

EFFECTS OF DISRUPTIVE GRAZING BY
THE MUD SNAIL ILYANASSA OBSOLETA
ON MUDFLAT NEMATODE POPULATIONS

A Thesis

Presented to

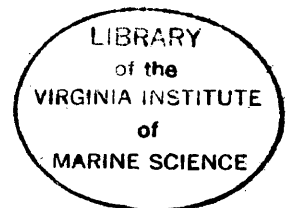
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

by

David Ludwig

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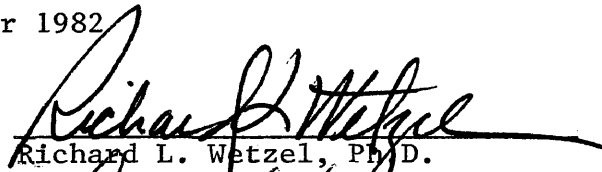
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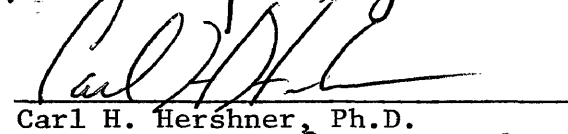
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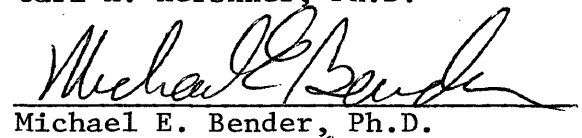
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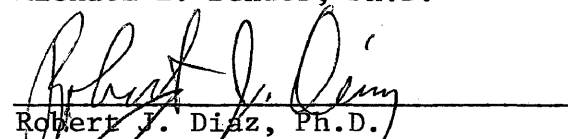

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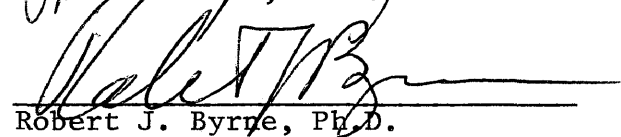
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This thesis is dedicated to two fine poets:

my sister Beth

my brother Dan

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Finally, I thank my parents, Frank and Elizabeth Ludwig. They encouraged my love of natural history, and only occasionally let on that escaped reptiles in the laundry basket were distressing.

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ABSTRACT

Population densities of the mud snail Ilyanassa obsoleta were manipulated in caging experiments on a salt marsh mudflat and in laboratory microcosms. Mud snails outcompete nematodes for food resources, but may increase resources available to deposit feeding groups. Mud snails reduce annelid (polychaete and oligochaete) populations by substrate disruption. Reduced annelid densities provide the nematode community with some release from predation and competition.

In mudflat sediments, the nematode community responds to both primary (predation) and secondary (environmental release, food competition) interactions. Multiple levels of interactive coupling should be considered in any systems level investigation in this habitat.

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INTRODUCTION

Wetland ecosystems have received bad press for decades in both scientific and popular literature. As late as 1958 the U.S. Department of Agriculture could say with pride:

"The conquest of the arid , semiarid, and wet lands continued into the 20th century...drainage enterprises in 1954 included more than 100 million acres."

and promise:

"The larger swamps and marshes are generally wetter than are the poorly drained crop lands...it may be physically possible to reclaim them...".

By the last quarter of the twentieth century, more than 45% of the original wetlands in the United States had been "reclaimed" (Jaworski and Raphael 1978) and in several states the figure topped 75% (Reilly 1978).

In the past twenty years, coastal wetlands have been increasingly viewed as important components in the functioning of estuarine ecosystems (Teal 1962, Nixon 1980). This recognition was officially embodied in the Water Pollution Control Act amendments of 1972, the Wetland Protection Executive Order of 1977, and the Clean Water Act of 1977. Much scientific effort was expended in the 1970's to classify and quantify structure and function in vegetated coastal wetlands (e.g. Day et al. 1973, Gosselink et al. 1973, Nixon and Oviatt 1973,

Silberhorn et al. 1974). In the late 1970's and early 1980's it was realized that intertidal mudflats are an integral part of the coastal system, coupling runoff from upland watersheds and marshes to open water estuaries (Nixon 1980). Mudflats trap nutrients when water ebbs from tidal marshes, and yield them to the marsh during tidal flood (Welsh 1978, Wolaver et al. 1980).

Despite the demonstrated and potential importance of mudflats, little information exists on structure and function of the component biota. What are community structure determinants in this habitat? On hard substrate systems, competition (Dayton 1971, Paine 1974), predation (Connell 1970, 1975), and grazing (Connell and Slatyer 1977, Lubchenko and Menge 1978) combine to organize the biota. How do these processes interact in intertidal mudflat ecosystems? A study of interactions between a dominant consumer (the gastropod Ilyanassa obsoleta Say) and annelid and nematode communities was undertaken to examine these questions.

Scientific Background

Predation is perhaps the most thoroughly studied interactive process in soft substrate habitats. On north temperate mudflats, many polychaete species are "overexploited" by predators through summer and autumn, leaving a community dominated by retractile, tubicolous species. During winter, predation is reduced and susceptible species are able to re-establish in the habitat (Riëse 1977a, b). Predation

by fish and crabs (Virnstein 1977, 1979, Holland et al. 1980) reduces density of macrofaunal organisms in subtidal sediments. Such demersal predators as Callinectes, Palaemonetes, Paralichthyes, Fundulus, and Leiostomous are often abundant over intertidal sediments during flood waters, and probably have a similar effect on mudflat macrobiota. Indeed Riese (1977c) has demonstrated the importance of predation by penaid and palaemonid shrimp in intertidal mudflat communities. Large polychaetes (Commuto 1976, and see discussion in Virnstein 1980), and a broad array of molluscs and crustaceans (Naqvi 1968) may also be significant predators of macrobenthic infauna.

Predation by macrofauna is also important in controlling meiofauna populations. The grass shrimp Palaemonetes pugio is a predator on meiofaunal organisms (Sikora 1977) and regulates populations of nematodes, polychaetes, oligochaetes, and copepods in salt marsh sediments (Bell and Coull 1978). Fish (Odum 1970, Buzas and Carle 1979), crustaceans (Gerlach and Schrage 1969, Sikora 1977, Bell and Coull 1978, Coull and Bell 1979), annelids (Hylleberg 1975, Gerlach 1978), and molluscs (Lee et al. 1976) all consume meiofauna, and may exert predation pressure on meiofaunal communities. It has recently been demonstrated (Bell and Sherman 1980, Palmer and Brandt 1981) that meiofauna are transported by tidal suspension of sediment flocculant. This might allow suspension feeding polychaetes and molluscs to consume meiofauna as well. Nematodes and copepods are within the size range of particles ingested by a variety of macrofauna (Taghon 1982).

Competitive interactions occur between members of similar "functional groups" (Woodin and Jackson 1979) which are broadly analogous to the "ecological equivalents" of Odum (1971). Competition may be either direct or indirect. Direct interactions require actual physical or behavioral contact between organisms. Direct, competitive effects are most important where space is limiting, as on hard substrates. Undercutting (Connell 1970) and behavioral aggression (Sheppard 1979) are examples of direct interactions. In the three-dimensional environment of sedimentary habitats, resource partitioning reduces direct competition for space (Dayton and Oliver 1980) and may therefore increase the importance of indirect competition. Indirect competition occurs between ecological equivalents via one or more physical, chemical, or biological mediator. A well known example of mediated competition is "trophic group amensalism" in which reworking and suspension of sediment by deposit feeding organisms excludes suspension/filter feeding types (Rhoads and Young 1970, Rhoads 1974).

Competition for food is surprisingly poorly understood in benthic ecosystems. Woodin and Jackson (1979) suggest that food is not generally limiting to organisms dwelling in sediments. Marine and estuarine sediments (except coarse and/or well sorted sands) are rich in energy and carbon resources (Tenore 1977) in the form of microalgae, fungi, bacteria, yeasts, dissolved substances, protozoans, and metazoans, of all sizes. This diversity of food "packages" would seem optimal for resource partitioning and an attendant reduction in competition (Johnson 1974). Competition for specific food resources, however, has been demonstrated in several studies. Weinberg (1979) described

sandflat polychaete communities which are structured in response to limiting levels of a particular resource: energy rich organic matter aggregates. On mudflats, similar competition among "relative specialists" might be postulated for specific food resources such as fecal pellets. Indeed, Levinton (1977) hypothesized that fecal pellets (and attendant microbes) were resource "bottlenecks" and thus limiting in subtidal muddy sand deposit feeding communities.

Macrofauna and meiofauna may also compete for specific food resources. Such interactions are difficult to demonstrate because meiofauna are nearly impossible to manipulate in an experimental context. Experimental manipulation of macrofauna, however, has produced evidence of macrofauna-meiofauna competition. Nichols and Robertson (1978) excluded the grazing snail Ilyanassa obsoleta from mudflat sediments and noted a rise in numbers of both diatom cells and diatom feeding nematodes. They interpreted this result as an indication of competition between snails and nematodes for microalgal food resources.

Substrate characteristics are important determinants of structure and function in benthic communities. Large macrofaunal organisms often partition available three dimensional space (Dayton and Oliver 1980). Such activities as tube building, burrowing, reef construction, and feeding provide interactive mechanisms among macrofauna groups and between macrofauna and meiofauna. Substrate disruption or disturbance reduces macroinfauna populations (Grant 1965, Woodin 1978). Biogenic substrate structure, including polychaete tubes (Woodin 1978) and submerged aquatic vegetation (Heck and Orth 1980) provide refuges from

disturbance and predation. Annelid tubes and burrows have important impacts at depth in sediments. Microfauna, meiofauna, and microflora all increase in proximity to Arenicola dwellings on mud flats (Aller and Yingst 1978). Similar effects occur near Spartina alterniflora roots on mudflats, where nematode populations may be 1.5 to 3.0 times greater than those in surrounding sediments (Ludwig, unpublished manuscript). The effects of tubes, roots, and burrows are probably due to increased oxidation and nutrient flux at depth (Aller 1978, Aller and Yingst 1978).

Purpose of the Research

This research was conducted to assess interactions between three important components of intertidal mudflat communities: the nassariid mud snail Ilyanassa obsoleta, nematodes, and annelids. The prosobranch gastropod Ilyanassa obsoleta was chosen for study because it is an abundant and conspicuous component of the fauna of intertidal mudflats in estuaries of the Middle Atlantic states. Population densities as high as 5860 individuals/meter² have been reported (Brown 1969) and biomass estimates range from 2 to 11 grams nonshell carbon/meter² (Pace et al. 1979). I. obsoleta may move over 15 feet/day (Grant 1965). Such high density, biomass, and activity in an organism which feeds as a disruptive grazer (Scheltema 1964) suggests that I. obsoleta may have important influences on populations of benthic infaunal organisms.

Nematodes provide a convenient tool for studying such influences. They are abundant, exhibit population responses over relatively short time spans, and their feeding mode (algae, selective or nonselective deposit feeder) is reflected in their buccal cavity morphology (Wieser 1953). I. obsoleta may effect nematode populations either directly, by predation or competition, or by effecting other organisms with interactive links to nematodes. Annelids are likely to mediate interactions between I. obsoleta and nematodes in intertidal mudflat sediments. Polychaetes and oligochaetes are abundant infauna in such habitats. Their size range makes them potential predators of and competitors with nematodes. Polychaete populations have been shown to decrease in the presence of large numbers of I. obsoleta (Grant 1965). Thus, I. obsoleta, by depressing annelid populations, may provide nematodes with some release from predation and competition.

This research was conducted for two general purposes. One was to develop efficient methodology for assessing biotic interactions in combinations including organisms with a broad range of size and activity. The other was to quantify direct and mediated interactions between the dominant, disruptive grazing snail I. obsoleta and benthic infaunal communities of nematodes and annelids.

Hypotheses

This thesis comprises results of two discreet, internally replicated experiments. One experiment was a manipulative caging study conducted in the field on a mudflat at Gate's Bay, Wachapreague,

Virginia. This experiment was designed to assess the effects of several densities of I. obsoleta on nematode density and feeding type distribution, sediment water content, and sediment chlorophyll a concentration. Six hypotheses were tested under this experimental design:

- i) I. obsoleta depresses nematode population density
- ii) I. obsoleta reduces proportion of algae feeding nematodes in mudflat sediments
- iii) small nematodes are selectively depressed by I. obsoleta (i.e. there is a "refuge" from I. obsoleta available to large nematodes)
- iv) proportion of nematode population at depth in sediment increases in presence of I. obsoleta (i.e. there is a "depth refuge")
- v) I. obsoleta depresses concentration of chlorophyll a in mudflat sediments
- vi) I. obsoleta changes sediment structure as measured by sediment water content

The second experiment used laboratory microcosms to obtain better quantitative resolution of effects of I. obsoleta on chlorophyll a concentration, nematode density and feeding type distribution, and possible secondary impacts of I. obsoleta on nematodes mediated by populations of polychaetes and oligochaetes. Three hypotheses were tested under this design:

- i) I. obsoleta preys on nematodes
- ii) I. obsoleta competes with nematodes for food
- iii) annelids mediate effects of I. obsoleta on nematode populations.

