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Recolonization of meiobenthos in oiled azoic subtidal muddy sands of the York River estuary, Virginia

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RECOLONIZATION OF MEIOBENTHOS IN OILED AZOIC SUBTIDAL

MUDDY SANDS OF THE YORK RIVER ESTUARY, VIRGINIA

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

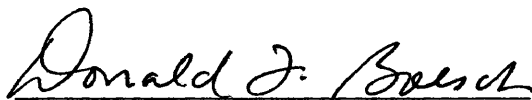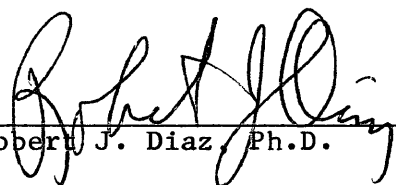---

by

Daniel M. Alongi

1981

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

the requirements for the degree of

Master of Arts
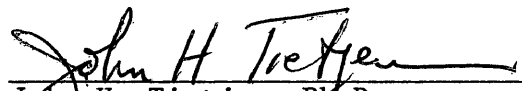

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ii

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ABSTRACT

In situ manipulative experiments were conducted over a three-month period (May - August 1980) to examine the recolonizing capabilities of meiobenthos on a shallow subtidal site in the lower York River, Virginia. Three concentrations of Prudhoe Bay crude oil were added to azoic muddy sands (100, 2500 and 10000 mg oil/kg dry wt sediment). Untreated azoic sediments served as controls.

The meiofauna initially attained densities equivalent to the natural community in the upper oxidized layer in all treatments within a one-week period but fluctuated greatly during the remainder of the sampling period. The rate of colonization was considerably slower in the anoxic layer of sediments. Nematodes did not significantly recover in the mid- and high-oil treatments. Due to the small scale of these disturbances no significant 'edge effect' was evident during the colonization process. Analysis of nematode community composition by reciprocal averaging ordination and nodal analysis revealed generally lower abundances but no distinct differences in species composition in the oiled substrates as compared to untreated and natural community controls. The colonizing nematode species assemblages may have fully recovered from these small-scale perturbations in 90 days. The elucidation of a complete return to ambient conditions may be a subtle process unelicitable by simple enumeration of phyla and/or application of univariate statistics.

Contrary to prior meiobenthic recolonization studies, a successional sequence was found for the nematodes colonizing the experimental trays. The sequence most closely approximated McCall's (1975) model of macrobenthic colonization of azoic substrates. The colonization pattern of Sabatieria pulchra presented an interesting ecological problem. This species, frequently dominant in polluted sediments, colonized as a K-selected, equilibrium species. Such a result lends credence to the hypothesis that nematodes dominating polluted habitats may not necessarily be opportunistic but eurytolerant, efficient species with good competitive qualities.

The ecological concepts of r and K selection may not be applicable to the life histories and attributes of small metazoa (≤ 1 mm) since these dogma were formulated on the basis of the ecology of predominantly larger organisms. The meiobenthos at this study area are stable assemblages responding quickly to stress in apparent concordance with the Boesch and Rosenberg (1981) stress tolerance model of estuarine benthos.

RECOLONIZATION OF MEIOBENTHOS IN OILED AZOIC SUBTIDAL

MUDDY SANDS OF THE YORK RIVER ESTUARY, VIRGINIA

INTRODUCTION

Disturbance, defined here as a perturbation causing significant
mortality of individuals, plays a substantial role in the structuring
of terrestrial and aquatic communities. The consequences of natural
and artificially induced perturbations have been studied over a wide
range of ecosystems (Peckarsky 1980, Shaw and Minshall 1980, streams;
Henebry and Cairns 1980, Christian et al. 1978, microbial communities;
Dix and Swan 1971, temperate forests; Platt 1975, Denslow 1980,
prairies; Deutsch 1980, rivers).

Disturbance phenomena have been extensively examined in marine
benthic systems with particular emphasis on macrobenthic communities
(Reish 1961, Dean and Haskin 1964, Dayton 1971, Rosenberg 1972, 1973,
1976, Duncan 1974, Dauer and Simon 1976; Boesch et al. 1976, Simon and
Dauer 1977, Rhoads et al. 1977, Pearson and Rosenberg 1978, Dean and
Hurd 1980, Santos 1979, Paine and Levin 1981). Several workers have
performed in situ experiments utilizing azoic substrates to study the
colonization and subsequent successional stages of macrobenthos (McCall
1975, Desbruyeres et al. 1980, Goren 1980, Fredette 1980, Schaffner
et al. 1981). These studies have been carried out in a wide variety
of habitats and conditions to permit a general conceptualization of
macrobenthic successional dynamics.

Immediately following disturbance, species possessing certain life
history characteristics (high fecundity, short life span, and high

dispersability) amenable to the exploitation of continually perturbed environments are found. These pioneering species are generally suspension-feeding or surface-deposit feeding organisms, which in turn are replaced by long-lived, equilibrium species capable of inhabiting the deeper anoxic sediments. Boesch (1979) noted that the rate of benthic recovery is also dependent upon the scale of disturbance and the persistence of those factors capable of maintaining it.

Conversely, the few studies which have examined response of meiobenthos to disturbance (Boaden 1962, Scheibel 1974, Conrad 1976, Rhoads et al. 1977, Sherman and Coull 1980, Thistle 1980, Desbruyeres et al. 1980, Alongi and Boesch 1981), were conducted under a narrow suite of environmental conditions and types of disturbance, rendering any similar generalization for meiobenthic community recovery problematic. The sparse data available suggest a rapid colonization sequence (less than one month for return to ambient conditions) for meiobenthic organisms. Their rapid dispersal capability has recently been ascribed primarily to transport via resuspended sediment in conjunction with active migration and habitat selection (Gerlach 1977, Sherman and Coull 1980, Thistle 1980).

Before the onset of such studies, however, the meiobenthos was hypothesized as being slow, rather inefficient colonizers due to the general absence of a pelagic dispersal stage (Coull and Bell 1980). This problem may be negated by their generally small size, rapid maturation and consequently high intrinsic rate of population increase.

The rate of recovery of meiobenthos following defaunation is probably dependent upon the spatial extent of the disturbance as well as the strength and duration of physical forces (e.g. tidal and wind currents and waves) capable of resuspending sediments.

With the above caveat in mind, one can envision a faster response of meiobenthos in regions where a prevalence of physical forces can permit mass migration of meiofauna via resuspended sediments and secondarily, by active migration. Conversely, the meiofauna might take longer to recover from defaunation in relatively quiescent areas where the frequency of sediment turbation is considerably less, thus hindering passive transport of meiofauna--the primary means by which meiobenthic organisms disperse. Since most meiobenthic taxa do not have pelagic larvae, the rate of meiofaunal recovery would be considerably reduced if active migration was the sole mode of transport, especially in a large scale disturbance.

Similarly, many macrobenthic species without planktonic dispersal phase (i.e. larvae), such as peracaridan crustaceans, have been found to be slow recolonizers. For example, Boesch (1979) discovered that the peracaridan crustaceans had not significantly recolonized one and one-half years following their elimination when anoxic conditions developed over a broad area of the inner and central shelf off New Jersey during the summer of 1976.

