | I. isolepis | C. stigmaeus | P. melanostictus |
|---|---|---|---|
| P. vetulus | 0.77 | 0.29 | 0.01 |
| I. isolepis | ---- | 0.39 | 0.05 |
| C. stigmaeus | ---- | ---- | 0.64 |

Table 13. Mean numerical proportions of dominant prey items in the guts of _Parophrys vetulus_ less than and greater than 35 mm SL.

| | SL L.T. 35 mm | SL G.T. 35 mm |
|---|---|---|
| **Small Benthic Prey** | | |
| _Magelona_ Palps | 0.28 | 0.03 |
| Juvenile Bivalves | 0.29 | 0.01 |
| Tellinid Siphons | 0.13 | 0.01 |
| Harpacticoid Copepods | 0.16 | 0.08 |
| SUM | 0.86 | 0.13 |
| | | |
| **Larger Benthic Prey** | | |
| Amphipods | 0.08 | 0.46 |
| Cumaceans | 0.03 | 0.30 |
| Decapods | 0.01 | 0.04 |
| Polychaetes | 0.0 | 0.06 |
| SUM | 0.12 | 0.86 |

Table 14. Average percent similarity (PSI) of <u>Parophrys</u> <u>vetulus</u> diets within and between replicate trawls on 23 January and 29 May 1979.

| | Replicates at same depth | |
| --- | --- | --- |
| | <u>Within Trawl</u> | <u>Between Trawl</u> |
| 23 January 1979 (20m) | 53% | 53% |
| 29 May 1979 (10m) | 50% | 3% |
| | Replicates at different depths | |
| | <u>Within Trawl</u> | <u>Between Trawl</u> |
| 23 January 1979 (20m and 30m) | 71% | 66% |
| 29 May 1979 (20m and 30m) | 65% | 12% |

Figure 7.  Location of study area.  Dotted lines enclose area from
which beam trawl samples were collected, "X" marks location of
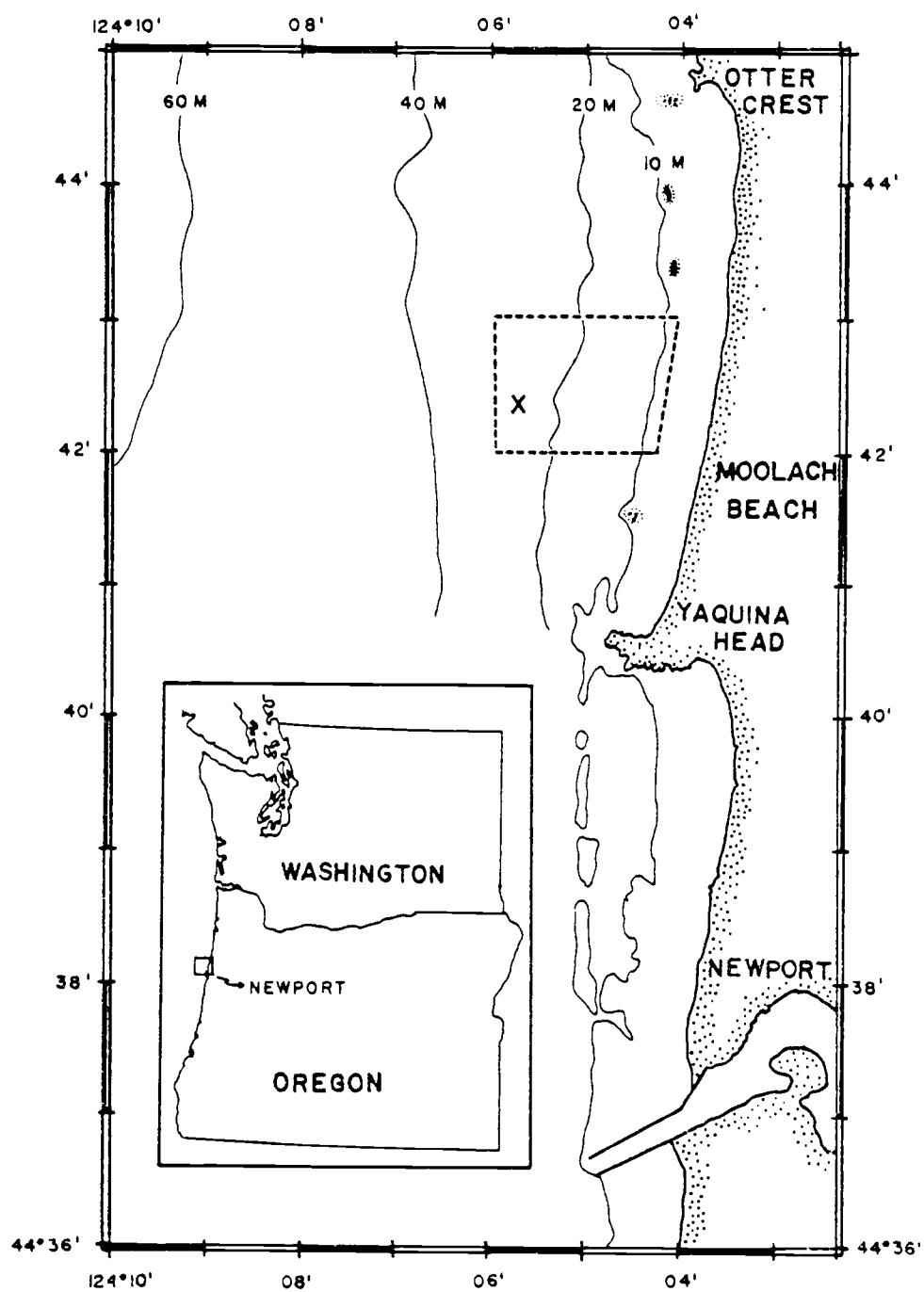box core and Smith-McIntyre grab samples.