MATERIALS AND METHODS

FIELD STUDIES

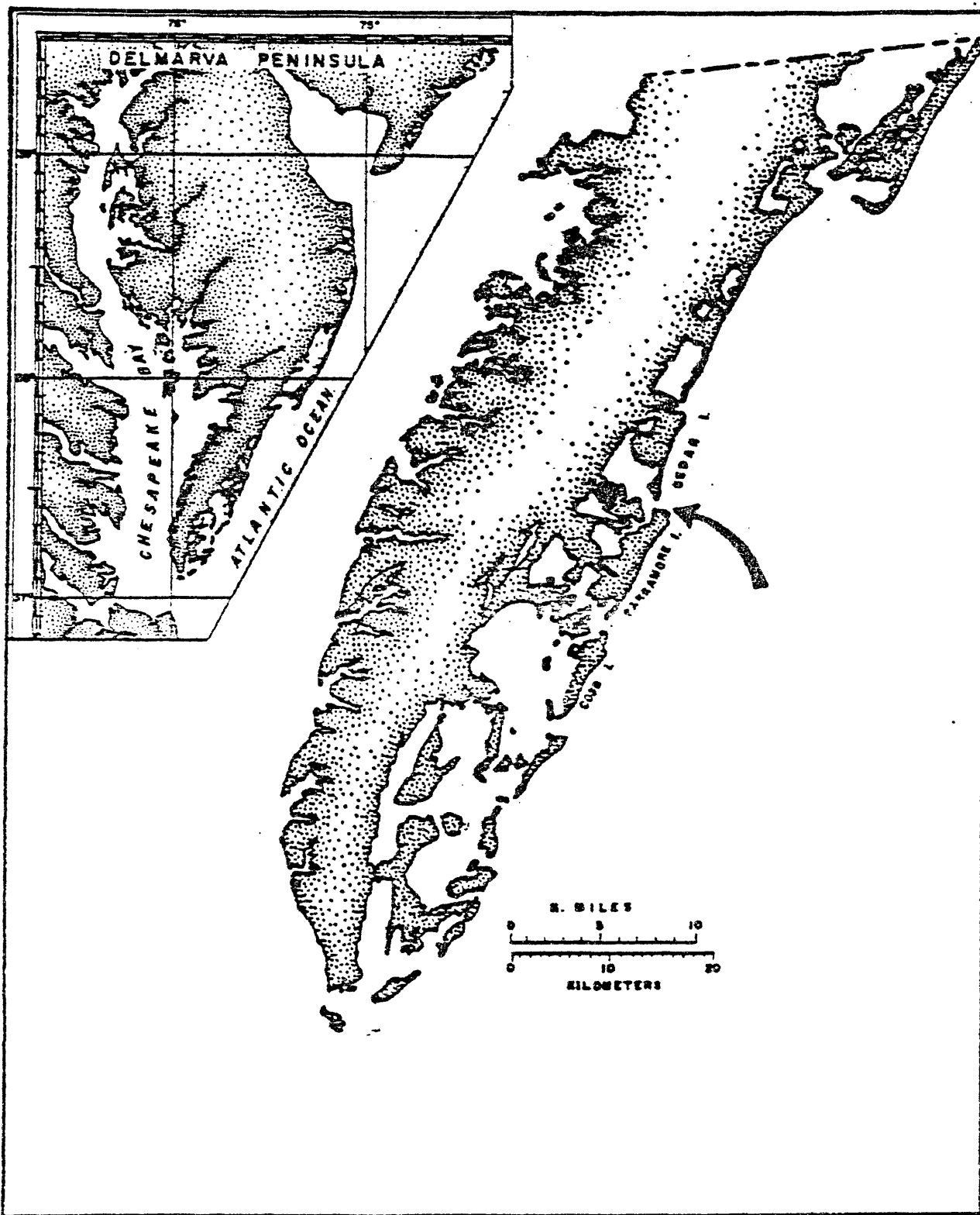
Study Site

Field studies were conducted in an estuarine marsh area about midway along Virginia's eastern shore peninsula. The ecosystem consists of shallow bays, extensive mudflats, and Spartina alterniflora salt marshes. Shallow bay-mudflat habitat makes up about 50% of the total system. The specific site at which the research was conducted is a small embayment called Gate's Bay. It is approximately 1 kilometer in diameter and is within several kilometers of the VIMS laboratory at Wachapreague (Figure 1). At mean low water the bay is 70 to 80% mudflat and has a single outlet for water exchange. There is a minimum of fresh water drainage into the system, and mean annual salinity varies between 31 and 33 parts per thousand. Tides are semi-diurnal with a mean range at Wachapreague Inlet of 1.2 meters and an increase of 0.02 meters at the town of Wachapreague. Spring tide ranges average 1.4 meters.

Experimental Design

Cages constructed of $\frac{1}{4}$ inch (6 mm) mesh hardware cloth were used to maintain mud snail densities and exclude such large natant forms as

Figure 1. Map of Virginia's eastern shore showing study site.

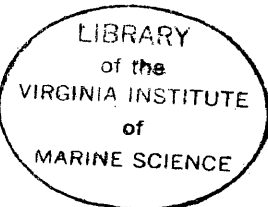


fish and crabs from experimental plots of mudflat sediment. Each cage enclosed an area of approximately 0.25 meter², and mesh was driven approximately 10 cm into the substrate. Cages were placed 1 meter apart, in a row 8 meters from and parallel to the marsh edge. A systematic rather than random placement was employed in an attempt to reduce large scale spatial heterogeneity and isolate treatment effects.

Snail densities and size frequency distribution have been assessed by quadrat sampling over 3 years by R. L. Wetzel and associated staff and students. In August samples the mean density is 375 snails/m², standard error of the mean= 260. Counts per meter² ranged from 0 to nearly 1500 individuals, reflecting the patchy distribution of this species on the Gate's Bay mudflat. Snails of shell height greater than 12 mm dominated August samples, comprising approximately 80 % of all individuals measured. Snails of this size are incapable of passing the hardware cloth mesh and were used in experimental treatments. No attempt was made to control densities of smaller I. obsoleta. Observations made during the experiment and quadrat counts from previous years (R. L. Wetzel, personal communication) indicate that small snails were not present in great numbers during these studies.

Experimental treatments were:

- i) caged control or snail exclusion plots ("OX" natural density)
- ii) 75 snails per 0.25 m² ("1X" natural density)
- iii) 150 snails per 0.25 m² ("2X" natural density)
- iv) uncaged, delineated natural mudflat plots, equal in size and shape to caged plots ("UNC")



Snail densities on uncaged plots were monitored by counting over the course of the study.

Triplicate samples for nematode density and feeding type analysis, and duplicate samples for sediment pigment concentration and water content were taken during daytime low tides on August 18, 20, and 23 (experimental days 0, 2, and 5, respectively). Each sample consisted of one core taken with a device cut from 1½ inch PVC pipe with a surface area of 11.3 cm². Corers were lined with a cylinder of acetate sheeting which permitted easy removal of the core after the acetate was cut away from the contained sediment. Samples were located within each plot using random number tables and matching the numbers to a grid system in each plot. No samples were taken within one core diameter (approximately 4 cm) of the mesh and ½ core diameter (approximately 2 cm) was maintained between all samples. Sediments were sampled to a depth of 7 cm. Cores were sectioned horizontally at 0.25 cm, 0.50 cm, 1.00 cm, 1.50 cm, and 2.00 cm. Cores for analysis of nematode density and feeding type were sectioned within 4 hours of sampling and each section was preserved separately in 10% buffered sea water formalin with rose bengal stain. Size distribution of nematodes was assessed by washing each section through nested 67 µm and 25 µm sieves. Nematodes remaining on the 67 µm sieve ranged in length from approximately 450 to 1600 µm and were classified as "large". Nematodes retained on the 25 µm sieve ranged from approximately 60 to 400 µm and were classified as "small". Cores for pigment analyses were frozen in their acetate liner for later removal, sectioning, and extraction.

Methodological Studies

One of the objectives of this research was to develop methods that would allow efficient and precise characterization of the nematode community of intertidal mudflat sediments. To meet this objective, I compared three extraction and enumeration techniques and used the best technique to assess density and distribution of nematode populations.

A 5 X 5 contiguous array of square plexiglas cores (inside diameter approximately 2.2 cm², 0.2 cm wall thickness, overall width of array 13 cm) was used for methodological studies. One such array was taken on 9 December 1978 and another on 4 May 1979. Each core was sectioned vertically at 2 cm depth (at or below the redox potential discontinuity) and the top fraction of each preserved in 10% buffered sea water formalin with rose bengal. Core contents were subsampled (method discussed below) and nematodes counted under a dissecting microscope. Green's index of dispersion (Elliott 1971) was calculated and used to assess nematode distribution and patch size (Findlay 1981).

Three methods of extraction and enumeration of nematodes were compared. These were:

- i) counting each nematode in an entire sample ("total count" procedure)
- ii) magnesium chloride elutriation
- iii) subsampling

On 9 December 1979 a 5 X 2 array of cores was taken adjacent to the array prepared for spatial pattern study. Five of these cores were

sectioned at 2 cm and preserved. Nematodes were counted in small, successive aliquots under the dissecting microscope until the entire sample had been so treated. This was the "total count" procedure. Five of the cores were sectioned and subjected to magnesium chloride elutriation (Hartzband and Boesch 1979). Each section was agitated in a jar with excess MgCl₂ solution. Sediment was allowed to settle for 30 to 60 seconds and the supernatant poured through a nested sieve series. This procedure was repeated 6 times per sample. Material retained on each sieve was preserved for later enumeration under the dissecting microscope. The 5 core row from the main 5 X 5 array that was contiguous with the 5 X 2 array was allocated for comparison of subsampling technique. These cores were sectioned and preserved. Subsamples were taken by placing the sample in a 500 ml erlenmeyer flask, making the volume up to a preselected level with water of ambient salinity, shaking, and removing a 10 ml aliquot with an autopipette subsampler. Several volumes were tested. Aliquots for counting were selected by correspondence with a random number table. First and last aliquots and all unselected aliquots were discarded. Replicate aliquots from several samples were enumerated for estimation of variance introduced by the subsample procedure.

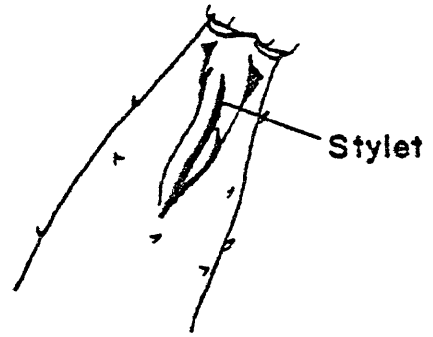
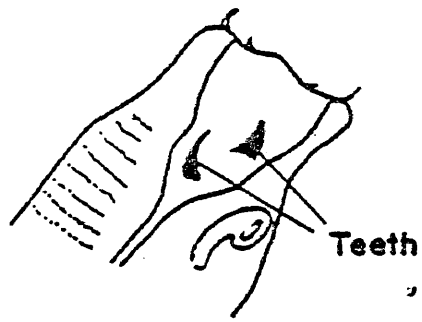
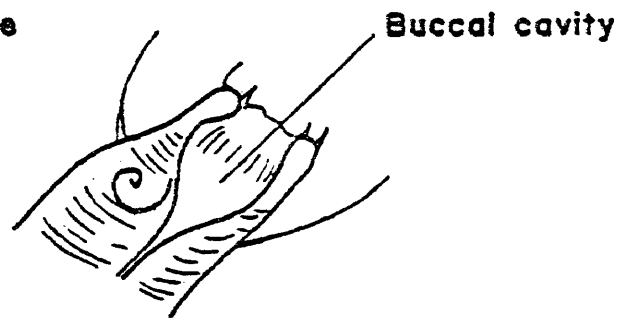
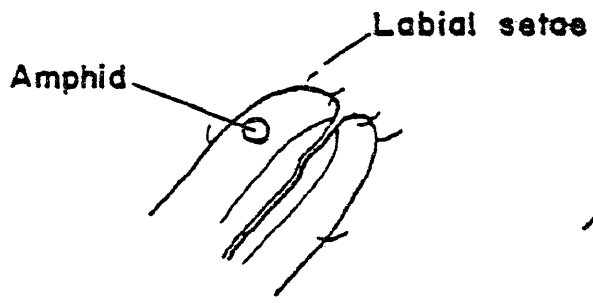
Appropriate core size was estimated by calculating Green's Index of Dispersion as a function of sample area. This index indicates random distribution of individuals at a value of 0 and maximum contagion at a value of 1. Regular distributions are indicated by

negative values of the index (Elliott 1971). In addition, a sample area which approximates "patch size" in a clumped distribution is indicated by an inflection in the relationship between the index and sample area.