Regardless of the balance between passive and active migration, search for a successional pattern of meiofauna has been hampered in previous studies by lack of adequate species identifications of various taxa. The studies of Sherman and Coull (1980) and Thistle (1980)

stress the importance of thorough taxonomic analysis, although rapid
colonization precluded a successional sequence ranging from early
colonizing opportunists to later colonizing, equilibrium species.
The concept of differential opportunism among meiobenthos is
presently not supported by evidence of sequence of colonization,
and is hindered by a severe lack of knowledge concerning the
population dynamics and life histories of individual species.
However, the evidence is still fragmentary enough in terms of
the diversity of habitats and types of disturbance studied to
allow for the possibility of its occurrence and subsequent
description based on our classic concepts of colonization and
succession (Odum 1969) and alternative models which have been
formulated (McCall 1975, Connell and Slatyer 1977).

The response of benthos to chronic disturbance caused by pollutants
has been extensively reviewed by Pearson and Rosenberg (1978) in which
they note that a consistent pattern of faunal change has been evidenced
in those studies examining the effects of organic enrichment on
macrobenthic communities. The authors have defined such patterns
of faunal change as consisting of three successional phases. The
first phase, called the 'peak of opportunists' or PO, is characterized
by high abundances of pollutant-tolerant, opportunistic species.
The second phase is a point along a temporal or spatial pollution
gradient in which total abundance, species richness and biomass are
low, but evenness diversity is high. Following this ecotone point,
a transition zone characterized by unstable communities is reached.
The instability is due to the dependence of such communities on the

availability of recruits from the water column. Such a successional

pathway questions the classic concepts of succession (Odum 1969) which

suggest that early colonists are exclusively capable of, and must,

alter a newly available habitat before further colonization can occur.

What possible recruitment sequence can be hypothesized for

nematodes in polluted sediments? Does nematode colonization of

impacted areas follow any of the succession theories provided by

McCall (1975), Connell and Slatyer (1977) or Pearson and Rosenberg

(1978)? Species capable of initially colonizing a perturbed

environment probably have evolved a high degree of tolerance

to the rigors of both physical and biotic factors which limit or

eliminate the occurrence of most species available for recolonization

(Connell 1975). One can easily conceive of one or more meiobenthic

species providing flexible enough in their levels of tolerance to

inhabit and dominate portions of a habitat unsuitable for others.

The sensitivity of whole meiofaunal groups to hydrocarbons seems

to vary greatly depending upon oil type and/or a wide variety of

abiotic conditions. For example, Wormald (1976) observed a

reoccurrence of meiobenthos one month after a diesel oil spill at

Hong Kong. Boucher (1980) reported a general decrease in nematode

abundance in intertidal sands 7 months after the Amoco Cadiz oil spill.

However, no changes were detected in nematode and copepod abundance in

sublittoral sands adjacent to the spill. Other studies indicate

equivalent insensitivity of meiofauna to petroleum (Rutzler and

Sterrer 1970, Sanders et al. 1972, Green et al. 1974, Barrett and

Kontogiannis 1975, Feder et al. 1976, Dalla Venezia and Fossato 1977,

Naidu et al. 1978, Elmgren et al. 1979, 1980). Giere (1979) and

Boucher (1980, 1981) maintain that the effects of petroleum

hydrocarbons may be seen in the total community but understood only

at the level of species. With the exception of the works by Giere

(1979), Boucher (1980, 1981), Sherman and Coull (1980) and Thistle

(1980), no other studies of effects of oil and/or recolonization

have identified even one meiobenthic taxon to species level. In

addition, no studies have employed daily sampling to examine the

initial colonization and subsequent recruitment of meiofauna in

sediments disturbed by oil. Knowledge of colonization by meiobenthos

in areas of oil pollution and other types of disturbance remain

largely unknown and contradictory.

As an attempt to clarify meiobenthic colonization patterns an in

situ manipulative study was performed with the following objectives:

1. Assess the colonization of meiobenthos following

catastrophic disturbance (defaunation) in an shallow subtidal

estuarine habitat,

2. Determine the effects of petroleum hydrocarbon

contamination on the rate of colonization and recovery by

meiobenthos,

3. Examine the response of meiobenthos to disturbance

in terms of community stability and successional models presently

available, and

4. Construct a mechanistic model of nematode recruitment

in both uncontaminated and oil polluted sediment if present

ecological models are untenable.

METHODS

Experimental Design

The study site was located in a shallow ($\sim$ 1 m deep) subtidal zone of the lower York River estuary (Fig. 1) off Gloucester Point, Virginia 37°15'N, 76°30'W). The site has a tidal range of 0.7 meters and an annual salinity of 15 to 25 °/oo (Haas 1977). Sediments at the study site consist of well-sorted muddy sands (2-8% silt and clay).

Sediments for the experiment were collected by shovel during mid-May 1980 near the study area. The sediments were placed into 24 polyethylene trays (Rubbermaid Incorporated, Wooster, Ohio) measuring 29.4 x 34.3 x 13.3 cm deep, and stored outside to dry for a period of two weeks. The substrate was examined after this period to ensure extermination of the macro- and meiobenthic fauna. The trays have an exposed surface area of 0.1 m^2 and were punctured on all sides to facilitate fluid exchange between tray sediments and the natural substrate.

The 24 containers were divided into four sets of six replicates. Sediment from one set of six replicates served as untreated controls and was hand-mixed for one hour in a pre-cleaned, acetone rinsed metal trough to ensure homogeneity. Control trays were filled to the brim with the mixed sediment, covered with aluminum foil, and placed in a storage bin. Sediments from each of the remaining three sets were mixed with three different oil concentrations (100, 2500, and 10000

Figure 1. Location map showing lower York River sampling site.

ATLANTIC OCEAN

CHESAPEAKE BAY

YORK RIVER STUDY SITE

YORK RIVER

JAMES RIVER

38° 00'

37° 00'

76° 00'

77° 00'

38° 00'

37° 00'

76° 00'

77° 00'