Figure 7.

Figure 8. Cumulative number of prey categories sampled as a function of sample size for <u>Parophrys</u> <u>vetulus</u> and <u>Isopsetta</u> <u>isolepis</u>. Each data point represents the mean of two separate trawl collections. Vertical bars are ±1 standard deviation.
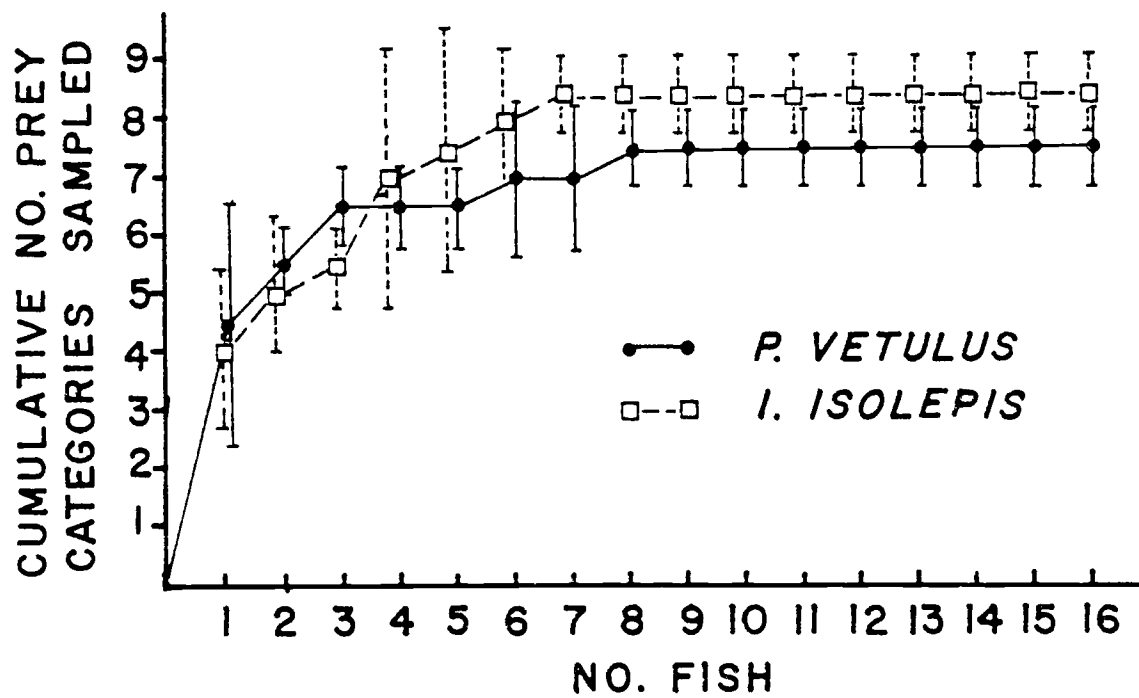
Figure 8.