Nematode Feeding Types

Nematodes from one core from each plot on each sampling day were used for feeding type characterization. Nematodes already sorted from sediment were placed in a gridded dish, and the first 10 nematodes were removed from each of 10 randomly selected quadrats for examination by phase-contrast microscopy. Nematodes were classified according to the scheme of Wieser (1953). Sketches of generalized nematode cephalae are presented in Figure 2 to illustrate the feeding types. Nematodes with no buccal cavity and no oral dentition or armament are considered selective deposit feeders (type 1A). Nematodes possessing an unarmed buccal cavity are nonselective deposit feeders (type 1B). Nematodes with a heavily armed buccal cavity (type 2B) are considered "predator/omnivores" by Wieser (1953), but species in this category, at least in South Carolina salt marsh sediments, are probably deposit feeders (Levy 1977). Nematodes with a lightly armed buccal cavity are algae feeders and/or grain scrapers (type 2A). For reasons which are discussed below, nematodes in this feeding type are most likely to respond to the presence of I. obsoleta. Therefore, the three deposit feeding types were lumped in analyses, and a ratio of number of algivores to number of deposit feeders used to characterize the feeding type distribution of nematodes in the sediments.

Figure 2. Generalized nematode cephalae, illustrating buccal morphology characteristics of the feeding types.
1A = selective deposit feeders, 1B = nonselective deposit feeders, 2A = algivores or grain scrapers, 2B = predator/omnivores or deposit feeders.



Chlorophyll Analysis

Chlorophyllide is a major degradation product of chlorophyll a in marine muds (Jeffrey 1968, 1974) and is indistinguishable from chlorophyll a when pigments are analyzed by the "classic" methods of Lorenzen (1967) and Strickland and Parsons (1968). A liquid-liquid phase partitioning procedure (Whitney and Darley 1979, Wun et al. 1980) was used to separate chlorophyll a and pheophytin a from chlorophyllides and carotenoids which interfere with spectrophotometric analysis. The method outlined here and employed throughout the study is that of Whitney and Darley (1979).

Two cores per plot per day were frozen within 4 hours of collection in the acetate liners. Within 4 weeks, cores were removed from the liners and sectioned horizontally at 1mm, 2.5 mm, and 5.0 mm. Each section was placed in a centrifuge tube, ground by hand in 10 ml of 100 per cent acetone and extracted in the dark at approximately 2 to 4 ° C. One hundred per cent acetone is used for the initial extraction to inhibit the action of chlorophyllase enzymes, which in algae, including diatoms, exhibit high activity (Barrett and Jeffrey 1964, 1971). Tubes were centrifuged and supernatant decanted and stored in the dark. The pellet was reground with 10 ml of 90 per cent acetone and extracted for 2 hours. The extracts were pooled and 10 ml of extract was added to a separatory funnel containing 3.5 ml of 0.05% NaCl and 13.5 ml of hexane. The funnel was shaken for 5 minutes, placed in a ring stand, and the phases allowed to separate. The

hyperphase was drawn off and divided, half was acidified with 2 drops of 50% HCl and both halves read against a hexane blank in a Spectronic 20 spectrophotometer set at 663 nm. Concentration of chlorophyll a was calculated according to Whitney and Darley (1979):

$$\text{mg Chl } \underline{a} / \text{ liter} = \frac{K \times A (663_o - 663_a) \times V}{L}$$

where K is a factor equating absorbance to concentration of chlorophyll a, =1.82, A is absorption coefficient of chlorophyll a in hexane layer, =11.05, L is cuvette path length, 663_o is absorbance without acidification, 663_a is absorbance with acidification. V is a constant which accounts for mutual miscibility of fluids used in the extraction and separation procedures. It must be measured using the specific brands and grades of reagents and laboratory temperatures at which the analyses are run.

Freezing and grinding of the sediment disrupts algal cell membranes and enhances chlorophyll extraction. Sonification is most desirable when performing pigment extraction of sediments and soils. Using sonification, the method outlined here is 98.5% efficient at recovering chlorophyll from estuarine sediments (Whitney and Darley 1979). Efficiency using grinding only is unknown.

Sediment Water Content

Two lined cores were taken randomly from each plot on each sampling day. These were returned to the laboratory for processing within 6 hours of collection. Liners were carefully removed from the

sediment, which was cut at 0.25, 0.50, 1.00, 1.50, 2.00, 3.00, and 5.00 cm. Each section was placed in a tared aluminum weigh pan, weighed, dried to constant weight, and re-weighed. Difference between the two weights was taken as a measure of sediment water content.

Data Analysis

Data were analyzed by nonparametric statistical procedures because of presumed violation of assumptions of otherwise appropriate parametric methods. Specifically, it was anticipated that the underlying distribution of nematodes on the mudflat would be aggregated rather than normal (but see Discussion) and that treatment effects could render variance of variables heteroscedastic. In addition, nonparametric procedures and corrections allow hypothesis testing to be conducted on data sets derived from small sample sizes (Wilcoxon and Wilcox 1964, Zar 1974).

The main interest in this study was whether or not variables were significantly different among treatments. In order for tests of treatment effects over the experimental period to yield meaningful results, it had to be shown that variables had no significant differences among plots before the experiment began. There were two levels to this analysis: within and among treatment plots. Differences among replicates within treatments were tested by Mann-Whitney 2-sample test (Zar 1974). Where this test yielded nonsignificant results, replicates were pooled and differences among treatments analyzed by Mann-Whitney test (when only 2 treatments were

employed in analysis) or by Kruskal-Wallis single factor analysis of variance by ranks (Zar 1974). When pre-experiment (Day 0) results were nonsignificant, similar tests were employed for analysis of treatment effects on subsequent days. When analysis of Day 0 data indicated pre-existing differences among plots for any variable, comparison was made within treatments among days. A nonparametric multiple comparison procedure (Zar 1974) was applied when Kruskal-Wallis results indicated significant differences among treatments.

MICROCOSM STUDIES

Experimental Design

Interactions of I. obsoleta and annelids and impact on nematodes were tested by adding groups in combination to microcosm sediments. Three replicate microcosms were established for each of the following treatments:

- i) meiofauna only
- ii) meiofauna plus macroinfauna
- iii) meiofauna plus snails
- iv) meiofauna plus macroinfauna plus snails

Microcosms were established in 19 cm diameter circular glass culture dishes. Sediment was collected from the top 2 cm of the mudflat to include maximum numbers of nematodes and sieved without dilution through 0.25 mm mesh. Material passing the sieve was homogenized by stirring and layered 1 cm deep in 13 dishes. This constituted the

"meiofauna only" treatment and formed the basis for addition of mud snails and macroinfauna. A similar quantity of sediment was collected from the mudflat and sieved gently with ambient salinity water. Material remaining on the 0.25 mm mesh was homogenized and equally divided. Half was distributed on sediment in 7 of the culture dishes and half was frozen, thawed, and distributed as a "killed control" on the remaining 6 dishes. Enough of the coarse sieve fraction was added to just cover the sediment surface in the dishes (ca. 40 ml). This constituted the "meiofauna plus macroinfauna" treatment. The seventh dish containing meiofauna plus macroinfauna was sampled before and after addition of the coarse sediment fraction in order to correct nematode counts for individuals added to the microcosms in material retained on the 0.25 mm mesh. Seven adult mud snails were placed in three dishes of each treatment ("meiofauna only" and "meiofauna plus macroinfauna"). This number of snails (equivalent to 245 individuals per meter²) is within the range for natural population densities on the Wachapreague mudflat (R.L. Wetzel, personal communication). Dishes were overlaid with ambient salinity water which was changed daily. Dishes were incubated in a greenhouse at approximately ambient insolation. Microcosms were incubated from 27 June to 7 July, 1980.

Sampling

At the end of the experiment, overlying water was drawn off and snails were removed. Samples for enumeration and characterization of nematodes were taken by hand using corers made from 3 cc plastic

syringes. Each corer sampled a surface area of 0.78 cm² to a depth of 1 cm. Six replicate cores were taken from each dish. Five were used to estimate nematode population density, and the sixth to identify feeding type distribution of individuals in the population. Sediment remaining in each dish was seived gently through 0.25 mm mesh. Materials retained on the seive constituted the macroinfauna sample. All samples were preserved in 5% buffered formalin in sea water with rose bengal stain. Feeding type characterization was conducted as described above.

Data Analysis

Data were analyzed using a nonparametric one-way analysis of variance by ranks, with the Γ correction for small sample sizes (Kruskal and Wallis 1952). Significant differences were further analyzed by a nonparametric multiple comparison procedure (Zar 1974). One macroinfauna sample was lost from the "meiofauna plus macroinfauna" treatment. Data were ranked without this sample for Kruskal-Wallis analysis. For the multiple comparisons, which require equal sample sizes, data were ranked a second time using the group mean as an estimate of the missing value (R. Diaz, personal communication).

RESULTS

FIELD STUDIES

Methodology

Nematode densities estimated under the three methods of extraction and enumeration were compared by Kruskal-Wallis single factor analysis of variance by ranks (Zar 1974). The null hypothesis of no difference among the methods was rejected ($p < 0.001$). Nonparametric multiple comparison procedures (Zar 1974, Wilcoxon and Wilcox 1964) showed that magnesium chloride extraction yielded estimates of significantly fewer nematodes per sample. Total counting was statistically indistinguishable from autopipette subsampling.

Time and effort efficiencies were recorded for counting by subsampling vs. total counts. Four to 8 hours were required to count every nematode in the 4.84 cm² core, top 2 cm of sediment. Using autopipette subsamples of 1/25 to 1/40 of the volume of the sample, one estimate could be obtained in 40 to 90 minutes. A series of replicate subsamples recorded from several haphazardly selected samples yielded coefficients of variation for the subsampling procedure ranging from 1.2 to 5.2%. Given the saving in time and effort, I considered the loss of precision acceptable and employed subsampling throughout the rest of the study. Calculated values of Green's Index ranged from 0.0013 to 0.0025 in May and 0.0006 to 0.0070 in December. These values are sufficiently close to 0 to indicate a randomly distributed

population, and the low order of magnitude of changes in the index with sample area (0.0005 to 0.0006 in May, 0.0002 to 0.0070 in December) relative to the value scale of the index (0 to 1) renders it unlikely that a meaningful estimation of "patch size" can be determined from these data. For these reasons, a core size of 1.5" diameter (11.3 cm²) was chosen for reasons of availability and expense.

Extraneous Cage Effects

The following organisms were found inside exclusion cages over the course of the experiment: Paralichthyes dentatus (1 individual), Fundulus heteroclitus (20), Palaemonetes sp. (2), and Ilyanassa obsoleta (1). Despite these intrusions, the cages were successful in reducing activity of large, natant forms over excluded areas of mudflat.

A series of measurements of photosynthetically active radiation was made under the mesh with a Li-Cor Model 185A Quantum meter. Results showed that the cages reduced light levels by 26 to 28% at the substrate surface. However, at low tide at Gate's Bay, light reaches levels sufficient to saturate or inhibit algal photosynthesis during clear weather (R. L. Wetzel, personal communication). The same instrument was used to determine that PAR levels were undetectable at the sediment surface when tide was at slack flood. Therefore, I feel that the action of the mesh in reducing PAR levels was probably not an important impact.

A further concern about the cages was that the mesh would reduce tidal currents sufficiently to allow deposition of suspended particles.

During the study, there was no noticeable accumulation of sediments associated with the cage structures. The cages were left in place a total of 22 days. During this time the mesh did not foul, nor did sediment accumulate.

Nematode Density

In August in the top 2 cm of Gate's Bay mudflat sediments, mean nematode population density was 980 individuals per cm^2 (standard error of the mean (S.E.= 80). In May, there were 2150 (S.E.= 60) individuals per cm^2 , and in December, 1810 (S.E. = 120) nematodes per cm^2 . These estimates were obtained by using 10 data points selected randomly from the distribution series (May, December) and Day 0 experimental cores (August). It should be noted that although these cores were of different sizes and so had the potential to affect density estimates in a non-regular fashion (see Vandermeer 1981), the random distribution of nematodes in the Gate's Bay sediments renders this unlikely. Standard errors around these values are relatively low, and in no cases do they overlap.