MILES
0   5   10   15   20   25
KILOMETERS
0   10   20   30   40
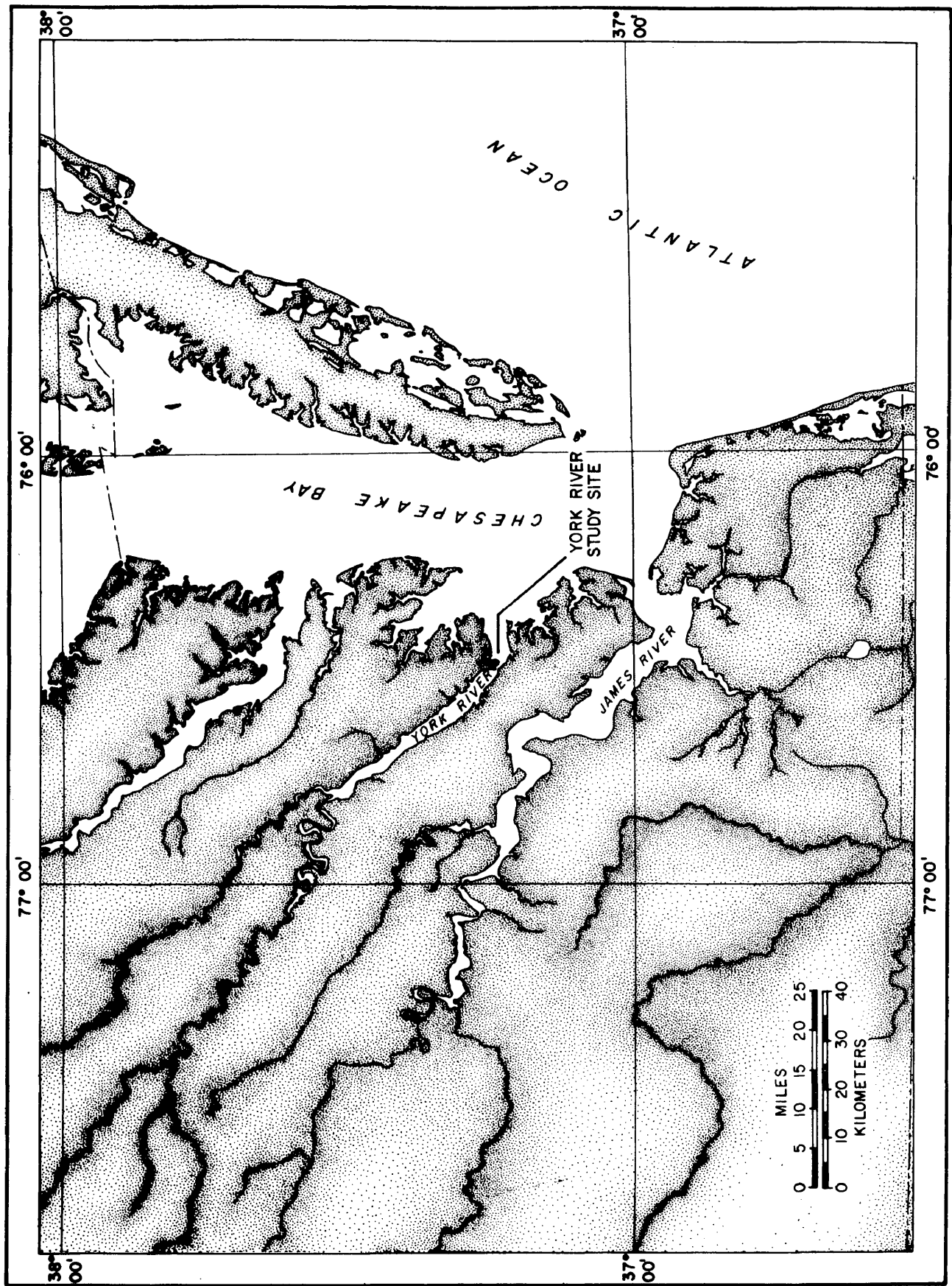
mg oil/kg dry wt. sediment). Different concentrations were used in order to adequately assess the potential effects of oil contamination on the recolonization process and represent a range of concentrations found in contaminated estuarine areas. The oil chosen for use in these in situ experiments was Prudhoe Bay crude, a relatively light weight oil from the North Slope of Alaska. The oil was supplied to the Department of Ecology-Pollution, VIMS, by the Battelle Pacific Northwest Laboratories, Richland, WA, and has been well characterized by both institutions (Riley et al. 1980, Smith 1981).

Sediments mixed with oil for each concentration were processed separately in the same acetone-washed trough, and hand-mixed briefly ($\sim$ 10 minutes) before oil addition for an even dispersion in the container. The appropriate amount of Prudhoe Bay crude was dissolved in 500 ml of heptane and added to the sediment in the trough (Table 1). The oil-contaminated sediments were hand-mixed for two hours per treatment, transferred to the trays, covered with aluminum foil, and placed in a storage bin. The 24 containers were labeled C1-6, LO1-6, MO1-6 and HO1-6 to indicate the treatment (C=Control, LO=low oil, MO=mid-oil, HO=high oil) and replicate (1-6).

The trays were placed into the substrate in the study area at low tide within 18 hours of oil addition to minimize further loss or alteration of hydrocarbons in the tray sediments. The containers were arranged in a 4 x 6 row matrix at least 0.3 m apart, covering an area of 25 m^2. Treatments were randomized within the matrix in order to decrease the effect of small-scale heterogeneity of biotic and abiotic variables on the different treatment types. Once all the

Table 1. Amounts of Prudhoe Bay crude oil and sediments used
          in recolonization experiment.

I. 100 mg oil/kg dry wt. sediment (0.113 ml/kg)*

Tray	Sediment Weight (kg)	Total Volume of Oil added (ml)
LO-1	12.0	1.4
LO-2	13.1	1.5
LO-3	12.5	1.4
LO-4	12.6	1.4
LO-5	12.2	1.4
LO-6	12.4	1.4

II. 2500 mg. oil/kg dry wt. sediment (2.83 ml/kg)*

MO-1	12.0	34.9
MO-2	12.6	35.6
MO-3	12.2	34.5
MO-4	13.1	37.0
MO-5	12.4	35.1
MO-6	12.6	35.6

III. 10,000 mg oil/kg dry wt. sediment (11.3 ml/kg)*

HO-1	12.6	142.5
HO-2	13.2	149.3
HO-3	12.0	135.7
HO-4	12.6	142.5
HO-5	12.9	145.9
HO-6	11.6	131.2

* based on oil density of 0.844 g/ml.

trays were in place, the aluminum foil covers were removed.

Since previous studies have shown the recovery of meiobenthos to be relatively rapid (Sherman and Coull 1980), samples for meiofauna were taken daily the first two weeks (Days 1-14), then approximately every other day for the next two weeks (Days 16, 18, 20, 22, 25, 26, 28, 31, 33), fortnightly during the second month (Days 47 and 61) and at Day 90 to comprise a sampling period of three months (May-August 1980).

A sequential sampling scheme was employed in which a different set of replicate trays sampled for meiofauna each sampling date. For example on Day 1, trays designated replicate-1 were sampled; on Day 2, replicates designated "2", etc., until on Day 6 the sampling sequence repeated with trays labeled replicate-1. All trays labeled as the fifth replicates were utilized only for hydrocarbon, sediment, and total organic carbon samples.

Two cores were taken from each treatment and from natural substrate at low tide with as little disturbance as possible. All meiofauna samples were taken (to a depth of 5 cm) with a hand-held plexiglass corer (2.54 cm inner diameter). The two cores from each treatment were taken from the approximate center and edge of each tray to test for a possible 'edge effect' during the recolonization process. All cores were fractionated at the redox potential discontinuity (RPD) into an upper oxidized portion of approximately 2 cm, and a lower 3 cm portion of anoxic sediment to test for possible differences in the rate of concentration between these layers. In the laboratory, all meiofauna samples were agitated

with an isotonic solution of magnesium chloride and the supernatant

decanted through 0.5 mm and 0.045 mm sieves. This process was

repeated three times for each sample. The contents of the 0.045 mm

sieve were preserved in 5-8% buffered formalin and stained with

Rose Bengal to facilitate sorting. The meiofauna was enumerated

under a dissecting microscope and identified to major taxa. Nematodes

were identified to species when possible.