Figure 9.  Seasonal change in food habits of <u>Parophrys</u> <u>vetulus</u> less

than 35 mm SL between November 1978 and July 1979.  Vertical

bars indicate average proportion of <u>Magelona</u> palps, "Mag.",

juvenile bivalves, "Biv.", clam siphons, "Sip.", and harpacticoid
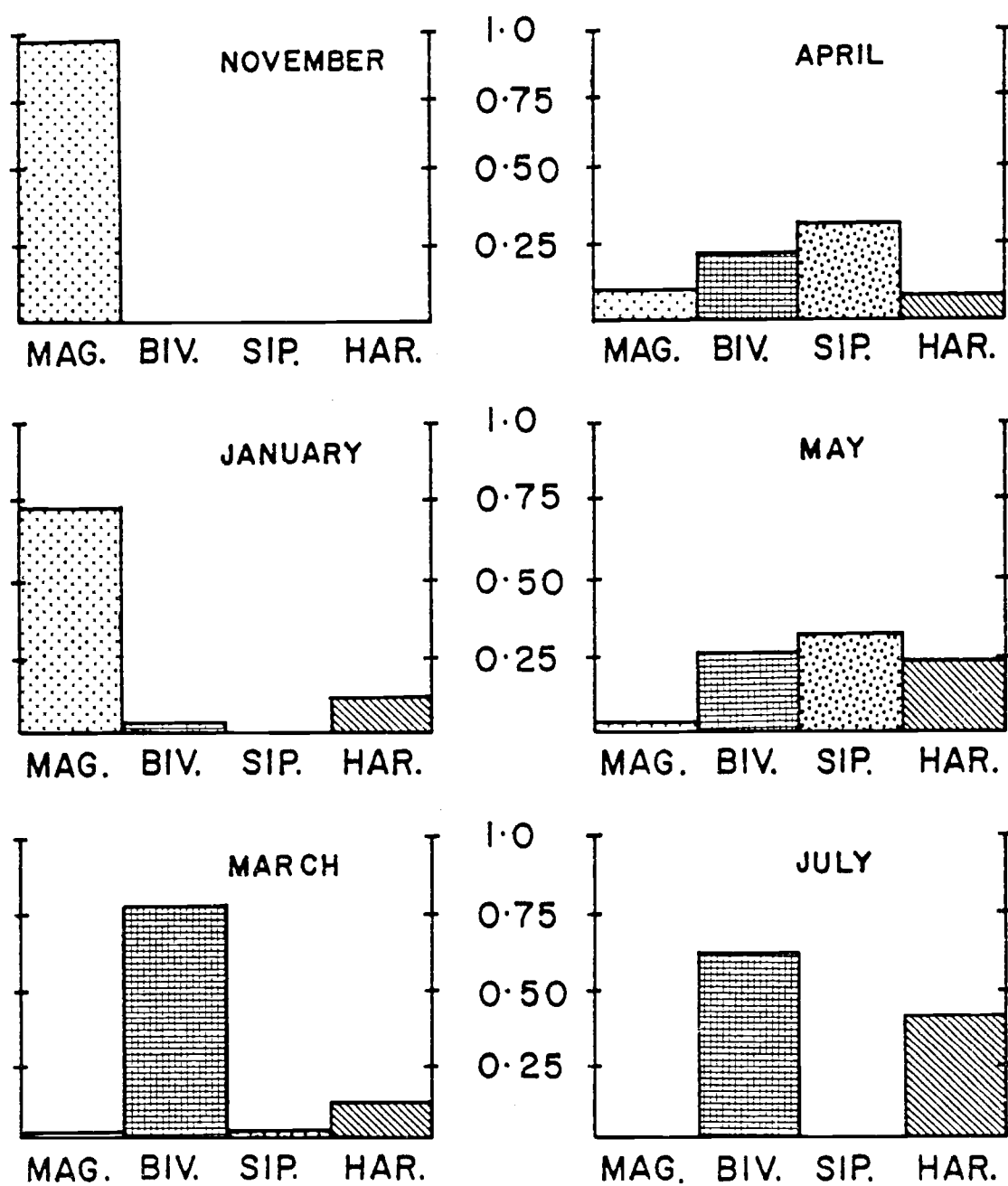
copepods, "Har.", in the diet.