Table 1 summarizes mean and standard error of estimated nematode density in the top 0.5 cm of sediment on all plots over the course of the experiment. Pairwise comparison of plots within treatments and days revealed no significant differences ($0.20 < p$) and plots were pooled within treatments for comparison among treatments. Figures 3 and 4 displays these results. Kruskal-Wallis ANOVA by ranks was

Table 1. Mean (N=3) nematode density (individuals/cm²± one standard error) in the top 0.25 cm of sediment.

	Plot#	Mesh Size (μ)		Total
		67	24	
Day 1	0X1	598±77	34±6	633±80
	0X2	526±60	12±6	538±63
	1X1	548±50	13±1	561±51
	1X2	444±24	14±2	459±21
	2X1	451±59	20±8	471±58
	2X2	518±17	13±1	531±17
	UNC1	382±93	11±1	393±93
	UNC2	580±35	12±1	593±36
Day 2	0X1	428±25	17±2	446±28
	0X2	447±9	28±1	475±9
	1X1	516±7	28±5	544± 3
	1X2	446±30	16±7	462±23
	2X1	471±15	23±7	494±21
	2X2	587±34	23±1	610±9
	UNC1	487±34	28±1	515±34
	UNC2	428±23	44±11	472±12
Day 5	0X1	507±46	20±16	527±49
	0X2	402±39	22±8	423±31
	1X1	605±32	6±3	611±35
	1X2	577±15	12±3	589±16
	2X1	617±14	16±4	633±17
	2X2	580±25	10±3	591±28
	UNC1	570±47	58±29	628±19
	UNC2	534±98	49±5	584±93

Figure 3. Nematode density by day and treatment in the top 0.25 cm of mud flat sediment.

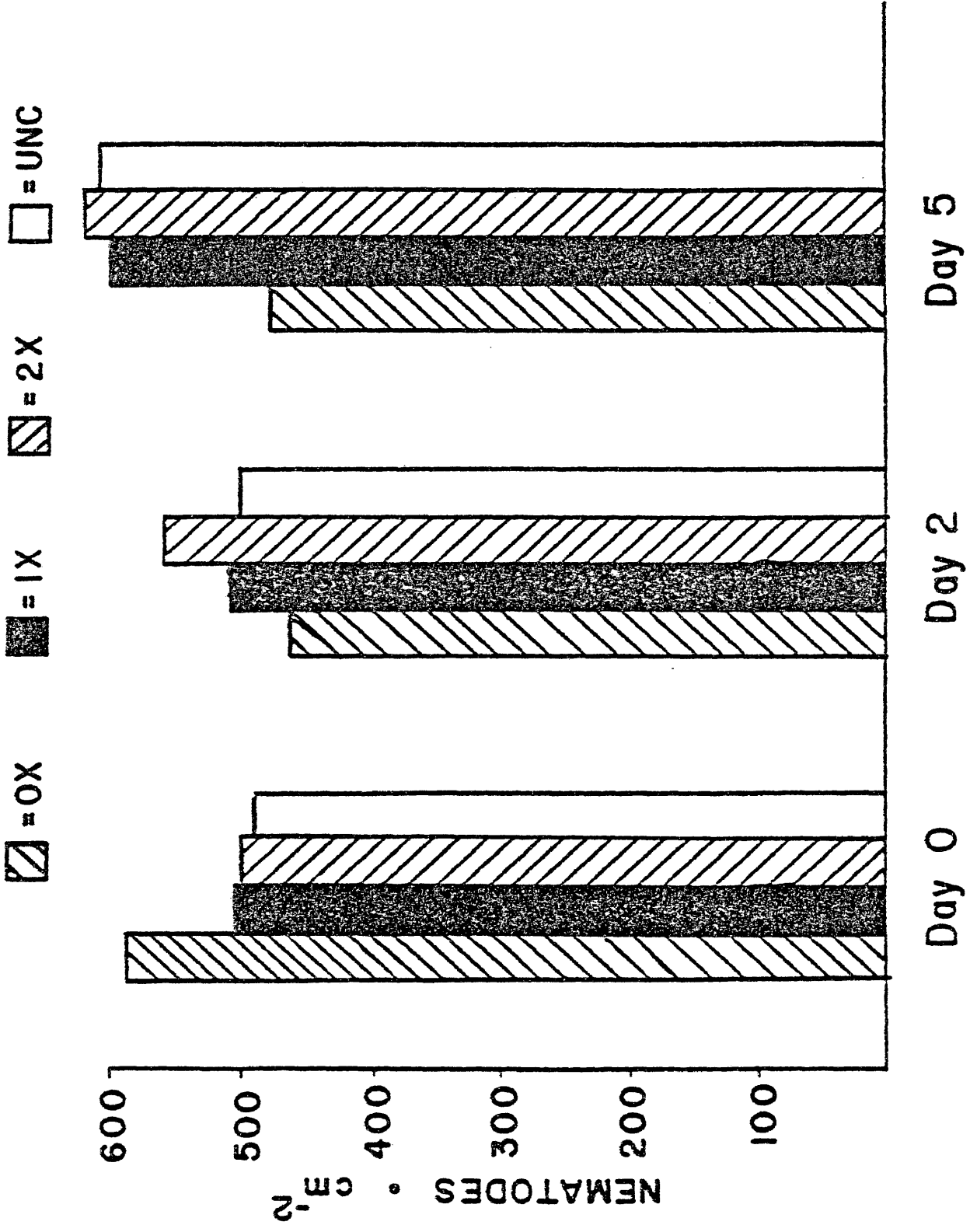
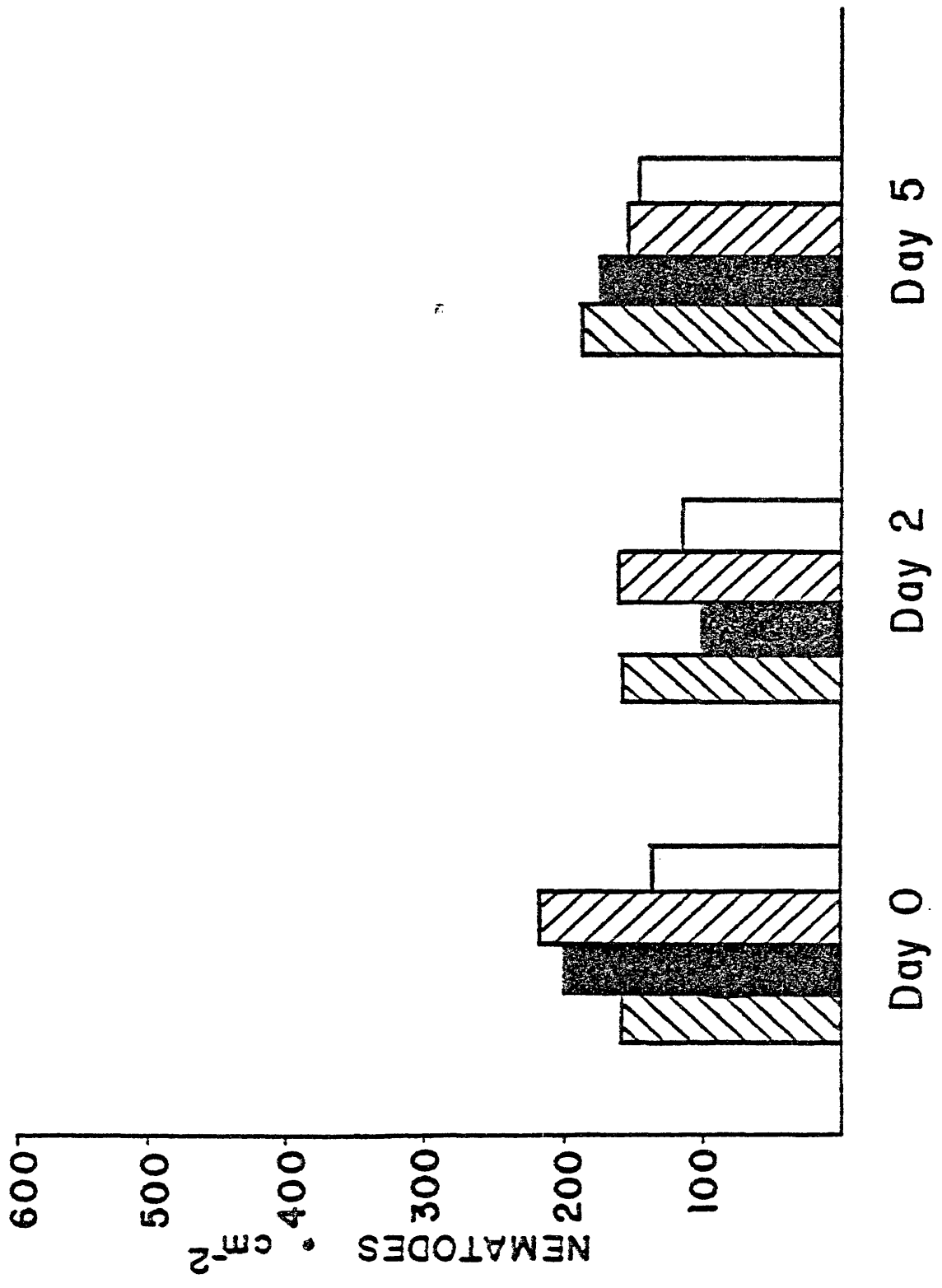


Figure 4. Nematode density by day and treatment at 0.25 to 0.50 cm depth in mud flat sediment.



applied among treatments within days. In no case was the null hypothesis of no difference among treatments rejected ($0.05 < p$). Overall nematode density at the sediment surface did not change in response to the experimental treatments.

Feeding Type Distribution

Table 2 shows distribution of nematode feeding types by treatment, day, and depth in sediment. Two sample comparison of feeding type index (number of type 2A/number type 1A + number type 1B + number type 2B, see Methods) revealed no significant differences among plots within treatments ($0.20 < p$), and treatments were pooled in subsequent analyses. Mann-Whitney comparison of pooled feeding type index in the top 0.25 cm sections on Day 0 indicated that plots 2X were significantly different from plots 0X ($p < 0.05$). This precluded comparison among treatments within days. Two sample comparison was therefore conducted within treatments among days and data are summarized in Figure 5. The null hypothesis of no difference is not rejected for the 0.25-0.50 cm section in any case. This indicates that below 0.25 cm of sediment, nematode feeding type distribution was not changed by experimental treatments. In the top 0.25 cm of sediment, the null hypothesis is rejected ($p < 0.01$) for the 2X snail density treatment. This density of snails caused a significant shift in feeding type index of the nematode population.

Figure 6 shows feeding type index of nematode communities as a function of depth, treatments, and days. Feeding type distribution

Table 2. Distribution of nematode feeding types among individuals. Mean %, N=6 in all cases except the deepest section where N=3.

		<u>Treatment 0X</u>				<u>Treatment 2X</u>			
		<u>1A</u>	<u>1B</u>	<u>2A</u>	<u>2B</u>	<u>Feeding Type</u>			
		<u>1A</u>	<u>1B</u>	<u>2A</u>	<u>2B</u>	<u>1A</u>	<u>1B</u>	<u>2A</u>	<u>2B</u>
<u>Depth (cm)</u>									
Day 0	0.00-0.25	19	11	56	16	14	7	67	12
	0.25-0.50	11	12	62	19	23	8	62	7
	0.50-1.00	37	13	36	14	40	11	29	20
	1.00-1.50	22	25	25	28	35	45	9	9
Day 5	0.00-0.25	13	8	63	15	10	21	48	21
	0.25-0.50	16	8	66	10	24	15	51	11
	0.50-1.00	19	9	43	29	22	17	45	17
	1.00-1.50	33	10	35	22	40	25	25	10

Figure 5. Feeding type distribution of nematodes in the top 0.25 cm of mudflat sediments by day and treatment.