Sediment Analysis

Samples for sediment and organic carbon analysis were taken on

Days 0, 1, 14, 20, 33, 47, 61, and 90. Sand, silt and clay composition

percentages were determined by sieve and pipette analysis by the

procedure described in Folk (1974).

Total organic carbon content, as total volatile solids, was

determined by the methods outlined in Standard Methods for the

Examination of Water and Wastewater (1975).

Hydrocarbon Analysis

Sediment samples for hydrocarbon analysis were taken immediately

prior to deployment and at weekly intervals through the study period

from the experimental treatments and control site. Due to limited

time and funds, only samples from Days 0, 28 and 90 were analyzed

for aliphatic and aromatic hydrocarbons separately. Sediment samples

from Days 28 and 90 were subdivided into two portions at the RPD.

All organic solvents used in the analysis were glass-distilled

and purity graded for gas chromatographic use (Burdick and Jackson,

Inc., Muskegan, MI and Fisher Scientific Co., Springfield, NJ.

Periodic gas chromatographic monitoring of the solvents was made to confirm purity. All glassware and utensils were detergent washed, rinsed in distilled water and acetone, and oven-dried (200°C for two hours) before use.

Core samples taken for hydrocarbons from the treatments were extruded into new, hexane-washed plexiglass core tubes and frozen at -15°C until analyzed. After thawing, 20 gram portions of each sample were placed in sterile glass dishes, covered with aluminum foil, and oven-dried at 50°C for 12 hours. The dried sediment was mixed, Sohlext-extracted for 16 hours with hexanes, and reduced in volume on a rotary evaporator with final stages of evaporation effected by a stream of dry nitrogen. Extracts from the study site control, untreated azoic control, and low-oil samples were adjusted to 1 ml, the mid-oil samples adjusted to 10 ml, and the high-oil samples adjusted to 40 ml by the addition of hexanes.

Column chromatography on silica gel was employed to separate the aliphatic and aromatic fractions. A 1 ml aliquot of the concentrated extract was placed on a 1 x 20 cm column of silica gel (activated at 240°C for 14 hours) topped with a 1.5 cm layer of activated copper powder and a 0.5 cm layer of pre-cleaned sterile sand. Elutions with 40 ml of hexanes yielded an aliphatic fraction. The aromatic fraction was eluted with 40 ml of 80/20 (v/v) hexane/methylene chloride. Both fractions were concentrated under a stream of dry nitrogen to a volume of 1 ml and 0.2 ml for the aliphatic and aromatic portions, respectively.

The fractions were analyzed for hydrocarbon constituents by capillary column gas chromatography. A Varian 2740 chromatograph fitted with a flame ionization detector, Grob-type injection port, and a 0.3 mm x 20 m glass capillary column coated with SE-52 was used to obtain gas chromatograms. Samples of 1.4 µl were injected with a toluene solvent plug using a hot-needle splitless injection technique (Grob and Grob 1969). The column temperature was programmed from 70-280°C at 6°C/min., and held at 280°C until all hydrocarbon components characteristic of Prudhoe Bay crude oil were eluted. A Hewlett-Packard 3354B laboratory data system provided a tabulation of peak integration and retention time for each chromatogram. Known standard mixtures of n-alkanes (C11-C32) and aromatic hydrocarbons (naphthalene, biphenyl, hexamethylbenzene, phenanthrene, pyrene, chrysene, perylene and benzo(g,h,i)perylene) chromatographed under identical conditions on the same day as the sample were used for identification and quantification of the hydrocarbon peaks in the same chromatograms. Peaks in the aliphatic fractions were mostly n-alkanes, and were easily recognizable by retention time and peak pattern. Aromatic fraction peaks were identified by retention time and pattern of abundance characterized by the Department of Chemical Oceanography, VIMS, and Battelle Pacific Northwest Laboratories, Richland, WA. Most aromatic constituents were identified to the level of unresolved envelope groups. This was considered adequate for the purposes of this study.

Amounts of oil in the extracted sediments were calculated by dividing the sum of the measured concentrations of the C11-C32

n-alkanes in the sediment by the measured concentration of these
compounds in fresh Prudhoe Bay crude oil. Percent loss of the
selected aromatic hydrocarbons were estimated by comparison of
the measured concentrations in the sediments and the amounts which
were present in the amount of fresh Prudhoe Bay crude oil originally
added to the sediment.

Data Analysis

Because the total number of samples collected was too large for
practical computation involved in numerical classification and
ordination, it was necessary to reduce the sample set by combining
top and bottom portions of all cores as well as the edge and center
samples within each of the treatments. A 2 x 2 contingency table
revealed no significant differences ($\alpha > 0.05$) between core layers
and edge and center replicates for each treatment. This reduced
the data set to 130 samples differentiated on the basis of sample
date and treatment type. The number of nematode species was reduced
by eliminating those species with densities $\leq$ 5 individuals$\cdot$10 cm^{-2}
in the study site control.

Classification of the samples and nematode species were performed
using the VIMS program COMPAH on square root transformed data
utilizing the Bray-Curtis similarity measure (Bray and Curtis 1957)
with group-average (inverse) and flexible sorting (normal) (Clifford
and Stephenson 1975, Boesch 1977). The Bray-Curtis similarity
measure can be expressed as:

$$S_{jk} = 1 - \frac{\sum_i |X_{ji} - X_{ki}|}{\sum_i (X_{ji} + X_{ki})}$$

where S_{jk} is the similarity between entities j and k; X_{ji} is the abundance of the ith attribute for entity j; and X_{ki} the abundance of the ith attribute for entity k. The cluster intensity coefficient was set at -0.25 in flexible sorting.

A cross-relation between normal and inverse classifications, termed nodal analysis and expressed in nodal diagrams (Boesch 1977), was performed in order to describe the collection groups on the basis of their characteristic species and the species described in terms of their patterns of occurrence over the sample groups. These comparisons of coincidence are expressed in terms of constancy, fidelity and abundance concentration for each species.

Constancy, the degree to which a species is consistently found in a habitat, was expressed as:

$$C_{ij} = a_{ij}/nj$$

where a_{ij} is the actual number of occurrences of the ith species in the sample group j and the n_j is the number of samples in the group. When a species occurs in all samples in a group the index will take a value of 1 and 0 when the species does not occur in a collection.

Fidelity, the degree to which a species selects or is relegated to a habitat, was computed as

$$F_{ij} = (a_{ij}\sum_j n_j)/(n_j\sum_j a_{ij})$$

using the same terms as in the constancy index. This is 1 when a species constancy in a sample group is equivalent to its overall constancy, greater than 1 when its constancy in a particular sample group is greater than its overall constancy, and less than 1 when its constancy is less than its overall constancy. A chi-square test was applied to test the significance of the deviation of the number of occurrences of a species from that expected within a sample group assuming even distribution.

Since constancy and fidelity are qualitative indices and imply nothing about patterns of abundance, abundance concentration was measured for each species in each sample group by dividing the mean abundance of the species in the sample group by its overall mean abundance.