Figure 9.

Chapter 5.   General Conclusions

The overall conclusions associated with the research goals

outlined in Chapter 1 are listed below.

a) Evaluation of temporal and spatial variability

1.   The nematodes of the inner Oregon continental shelf are generally

similar in their taxonomic and numerical composition to those living

elsewhere in comparable sediments.

2.   Unlike previous reports, significant seasonal changes in nematode

densities were observed.  A twofold increase in abundance occurred

over a 4 month period.  Estimates of nematode densities based on one

sampling date may not accurately reflect "long term" or "average"

conditions.

3.   Over one-half of the variance associated with spatial changes in

nematode abundances within the 3.3 km$^2$ study area was attributable to

the small-scale differences found within 0.25 m$^2$ box cores.  Since

most of the natural variability present in sandy bottom meiofauna

populations apparently occurs on such small scales, future sampling

programs and manipulative experiments can utilize relatively small

replicate control and experimental plots.

4.   Harpacticoid copepods are very rare within the study area.

Average densities were less than 1% of those found for nematodes.

b) Structure of meiobenthic assemblages

1.   The broad scale (between-station) spatial differences in the

nematode fauna of the study area correlate with the frequency of

wave-generated sediment disturbance.  Determination of the proximal

factors responsible for these differences requires additional study,
but may include either size-selective predation or morphological and
reproductive adaptations to sediments which are frequently reworked
by currents.

2.  Small-scale (within-station) distributions of dominant nematode
species appear to result from an equilibrium of two opposing proces-
ses.  Physical disruption of the sediments by wave activity tends to
randomly disperse individuals, while the intraspecific requirements
for reproduction tend to attract members of the same species and
bring them together.

3.  Even though densities of the dominant nematodes varied over time,
the rank order of their abundance remained unchanged.  No known
mechanism adequately explains this consistency in species proportions.
Similar persistence in the dominance structure of North Pacific
central gyre plankton communities has been documented.  Although
their environments are very differnt, nematode assemblages off Moolach
Beach and plankton communities in the North Pacific central gyre may
be controlled by similar ecological processes.

4.  Coexistence of the nematode species within small areas ($<1 \text{ m}^2$)
off Moolach Beach does not appear to be maintained by localized
disturbances.  Spatially, species are randomly distributed with
respect to each other while temporally their changes in density tend
to parallel each other.  If a subset of these nematodes were oppor-
tunistically exploiting new or disturbed habitat patches while others
were inhabiting less recently perturbed areas, then significant
negative interspecific correlations should have resulted.

c) Trophic importance of meiofauna

1. The vast majority of meiobenthic animals were not utilized by juvenile flatfishes as a food source. Only a few large epibenthic species of harpacticoids and two species of nematodes which occurred in the uppermost 1 cm of sediment were consumed. These results are in keeping with previous generalizations concerning the failure of most sand-dwelling species to be eaten by animals belonging to higher trophic levels. This does not rule out the possibility that meiobenthic animals are preyed upon by amphipods, polychaetes, and mysids which are themselves eaten by fishes. Far more information is needed on the details of these trophic relationships before definitive statements concerning the importance of meiofauna can be made.

2. Large, epibenthic harpacticoid copepods such as Halectinosoma spp. are consistently found in the diets of English and Butter soles smaller than 35 mm standard length. These copepods may provide significant nutrition for these fishes during their first few weeks after metamorphosing and settling to the sea floor.

d) Relationship between spatial distributions of prey and the diet of fishes

1. This particular research goal could not be addressed directly, since abundances of harpacticoid copepods were too low to describe their dispersion patterns. The seasonal change in spatial distributions of Moolach Beach nematodes suggests, though, that small prey, e.g., harpacticoides and polychaetes, are also more aggregated in the summer than winter. Since 0-age English sole recruit to this area

between November and July, seasonal variation in spatial patterns may affect feeding rates. Confirmation of this possibility would best be accomplished by monitoring the diet of English sole in conjunction with changes in the abundance and spatial distribution of most common prey (Magelona, Tellina).

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