■ = 1A ▨ = 1B □ = 2A ▩ = 2B

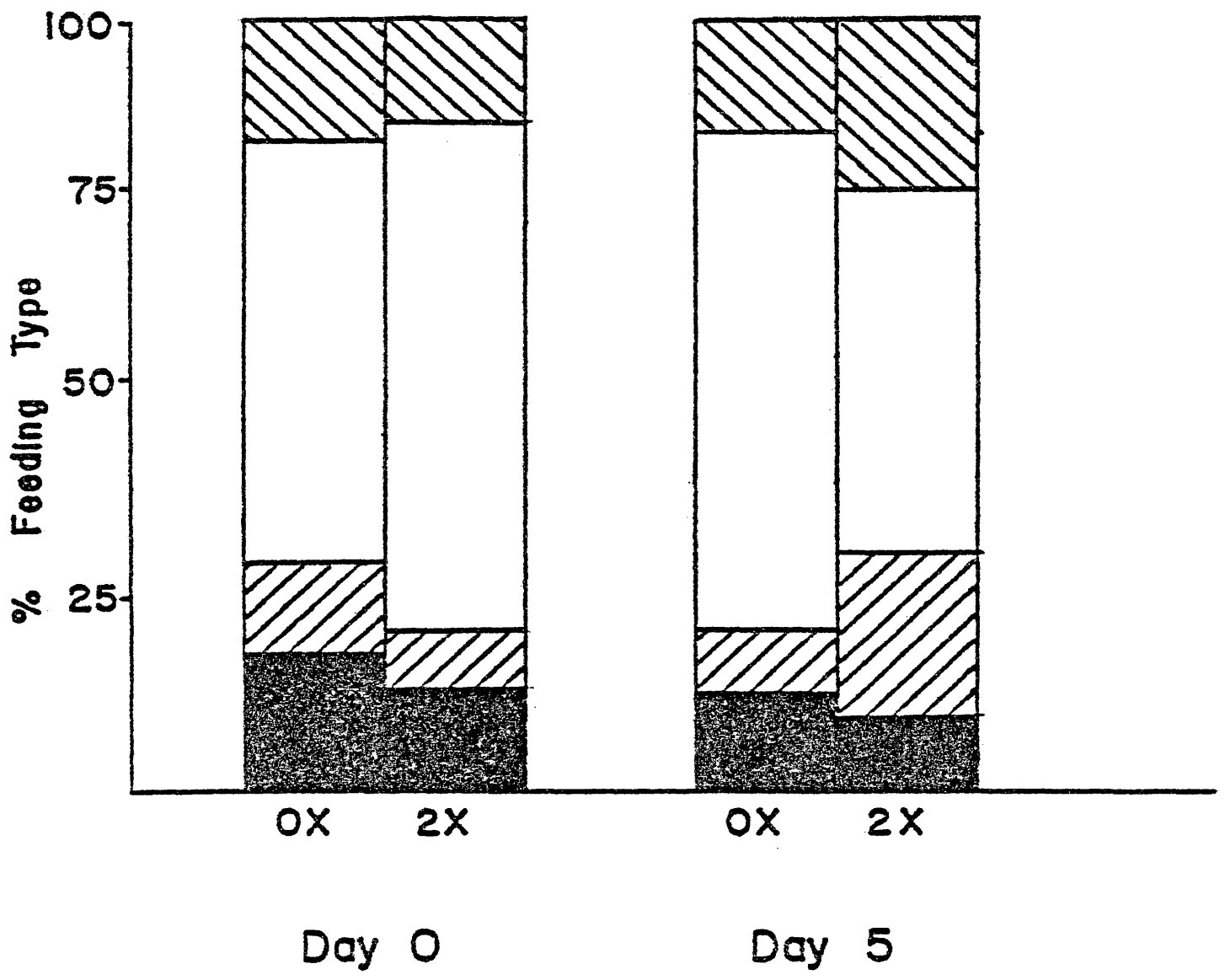


Figure 6. Index of algivory of nematode community by day, depth in sediment, and experimental treatment.

changed below the first 0.50 cm of sediment in all cases, from dominance by algae feeders (index > 1) to dominance by deposit feeders (index < 1).

Vertical Distribution

Table 2 and figure 7 show the relationship of nematode numbers to depth in sediment for treatment plots only. Kruskal-Wallis analysis of proportion of total nematodes found below 0.25 cm was nonsignificant ($0.20 < p$) on either day 0 or day 5. Thus, increasing snail densities did not cause increase in proportion of nematode population at depth in sediment.

Size Distribution

Table 1 summarizes nematode populations by size category in Gate's Bay sediments. Proportion of the population by size category in the top 0.25 cm of sediment was tested by Kruskal-Wallis analysis. The null hypothesis was not rejected ($0.25 < p$), leading to the conclusion that experimental treatments had no impact on size distribution of nematodes in the surface of the sediment.

Chlorophyll a

Table 3 shows mean and standard error of chlorophyll a concentration with depth in sediment for all plots and days. The number of replicates per cell (2) is too few to permit reliable use of any two sample comparison procedure (see Zar 1974). However, the mean

changed below the first 0.50 cm of sediment in all cases, from dominance by algae feeders (index > 1) to dominance by deposit feeders (index < 1).

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Figure 7. Distribution of nematode population by depth in sediment, day and experimental treatment.

 = Above 0.25 cm

 = 0.25 - 5.0 cm

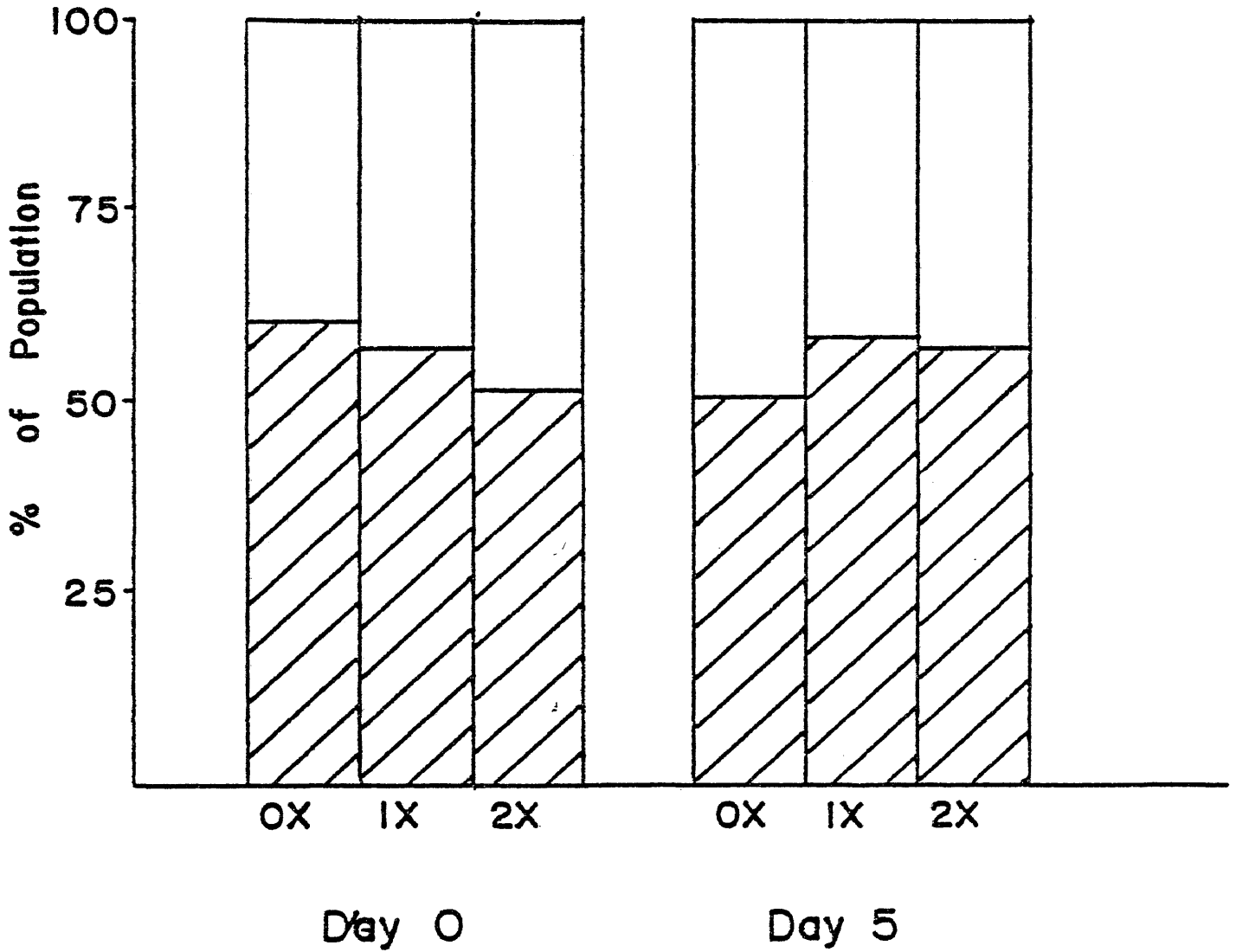


Table 3. Mean (N=4) chlorophyll a concentration (mg/m²/mm ± one standard error) in sediments.

		<u>Treatment</u>			
		<u>0X</u>	<u>1X</u>	<u>2X</u>	<u>UNC</u>
<u>Depth (mm)</u>					
Day 0	0.0-1.0	13.3±1.1	10.8±0.9	9.9±2.1	8.2±1.5
	1.0-2.5	3.3±0.7	4.6±0.1	4.0±0.7	3.4±0.1
	2.5-5.0	1.3±0.4	2.3±0.6	2.5±0.9	1.4±0.3
Day 5	0.0-1.0	16.7±0.9	11.5±2.7	2.0±0.4	5.7±1.5
	1.0-2.5	4.9±0.4	2.4±0.5	4.0±1.5	3.3±0.5
	2.5-5.0	4.2±0.3	4.0±0.5	1.4±0.5	1.1±0.1

chlorophyll concentration on no pair of plots varies by more than 20% of the mean within any day, and in most cases by less than 10%. For this reason, I have pooled data within treatments for comparison among treatments and days, but the reader should bear in mind that this justification is weaker than that provided above for pooling of nematode data. Pooled chlorophyll data are displayed in figure 8. Kruskal-Wallis ANOVA of chlorophyll a among treatments within depths and days revealed significant treatment effects ($p < 0.001$) on day 5 only in the top 1.0 mm and 2.5-5.0 mm of sediment. Multiple comparison results revealed the following groups in the top 1mm of sediment where breaks in the underscore indicate significant differences ($\alpha = 0.05$):

2X UNC 1X 0X

Core sections taken from 2.5-5.0mm grouped as follows ($\alpha = 0.05$):

UNC=2X 1X=0X

Sediment Water Content

Table 4 shows mean and standard error of percent water in sediment core sections for all depths and days. Pairwise comparisons are again precluded by the low number of replicates. However, based on the low standard error within treatments and days, I have pooled data within treatments for comparison among treatments within days. On day 0 in the first 0.25 cm of sediment, Kruskal-Wallis analysis led to rejection of the null hypothesis of no difference among plots. Therefore, subsequent analyses were conducted within plots and sediment depth

Figure 8. Concentrations of chlorophyll a by day, depth in sediment, and experimental treatment.

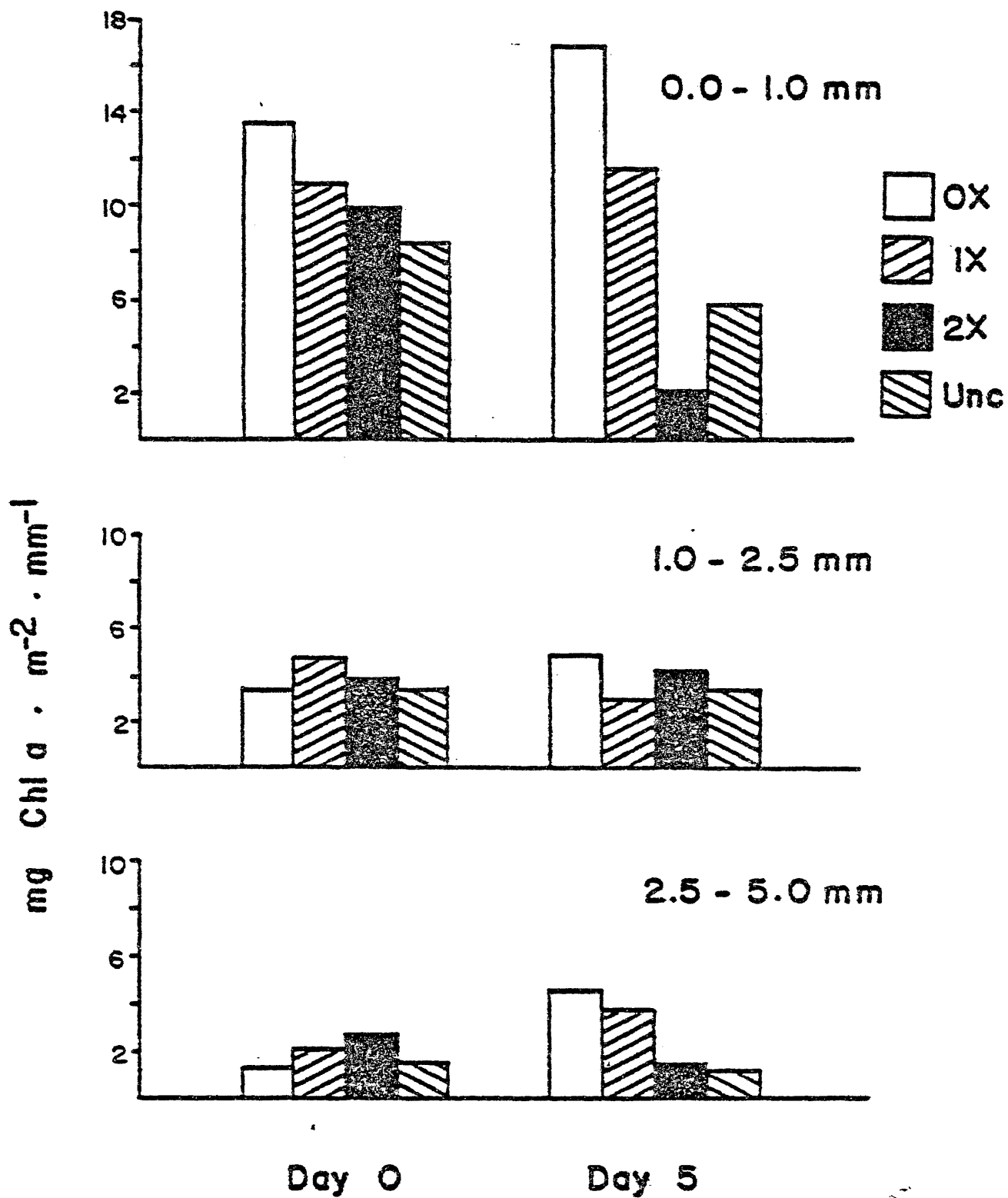


Table 4. Mean (N=4) % water in sediment. Standard error less than 1.5 in all cases.