Reciprocal averaging ordination (Hill 1973) was employed for the nematodes on reduced sets of square root transformed data. This technique, also known as correspondence analysis (Chardy, Glemarec and Laurec 1976), has proved to be efficacious in ecological interpretations (Fasham 1977, Gauch et al. 1977), in that it projects sample groups (normal analysis) and species (inverse analysis) in the same ordination space. The ordination computations of extraction of eigenvectors and determination of sample and species scores on successive axes of variation were executed using the program ORDIFLEX of the Cornell Ecology Program Series (Gauch 1977). For the normal analysis, the sample set was further reduced in order to clarify the progression of nematode colonization in each treatment over the sampling period. The day 1 and day 90 samples were plotted

individually. The other 24 sampling dates per treatment were plotted as 8 scores with each score representing an average of three sampling dates.

Species diversity was measured by the Shannon information function (H') (Pielou 1975). Evenness (J') was calculated after Pielou (1975) and species richness was estimated by SR = S-1/ln N, where S is the number of species and N the number of individuals in a sample (Margalef 1958). These indices were compared with abiotic variables (percent total organic carbon, total hydrocarbon concentration, etc.) by Kendall's coefficient of rank correlation ($_\tau$).

RESULTS

Sediment Texture and Organic Carbon

Sediments in all experimental treatments changed little over the sampling period. Differences fell within the range of variability of the study site controls (Figs. 2-6). A one-way ANOVA performed to compare sediment parameters (arc sine transformed percent sand, silt, and clay) between the experimental treatments and study site control, revealed a significant difference ($p < 0.05$) only in percent sand between the mid-oil and control sediments.

Percent total organic carbon exhibited minor variability within and among the experimental treatments and controls over the 90 days of exposure, generally falling within a range of 0.1-0.8 percent (Fig. 7). Only the Day 1 sample from the tray control exhibited a higher composition of organic carbon than the 0.1-0.8 percent range found for the other treatment samples. No significant differences ($p > 0.05$) exist for percent total organic carbon between and among experimental treatments and controls. Although the presence of oil generally leads to a concomitant increase in organic carbon concentration, no significant correlation ($p > 0.05$) was established between total organic carbon and total oil concentration in any of the sediments treated with crude oil.

Hydrocarbon Analysis

Changes in the concentration and percent loss of Prudhoe Bay

20

Figure 2. Changes in sediment parameters in study site control.

Numbers denote sampling dates.
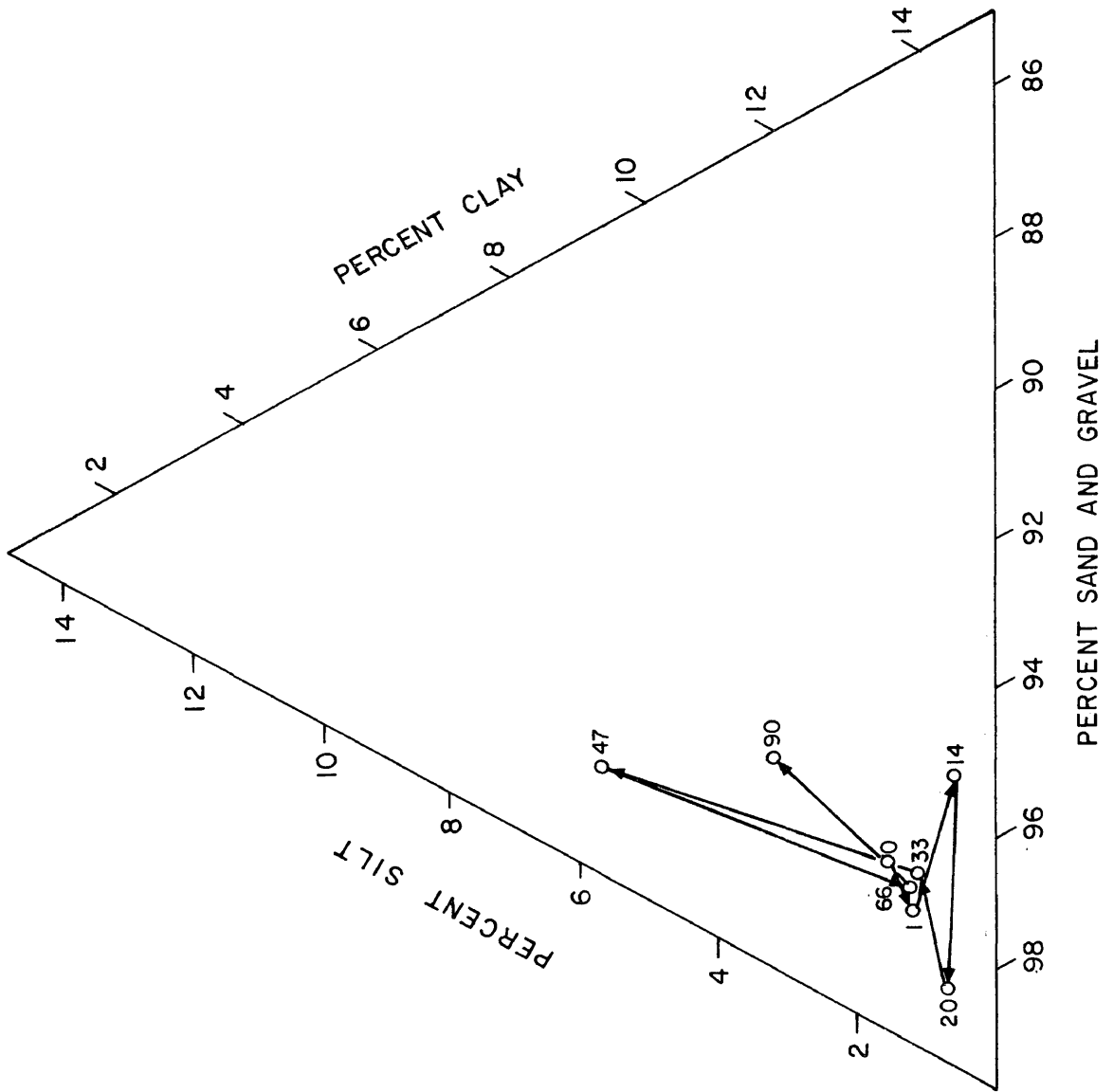
Figure 3. Changes in sediment parameters in tray control. Numbers

denote sampling dates.