	Depth (cm)	OX	Treatment		UNC
			1X	2X	
Day 0	0.00-0.25	37.5	41.7	42.2	42.1
	0.25-0.50	38.1	40.9	40.3	40.7
	0.50-1.00	36.8	40.3	39.4	39.4
	1.00-1.50	36.6	38.8	37.4	37.6
	1.50-2.00	37.9	41.6	38.1	38.1
	2.00-3.00	39.7	44.7	40.1	42.0
	3.00-5.00	41.8	43.5	43.7	43.8
Day 2	0.00-0.25	44.4	46.2	43.8	41.1
	0.25-0.50	39.4	43.5	39.9	41.7
	0.50-1.00	38.5	42.0	38.6	41.1
	1.00-1.50	37.7	40.1	37.6	41.9
	1.50-2.00	36.6	40.8	37.0	43.6
	2.00-3.00	38.3	42.3	38.7	45.4
	3.00-5.00	41.6	44.4	41.7	44.8
Day 5	0.00-0.25	41.8	41.3	40.3	38.4
	0.25-0.50	39.2	41.2	40.2	40.4
	0.50-1.00	40.6	40.7	36.8	36.2
	1.00-1.50	39.1	39.5	38.2	38.9
	1.50-2.00	38.6	38.7	37.8	39.4
	2.00-3.00	40.3	39.5	39.2	44.6
	3.00-5.00	42.0	43.6	41.6	44.2

among days. The null hypothesis was rejected in the first 0.25 cm of sediment for treatments 0X, UNC, and 1X. Multiple comparison of 0X plots yielded the following groups:

D0 D5 D2

Multiple comparison of significant results in UNC and 1X plots were ambiguous, indicating commission of Type II error. Such results are impossible to interpret.

MICROCOSM STUDIES

Tables 5 and 6 and figures 9 through 13 show densities of polychaetes, oligochaetes, and nematodes, and ratio of algivorous to deposit feeding nematodes in each microcosm. Samples taken before and after addition of live coarse sediment to the 13th microcosm showed that 670 ± 73 nematodes/cm² (mean \pm 1 standard error, N=3) were added in the coarse seive material. Nematode counts from microcosms containing live coarse fraction were corrected for this addition by subtracting the mean number of nematodes added from the mean number of nematodes in each replicate plot.

Kruskal-Wallis analysis showed that nematode densities were significantly different among the treatments ($\chi = 14.3$, $v=5$, $p < 0.025$). The "meiofauna only" and "meiofauna plus snails" treatments were not different from each other ($0.10 < p$) but were significantly ($p < 0.01$) higher than both treatments containing macroinfauna (table 7 and figure 9).

Table 5. Density (mean #/10 cm², N=5) and Index of Algivory of nematodes in microcosm sediments.

<u>Treatment</u>	<u>Replicate</u>	<u>Density</u>	<u>Algivory Index</u>
meiofauna only	a	3440	3.6
	b	3860	4.5
	c	3330	3.8
meiofauna plus macroinfauna	a	2150	3.5
	b	2230	2.2
	c	3000	1.6
meiofauna plus snails	a	3410	1.1
	b	3860	1.4
	c	3670	1.6
meiofauna plus macroinfauna plus snails	a	2170	1.6
	b	2030	1.1
	c	2310	1.4

Table 6. Total numbers of annelids per microcosm (270 cm²).

<u>Treatment</u>	<u>replicate</u>	<u>polychaetes</u>	<u>oligochaetes</u>
meiofauna only	a	31	84
	b	43	123
	c	47	124
meiofauna plus macroinfauna	a		sample lost
	b	77	1771
	c	84	2002
meiofauna plus snails	a	58	127
	b	43	101
	c	44	113
meiofauna plus macroinfauna plus snails	a	57	1603
	b	67	1892
	c	70	1902

Figure 9. Nematode density in microcosm sediments by experimental treatment.

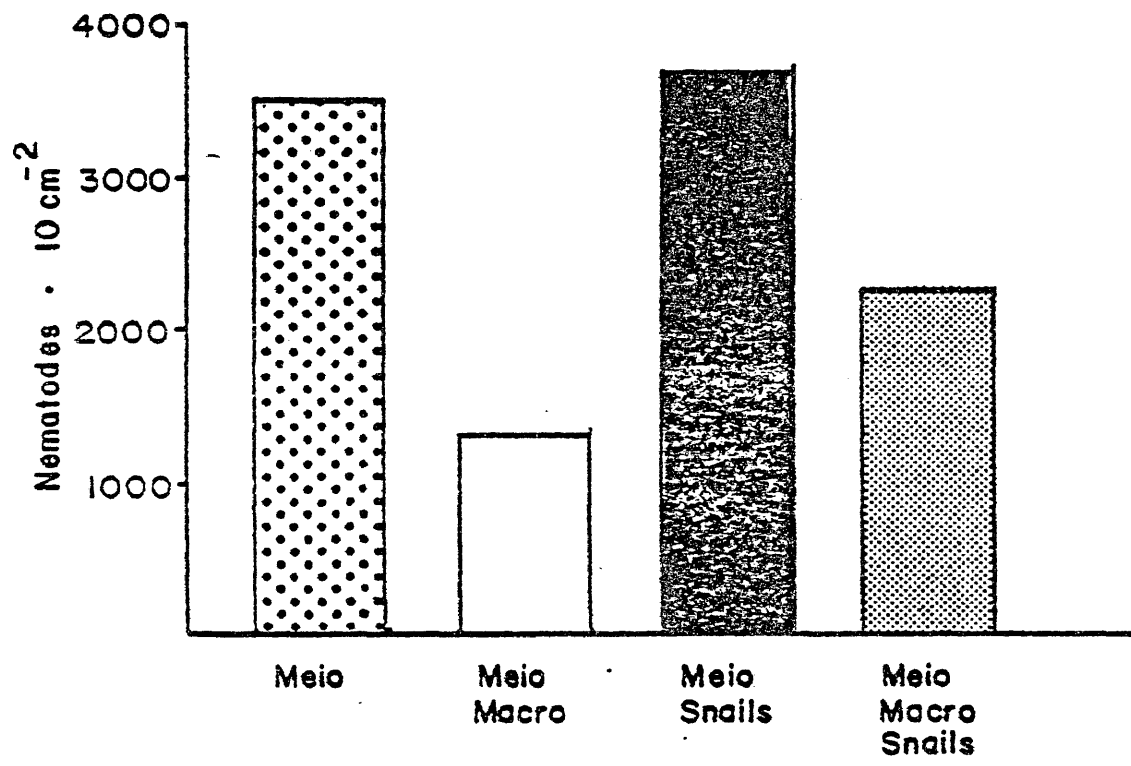


Figure 10. Distribution of nematode feeding types in microcosm sediments by experimental treatment.

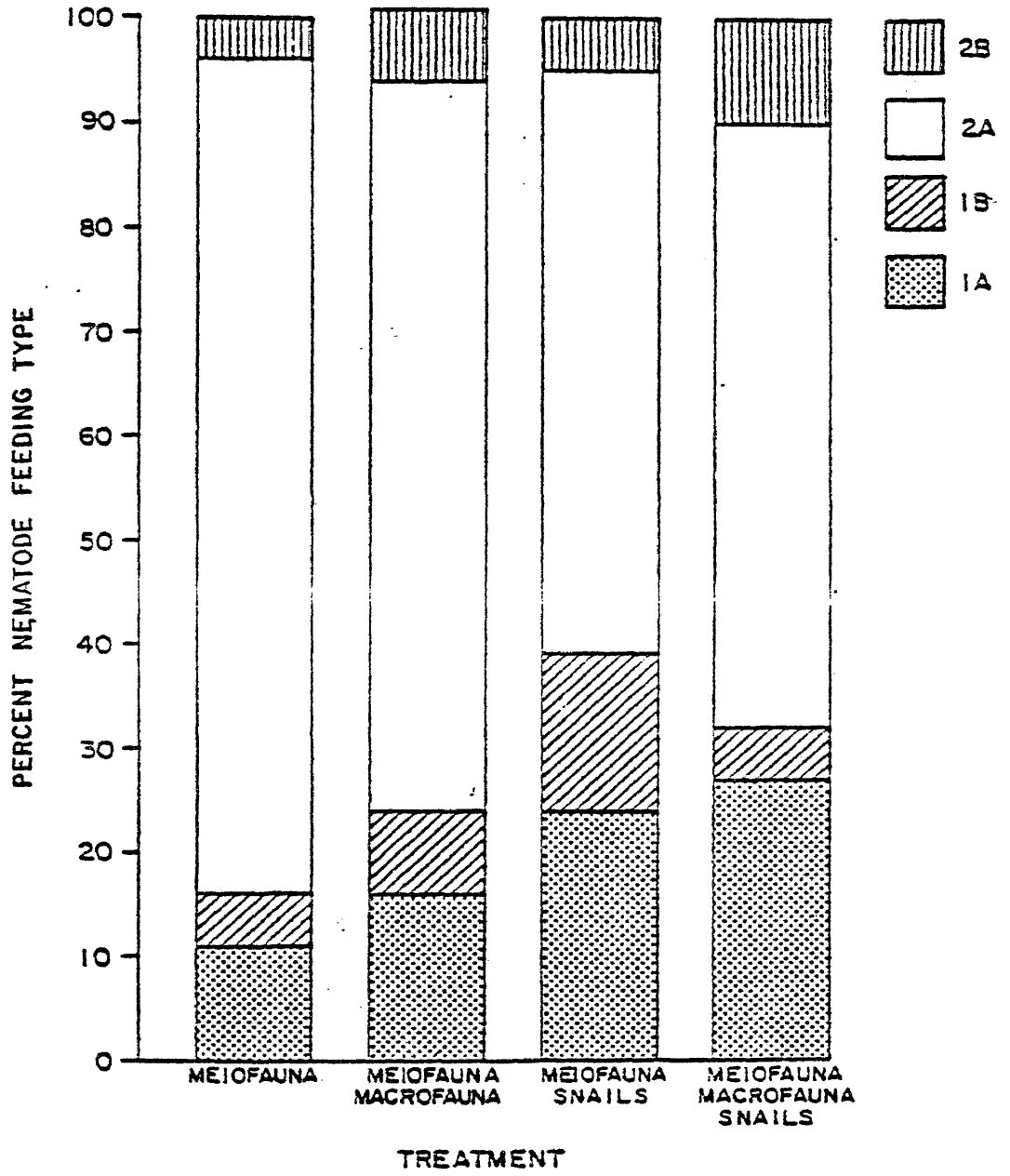


Figure 11. Index of algivory of nematodes in microcosm sediments by experimental treatment.

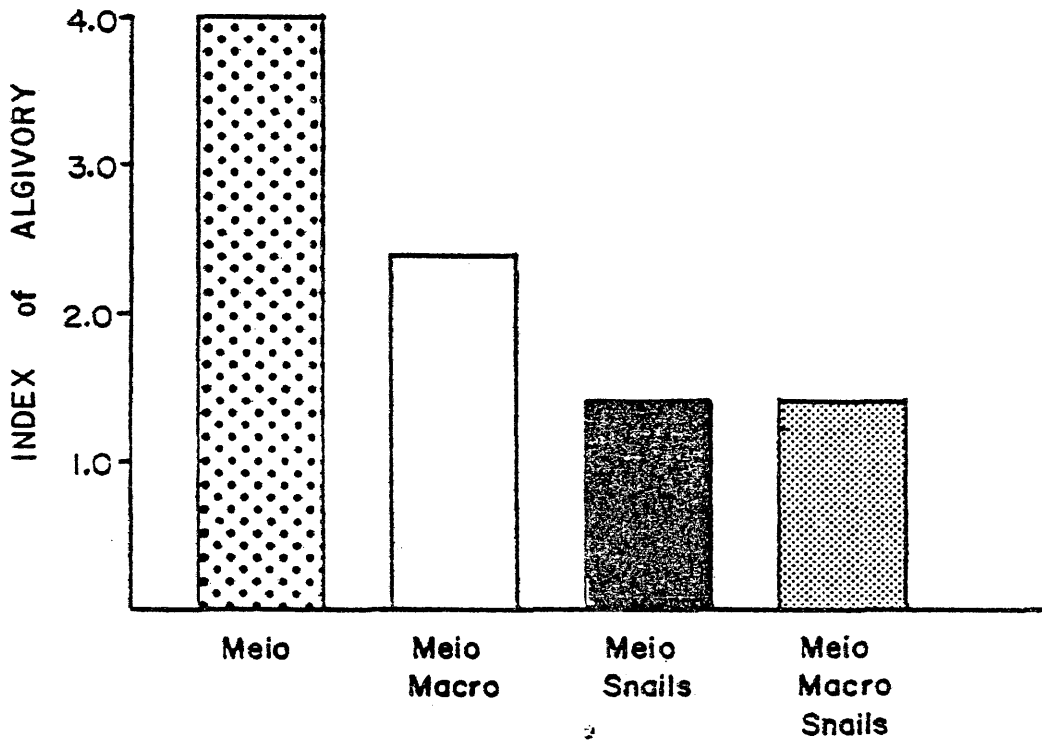


Figure 12. Oligochaete density in microcosm sediments by experimental treatment.

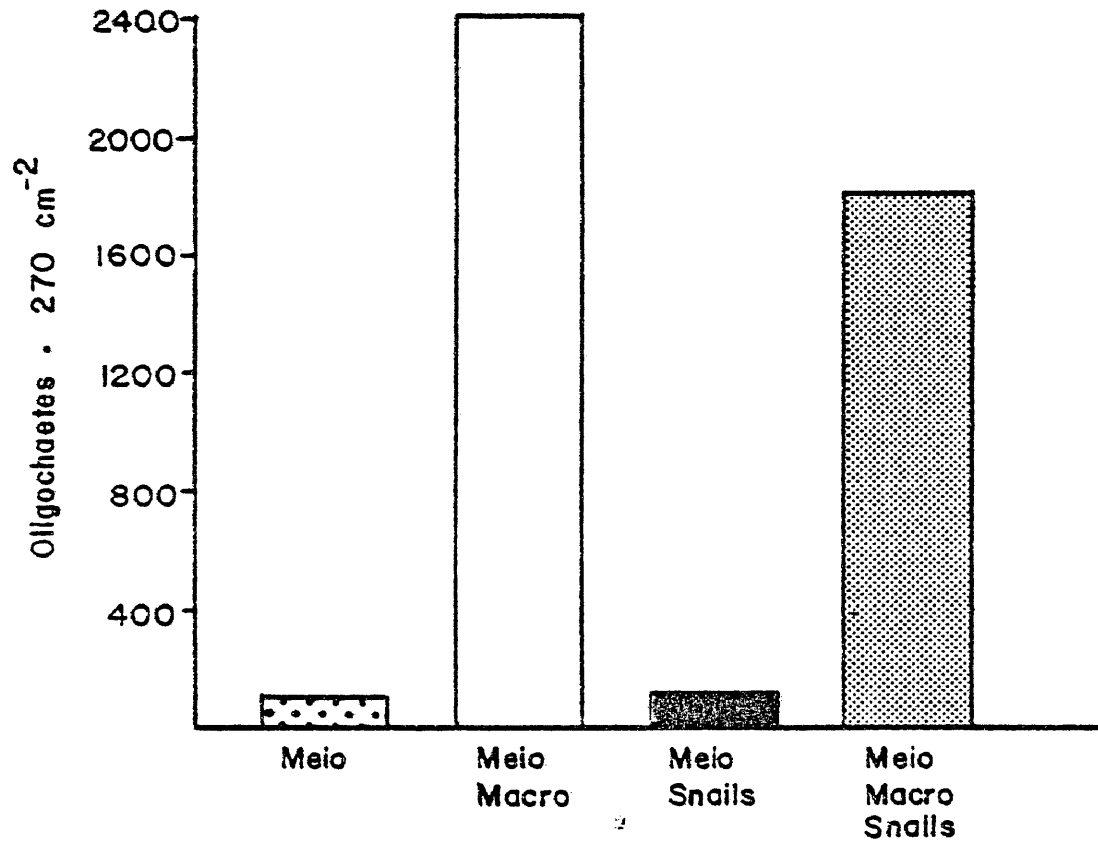


Figure 13. Polychaete density in microcosm sediments by experimental treatment.

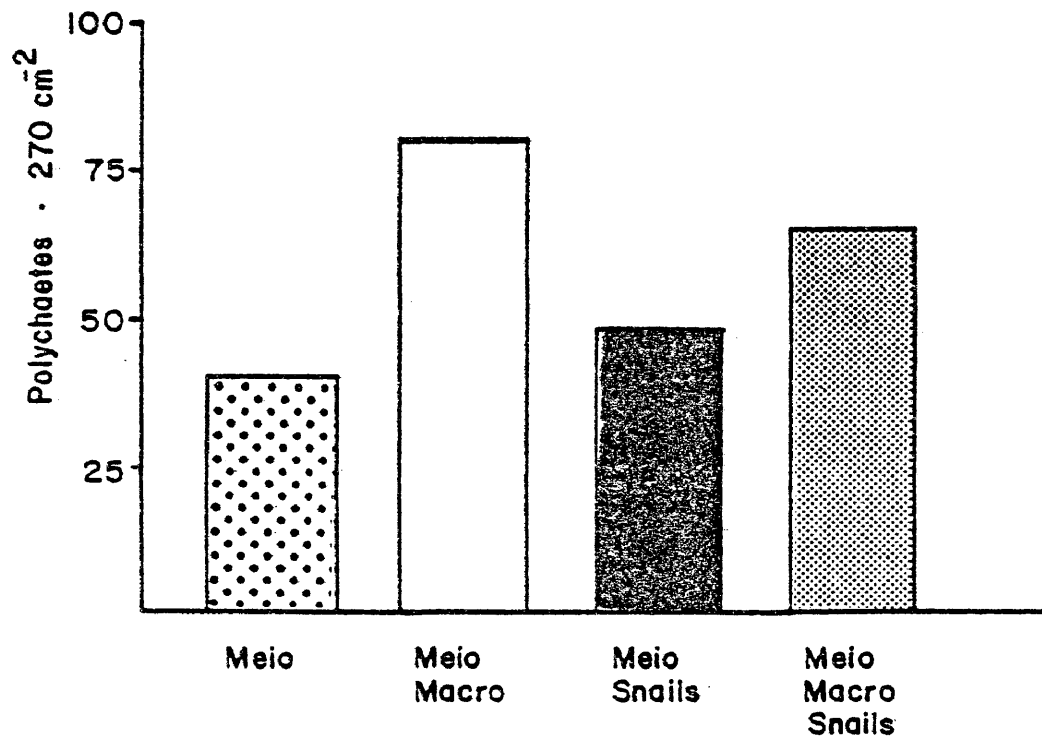


Table 7. Summary of multiple contrast analyses of microcosm results. Treatment abbreviations: ME = "meiofauna only", ME+SN = "meiofauna plus snails", ME+MA = "meiofauna plus macroinfauna", ME+MA+SN = "meiofauna plus macroinfauna plus snails". Breaks in underscore indicate significant differences at 0.10 level.

<u>Parameter</u>	<u>Multiple contrast</u>			
polychaete density	<u>(ME)</u>	<u>(ME+SN)</u>	<u>(ME+MA+SN)</u>	<u>(ME+MA)</u>
oligochaete density	<u>(ME)</u>	<u>(ME+SN)</u>	<u>(ME+MA+SN)</u>	<u>(ME+MA)</u>
nematode density	<u>(ME+MA+SN)</u>	<u>(ME+MA)</u>	<u>(ME)</u>	<u>(ME+SN)</u>
algivory index	<u>(ME+MA+SN)</u>	<u>(ME+SN)</u>	<u>(ME+MA)</u>	<u>(ME)</u>

Treatment plots yielded significantly different proportions of algivorous nematodes ($\chi = 14.8$, $v=5$, $p < 0.025$). This information is displayed in figures 10 and 11. All treatments were lower than the "meiofauna only" treatment, and both treatments containing snails formed a group that was lower than the "meiofauna plus macroinfauna" treatment (table 7).

Oligochaete densities were significantly different among the treatments ($\chi = 14.1$, $v=5.5$, $p < 0.025$). Multiple contrast (table 7 and figure 12) showed that the "meiofauna plus macroinfauna plus snails" treatment was significantly lower ($p < 0.10$) than the "meiofauna plus macroinfauna" treatment. An identical pattern of difference was found for the Kruskal-Wallis and multiple contrast analyses of polychaete numbers ($\chi = 13.6$, $v=5.5$, $p < 0.05$, and table 7 and figure 13).

DISCUSSION

FIELD STUDIES

Methodology

Decantation and seiving with 6% magnesium chloride was clearly inadequate for sampling nematodes in the mud at Gate's Bay. This may be due in part to the presence of caudal glands on a large proportion of nematodes in this habitat. Observation suggests that 70 to 80% of individuals extracted possessed visible caudal glands. These structures may allow the animals to adhere to heavy sediment particles, increasing their sinking rate and reducing their recovery in decanted samples. This extraction method has been employed successfully in coarser sediments of the continental shelf (Hartzband and Boesch 1979). It would be most interesting to know whether or not a comparable percentage of nematodes in this habitat have functional caudal glands. The importance of adhesion may be enhanced in intertidal sediments subject to tidal and storm flow and persistent disruptive grazing. Sediment type may also play a role in efficacy of MgCl narcotization. Uhlig et al. (1973) concluded that elutriation with narcotization by 7% MgCl was adequate for extracting meiofauna from coarse sediments and not from fines sediments.

Total counting was statistically indistinguishable from subsampling as a means of enumerating nematodes. Total counts are time consuming and of reduced effectiveness when used with preserved material (Uhlig

et al. 1973). Subsampling has not, to my knowledge, been used in estimation of total nematode numbers, although various methods have been employed to subsample previously sorted material for identification (Levy 1977, Hartzband and Boesch 1979).

Subsampling by autopipette proved to be remarkably effective in enumerating nematodes in Gate's Bay muds. Use of subsampling should be explored in other ecological studies where large numbers of samples must be processed with limited time and funds, and where some loss of precision is not considered critical.

Core Size and Nematode Patchiness

Many recent studies of marine and estuarine meiofauna distribution fail to justify sampling areas utilized (e.g. Levy 1977, Bell et al. 1978, Nichols and Robertson 1978, Sherman and Coull 1980, Bell and Coull 1980). This is unfortunate in view of the reported "patchiness" of nematode distribution in sediments (Vitiello 1968, Warwick and Buchanan 1970, Gray and Rieger 1971, Arlt 1973, Gerlach 1977, Bell et al. 1978) and because sample precision varies with sample size (Tietjen 1980). On sandy beaches, recovery efficiencies of different size cores indicate that nematode patches are approximately 3.75 cm² (Gray 1971). In salt marsh sediments, a 2.54 cm² core approximates overall meiofauna patch size (Bell 1979). In a detailed study of meiofauna distribution, Findlay (1981) utilized graded sample sizes and calculated Green's index of dispersion as a function of sample area to indicate randomness, aggregation, and patch size. I employed

a similar approach. Calculated values of Green's index are all close to 0, indicating that, at the sample areas used, nematodes are distributed randomly. Findlay (1981) assumed changes of 0.3 index units/cm² to indicate patch size. In comparison, my values show little change with sample area. Nematodes on the Gate's Bay mudflat are distributed randomly, at least at a scale of 4.84 cm² or larger. Patchiness at a scale smaller than this would not be detected by my method. At the 4.84 cm² scale the nematode community is poorly "organized" in that it lacks interactions that would produce either evenness or patchiness. This is in contrast to the situation in salt marsh sediments, where patchiness from several sources is imposed upon the nematode community (Bell et al. 1978, Bell 1980).