PERCENT CLAY

14

12

10

8

6

4

2

14

12

10

8

6

4

2

86

88

90

92

94

96

98

PERCENT SILT

PERCENT SAND AND GRAVEL

47

90

1

20

14

33

61
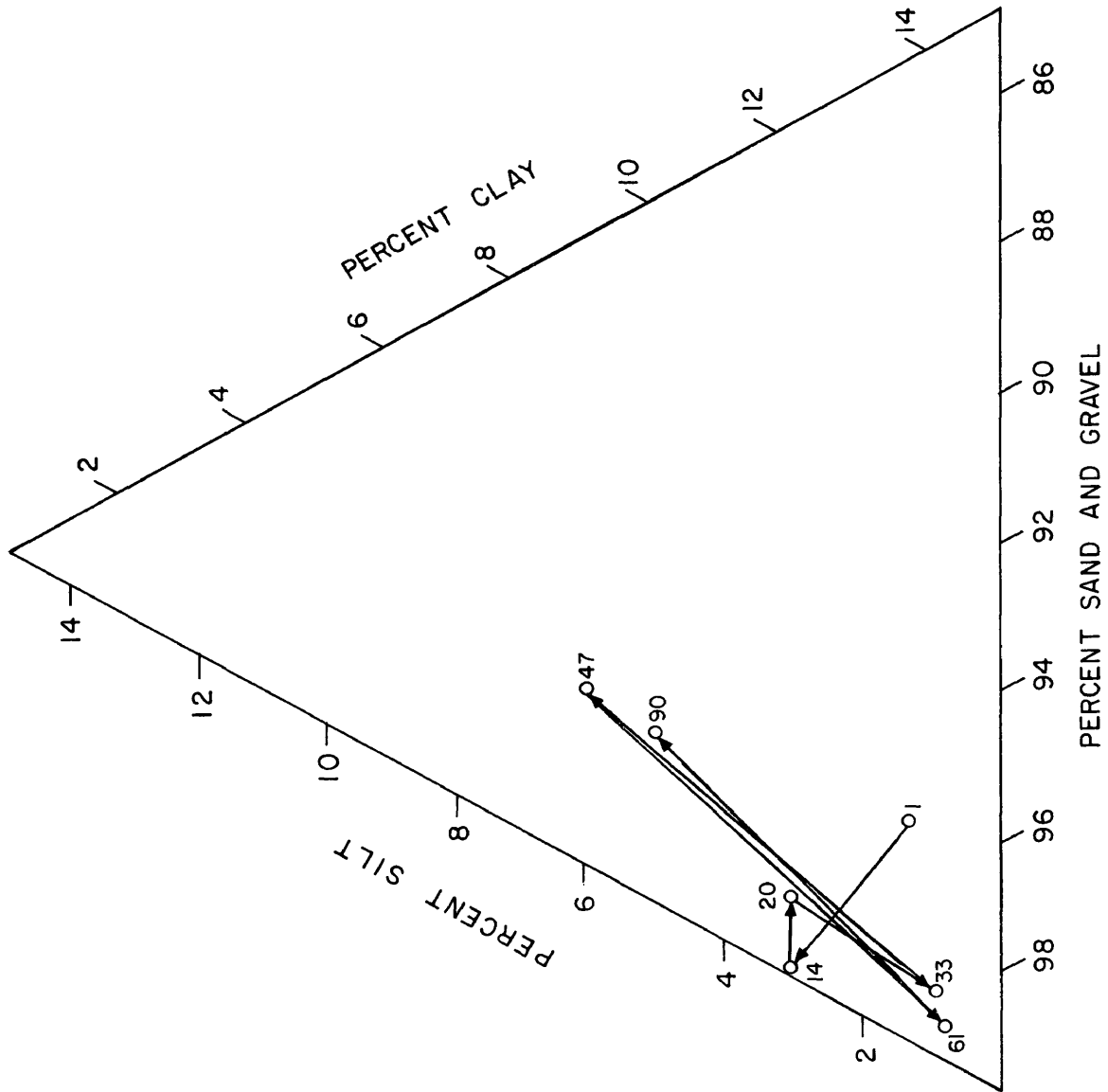
Figure 4. Changes in sediment parameters in low oil treatment.

Numbers denote sampling dates.

PERCENT CLAY

PERCENT SAND AND GRAVEL

PERCENT SILT

61

90 47

14

33

20

10

23
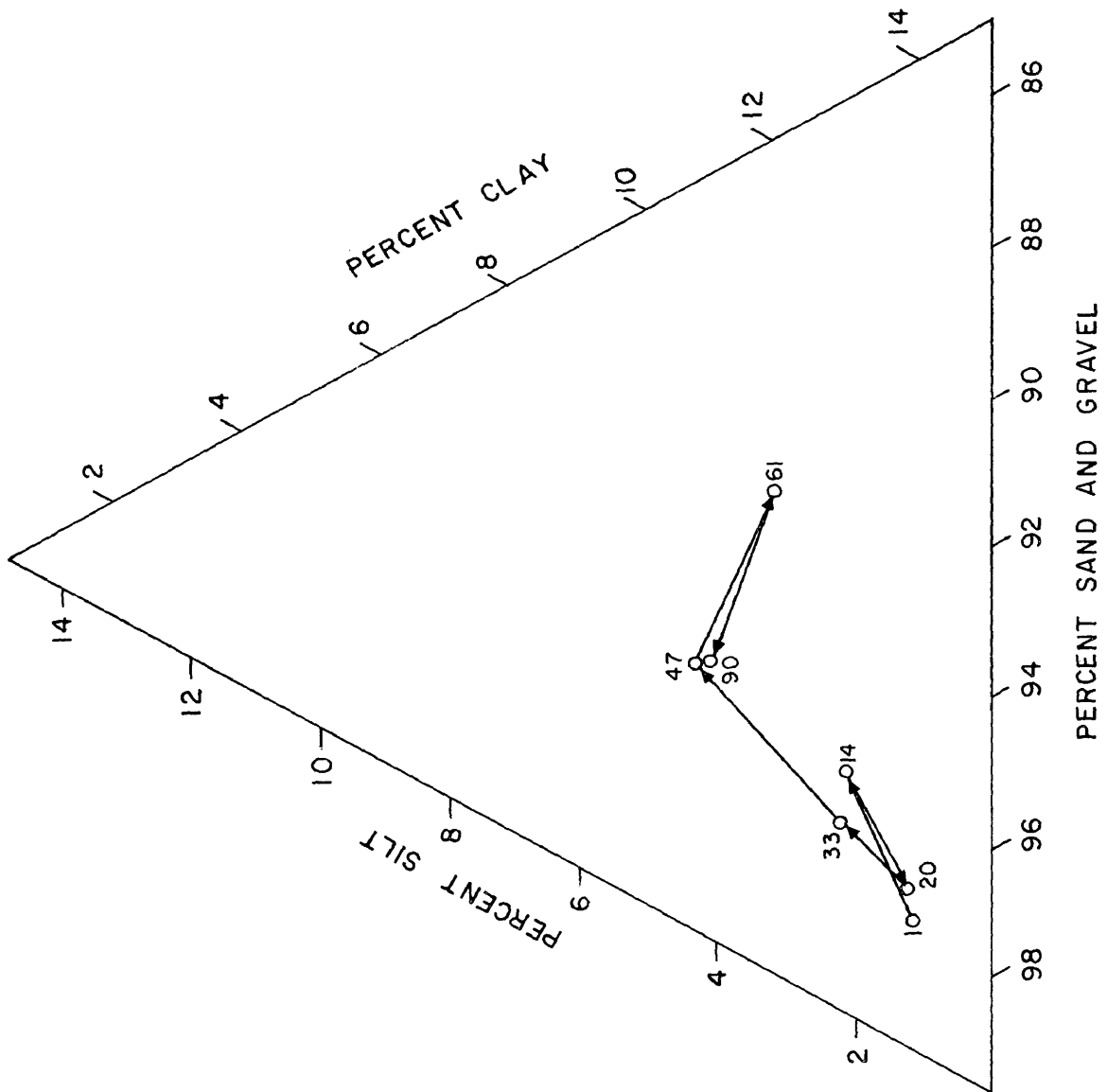
Figure 5. Change in sediment parameters in mid oil treatment. Numbers denote sampling dates.