Nematode Density

In subtidal nematode communities, seasonal density changes are marked but vary in timing and degree with geography and habitat (Tietjen 1969, Coull 1970, Juario 1975, Levy 1977, Platt 1977b). In shallow subtidal estuarine muds, Warwick (1971) reported a lack of seasonal variation in density or species composition of nematodes. However, in subtidal salt marsh creek sediments, Sikora et al. (1977) found peak nematode abundance in late spring and lowest populations in August. Their observations accord well with my data. Nematode populations in August on the mudflat at Gate's Bay are approximately half those in May and December, with no overlap in standard errors. This late summer reduction may be due to combined action of biotic and

physico-chemical forces. Although nematodes are capable of inhabiting anoxic sediments (Wieser and Kanwisher 1959, Fenchel and Jansson 1966, Fenchel 1969, Boaden and Platt 1971, Platt 1977a), peak populations occur at and above the RPD layer and closely track the discontinuity when it migrates (McLachlan 1978). In August at Gate's Bay, the RPD is generally near the sediment surface, with diel migrations above and below the sediment-water interface (R.L. Wetzel, personal communication). Nematode populations may be forced into the zone of sediment transport by the physico-chemical environment, where they are at increased risk from a variety of predatory and grazing forms. McLachlan (1978) reached a similar conclusion, and stated:

"The greater tendency toward random distribution in summer suggests that chemical factors control abundance and vertical distribution; but horizontal dispersal is controlled biologically by predation and competition to a greater extent in summer..."

Of particular interest is the fact that nematodes are transported under tidal influence (Bell and Sherman 1980) and may become available to filter feeding macrofauna.

Lack of treatment effects on overall density of nematodes is surprising in view of the reported increase in density of nematodes in response to I. obsoleta exclusion (Nichols and Robertson 1978). Nichols and Robertson (1978) interpreted their results as a demonstration of competition between nematodes and mud snails for diatoms, which they felt were at limiting levels in the subtidal sands in which their study was conducted. At Gate's Bay, exclusion of I. obsoleta yielded a significant increase in algal biomass measured as

chlorophyll a, with no significant increase in nematode density. Thus, the nematode community as a whole is limited by factors other than food. Increased predation and decreased space, as discussed above, may serve to depress nematode populations. However, exclusion of I. obsoleta was accompanied by an increase in proportion of algae feeding nematode types (see below). I conclude that both density independent (physico-chemical) and density dependent (biotic interaction) factors serve to structure the nematode community.

Feeding Types and Vertical Distribution

Nematodes can partition food resources with fine resolution, discriminating between genera and "species" of algae, fungi and bacteria (Tietjen and Lee 1973, 1977, Alongi and Tietjen 1980). Despite this discriminatory power, buccal morphology has proven reliable in differentiating general trophic categories of nematodes (Levy and Coull 1977). I lumped all 3 non-algae feeding categories into one category referred to as "deposit feeders" and compared the ratio of algae feeding types to deposit feeding types among experimental treatments. In the top 0.25 cm of sediment, the 2X snail treatment caused a shift in nematode feeding type distribution away from dominance by algivores. This effect is probably due to reduction in benthic algae as a resource, since this treatment also caused a significant reduction in chlorophyll a. This conclusion is strengthened by the observation that there is no significant effect of caging on either nematode feeding type distribution or chlorophyll a

concentration in the sediment below 0.25 cm and 0.10 cm, respectively. I. obsoleta obtains a large proportion of its energy resources from benthic algae (Wetzel 1977) and thus is a competitor for this resource with nematodes. My results suggest that nematode density is reduced in summer by physico-chemical factors, but that the population surviving is organized by available resources such that algivores tend to dominate the community. This inference is also discussed below as part of the microcosm study, where alternate hypotheses are considered. I have no data available to support the conclusion that algal biomass is at limiting levels in Gate's Bay sediments in August. However, chlorophyll a is strongly concentrated in the top 1 mm of sediment, and meiofauna in the top 2.5 mm. This summertime crowding effect imposed by the rigorous physico-chemical conditions may truncate biotic interactions into a small space such that overall resource competition may be intensified. This point bears further investigation, and invites manipulative experiment. Maintaining oxidizing regimes at depth in the substrate, stimulating algal production, and measuring depth distribution of meiofaunal organisms could show whether or not truncation and crowding of sediment column organisms occurs and how it effects biotic interactions. These experiments are suggested by results of my vertical distribution analysis. Table 1 shows that nematode densities are lower at depth in the sediment, and results of feeding group analysis with depth show that the community exhibits a significant shift away from algivory below 0.25 cm. Thus, there appears to be a rich sediment surface

community of algae and associated meiofauna, which is differentiated from a less abundant, detritus based community at depth. The role of I. obsoleta in structuring the sediment column is, unfortunately, poorly indicated by results of the sediment water column analysis. Results are ambiguous and in several cases could not be tested by multiple contrast. The impact of I. obsoleta on sediment structure and water content is probably overshadowed by other environmental forces or lack of experimental resolving power.

MICROCOSM STUDIES

Significant differences in both the ANOVA and multiple contrast analyses are at least partly due to the experimental manipulation, that is, the sieving procedure. Since nematode numbers were corrected for individuals added in the coarse sieve fraction, this manipulation only effects the annelid results. In analyses of both oligochaete and polychaete numbers, the multiple contrast test separated the "meiofauna only" and "meiofauna plus snails" treatments as a group from both treatments which received live coarse fraction. This is due to individuals sieved from the sediment on the 0.25 mm mesh. It should be noted that nearly 50% of polychaetes passed the mesh, while only 4% of oligochaetes did so.

The first hypothesis of this experiment is that I. obsoleta consumes nematodes. In the absence of a priori reasons for assuming that I. obsoleta can selectively ingest nematodes of different species, this predation should be reflected in a general drop in nematode

density in the presence of snails. Such a decrease did not occur: the "meiofauna plus snails" treatment contained nematode densities which were not significantly different from the "meiofauna only" treatment. It seems unlikely that I. obsoleta, as a nonselective deposit feeder (Scheltema 1964, Brown 1969) can avoid consuming some nematodes. The microcosm results suggest, however, that I. obsoleta does not eat nematodes in substantial numbers.

The second hypothesis, i.e. I. obsoleta competes with nematodes for food, was previously investigated by Nichols and Robertson (1978). They reported that exclusion of I. obsoleta from subtidal sediments resulted in a rise in numbers of both algivorous nematodes and diatom cells. My results tend to support their conclusion that I. obsoleta outcompetes nematodes for algae. Both treatments containing mud snails had significantly lower proportions of algivorous nematodes than either treatment without snails. Experiments conducted in microcosms using a similar design with 8 and 16 snails per plot showed that I. obsoleta caused a significant ($p < 0.05$) reduction in sediment pigments after 6 days (Ludwig, unpublished manuscript). Pace et al. (1979) obtained similar results in snail enclosures on a natural mudflat and demonstrated that the reduction in pigments was not due to mechanical disruption of substrate by the snails, but was a result of feeding. Since I. obsoleta obtains most of its energy from microalgae (Wetzel 1977, Haines and Montague 1979), it quite probably competes for this resource with algae feeding nematodes. The decrease in algivorous nematodes was accompanied by an increase in deposit feeding

types. Nematode populations have been shown to respond positively to substrate changes caused by crustacean grazing (Brown et. al. 1978). If I. obsoleta caused increased quality or quantity of material to be available to deposit feeding nematodes, and enough nematode eggs were present in the microcosm sediments to allow a short turnover time, there could have been a real positive effect of I. obsoleta on these feeding types.

The third hypothesis is that annelids mediate the effects of mud snails on nematode populations. Acceptance of this hypothesis requires demonstration of significant impact of annelids on nematodes, and of mud snails on annelids. Both effects occurred in the microcosms. Presence of I. obsoleta caused significant reductions in populations of both polychaetes and oligochaetes. The impact of I. obsoleta on polychaetes seems to be restricted to larger individuals, since the "meiofauna plus snails" plots had polychaete densities which were not significantly different from the "meiofauna only" plots. The effect of mud snails on polychaete populations may be due to substrate disruption by snails moving over the sediment. Streblospio benedictii and Scoloplos robustus were dominant polychaetes in all replicates (making up 61 to 98% of individuals) and are tubicolous and burrowing species, respectively. Disruptive grazing by snails may prevent construction or maintenance of tubes or interfere with burrowing by the polychaetes. Grant (1965) noted such a disruptive effect of mud snails in Massachusetts, where large numbers of I. obsoleta moving onto a sand flat caused reduction in populations of tubicolous and

soft-bodied infauna. Impact of mud snails on oligochaetes is probably due to disruption rather than food competition. I. obsoleta feeds primarily on algae (Wetzel 1977) while oligochaetes consume mainly other microbes (Giere 1975).

Effects of macroinfauna on nematodes may take several forms. Seven polychaete species were found in microcosm sediments: Streblospio benedictii, Scoloplos robustus, Capitella capitata, Polydora sp., Nereis succinea, Eteone sp., and an unidentified cirratulid. These species are all classified as deposit feeders by Fauchald and Jumars (1979) and their gut contents include algae and occasionally nematodes (Sanders 1960). Thus, polychaetes may effect nematodes in three ways: 1) direct, generalized predation, 2) competition for algae, and 3) competition for available detrital carbon and microbes. All three of these mechanisms probably operate at once. Annelids caused significant reduction in proportion of algivorous nematodes, but competition for algae is not the only negative impact on the nematode community. Total numbers of nematodes were significantly lower in the plots with added macroinfauna, suggesting direct predation on nematodes by annelids.

In summary, nine hypotheses were presented in the Introduction to this thesis. These are reiterated below, and their resolution discussed in light of results presented above.

Hypothesis 1 is that I. obsoleta depresses nematode population density. This was not found to be true under any treatment of either experimental regime. Hypothesis 2 is that I. obsoleta reduces the

proportion of algae feeding nematode types in the sediment. This was found to be true in the 2X treatment of the field manipulation and under the laboratory conditions in the microcosm experiment.

Hypothesis 3 is that there is a size refuge from the effects of I. obsoleta available to larger nematodes. No such refuge was found to exist. Hypothesis 4 proposes a depth refuge from the effects of mud snails. Again, population densities of nematodes were unaffected at any depth in the sediment column. However, below the top 0.25 cm of substrate, algivorous nematodes comprised a lower proportion of the population, and feeding type distribution was unchanged at depth.

Hypothesis 5 is that I. obsoleta depresses concentration of chlorophyll a in the sediment. This was found to be true for the 2X treatment in the field manipulation. Hypothesis 6 proposes an impact of mud snails on sediment water content. Results of this analysis are ambiguous at best, but suggest that any possible impacts of mud snails may be overshadowed by other factors or lack of experimental resolution.

Hypothesis 7 is that I. obsoleta is a predator of nematodes. As predicted from results of hypothesis 1 above, this was found not to be the case. Hypothesis 8 proposes food competition between nematodes and mud snails. This seems to occur, and in a manner suggesting that microbial algae are the resource of competition. The final hypothesis proposes mediation of the impacts of mud snails on nematode populations by benthic annelids. This was found to be true, in that annelid populations respond to the presence of I. obsoleta and also effect nematode populations in a variety of ways.

CONCLUSION

Presence of the disruptive grazing snail Ilyanassa obsoleta on mudflat sediments has significant interactive impacts on meiofauna and macroinfauna community structure. In late summer, anoxia of sediments at depth truncates biotic interactions into the top layer of substrate. In this environment, the mud snail is a superior competitor for algal food resources, but may provide enhanced quality or quantity of food to deposit feeders. In this way, presence of I. obsoleta shifts trophic structure in the mudflat nematode community, reducing dominance by algivores. In future studies incorporating nematode trophic dynamics, the nematode community should be considered in two trophic categories: algae feeders and deposit feeders. Nematodes in each of these classes feed on different forms of primary input and respond to different environmental control processes.

Mudflat annelid populations respond primarily to sediment disruption by I. obsoleta, and populations of polychaetes and oligochaetes are reduced in the presence of mud snails. As a result, I. obsoleta provides the nematode community with some release from predation and competition pressure from annelids.

In mudflat sediments, the nematode community responds to both primary (predation) and secondary (environmental release, food competition) interactions. Multiple levels of interactive coupling should be considered in any systems level investigation in this habitat.

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