PERCENT CLAY

PERCENT SILT

PERCENT SAND AND GRAVEL
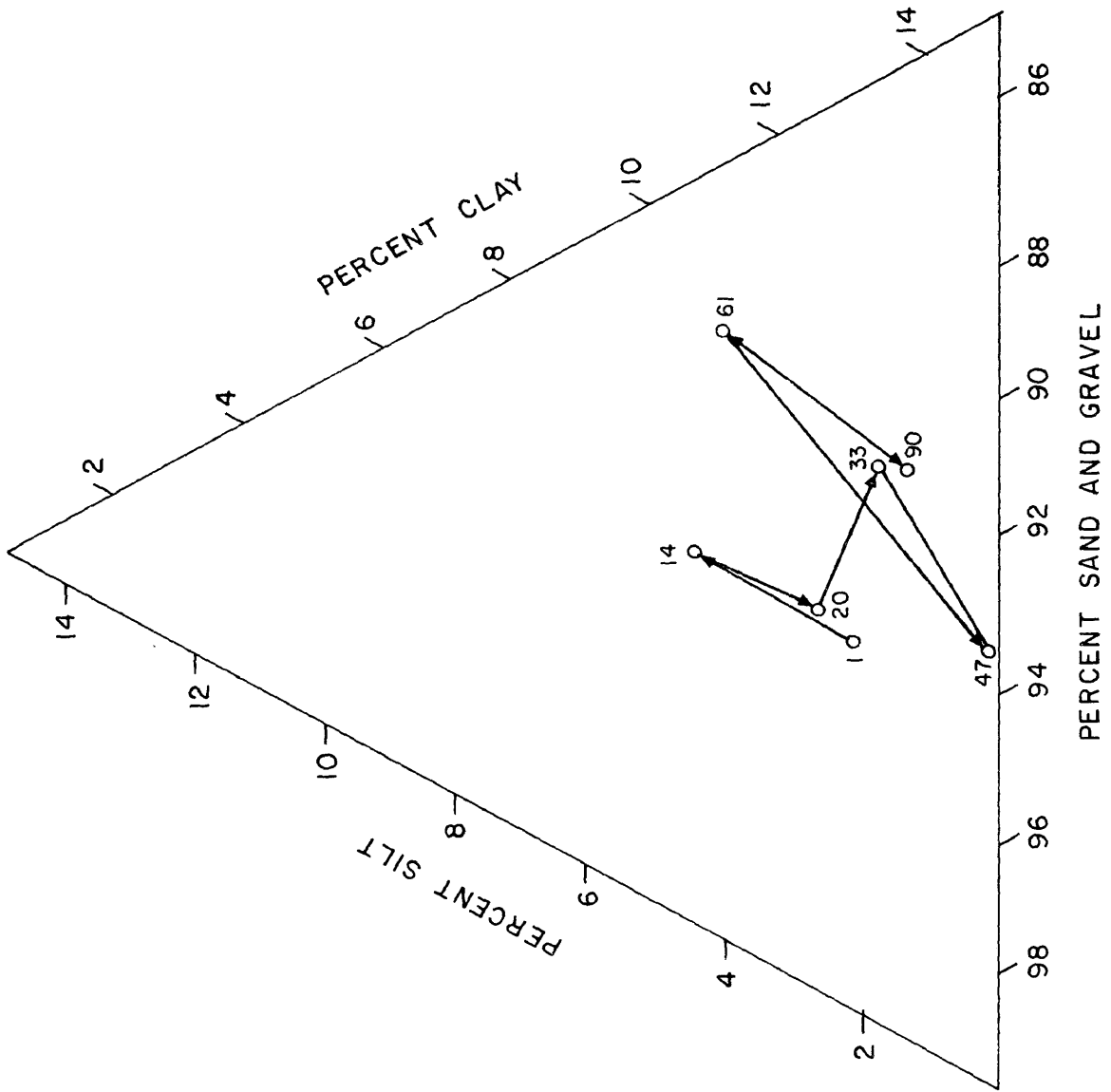
Figure 6. Changes in sediment parameters in high oil treatment. Numbers denote sampling dates.
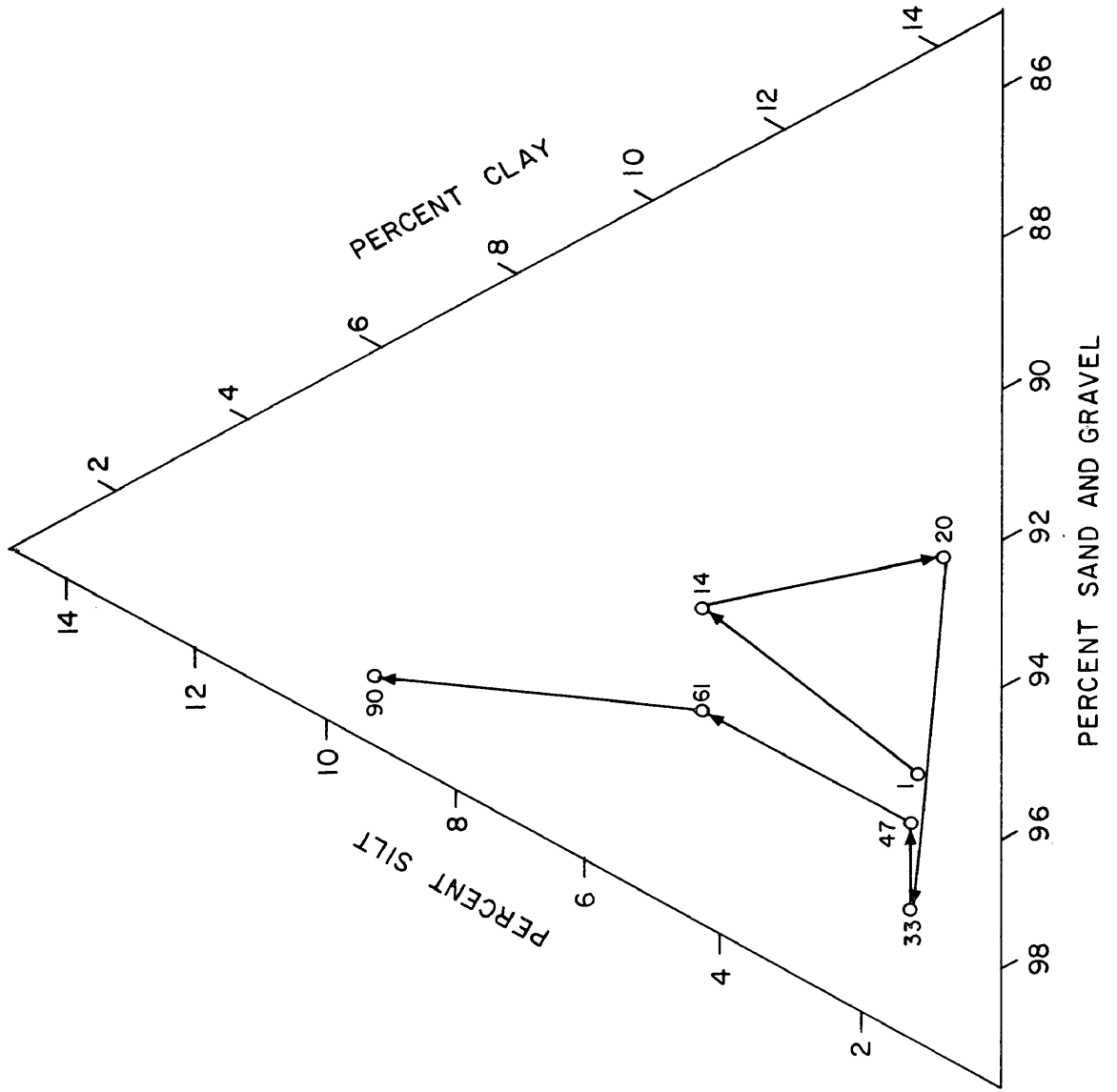
Figure 7. Changes in percent total organic carbon in experimental

treatments and study site control over the sampling period.
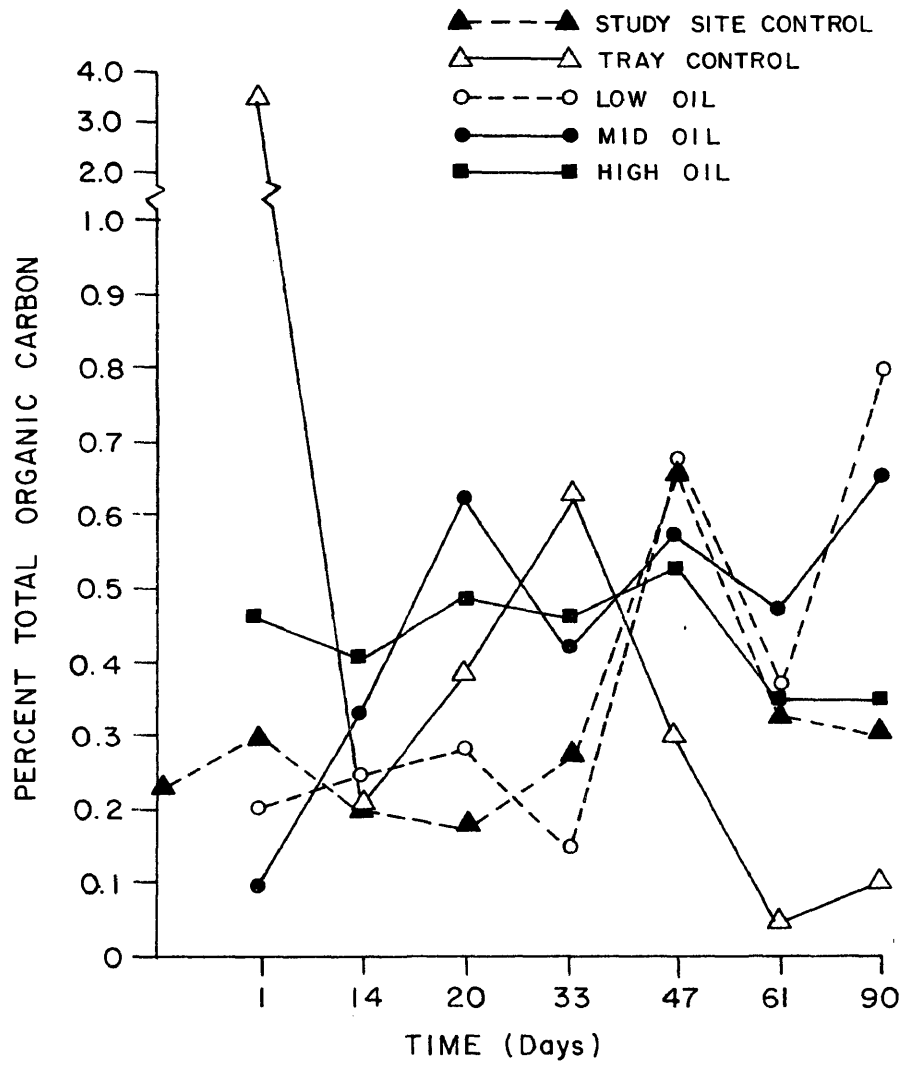
crude oil (in fresh Prudhoe Bay crude oil equivalents) from the experimental treatments are summarized in Table 2. Based on the concentrations of the $\underline{n}$ C11-$\underline{n}$ C32 paraffins, loss of total oil before tray emplacement at the study site occurred, probably due to several factors. Relatively warm temperatures prevailed during the mixing of oil and sediment, and other predeployment activities, leading to a loss of the more volatile components. An apparent loss may result from handmixing for two hours, since the mixture is not expected to be completely homogeneous. In addition, analytical procedures such as sediment drying and solvent evaporation, involve evaporative losses of the more volatile lower molecular weight paraffins ($\underline{n}$-undecane) and aromatics (naphthalenes, alkyl-benzenes) (Lake $\underline{et}$ $\underline{al}$. 1980; Smith and deFur 1980). In spite of the great inherent variability, a general trend of substantial loss is evident over the time period. After 90 days of exposure, 39%, 82-94% and 45-69% loss of total oil was incurred in the low, mid and high oil treatments, respectively.

The most rapid degradation of petroleum hydrocarbons occurs at the surficial layers since biodegradation is an aerobic process (Gardner $\underline{et}$ $\underline{al}$. 1979, Hughes and McKenzie 1975, Lee 1978, Lee $\underline{et}$ $\underline{al}$. 1979). Oil buried below the oxidized layer can remain unmodified for years (Hughes and McKenzie 1975, Gardner $\underline{et}$ $\underline{al}$. 1979). Consequently, it is of interest to note that losses of oil between the oxidized and lower sediment layer were not substantially different in any of the treatments (Table 2). In general, the loss of oil from the tray sediments appears to be a function of time

Table 2. Amount of Prudhoe Bay crude oil equivalents (mg/kg dry sediment=ppm) and percent loss (in parentheses) in experimental tray sediments. Values for tray sediments represent estimates above study site control levels.

Natural and Untreated Tray Control Samples

Day 0 Study Site Control	1.5
Day 90 Study Site Control	0.4
Day 0 Tray Control	0.9
Day 90 Tray Control	2.1

Contaminated Tray Samples

I. Low oil initial target concentration = 100

Day 0 LO	45.1(55)
Day 28 LO top	135.4
Day 90 LO top	60.4(39)
Day 28 LO bottom	61.3(39)
Day 90 LO bottom	60.8(39)

II. Mid oil initial target concentration = 2500

Day 0 MO	8093.0
Day 28 MO top	870.9(65)
Day 90 MO top	449.1(82)
Day 28 MO bottom	1701.3(32)
Day 90 MO bottom	157.4(94)

III. High oil initial target concentration = 10000

Day 0 HO	9076.5(9)
Day 28 HO top	8029.3(20)
Day 90 HO top	5473.0(45)
Day 28 HO bottom	8387.5(16)
Day 90 HO bottom	3052.5(69)

rather than oil concentration and/or sediment depth. This may be due to the fact that although most microbial activity is restricted to the surface layers, macro- and meiobenthic organisms bioturbate the sediment to as great as 15 cm depth (Rhoads 1967). This 'conveyer-belting' of deeper substrate to the surface allows the microbial fauna to degrade subsurface hydrocarbons. The rate of hydrocarbon degradation may be expected to increase as the number of animals which bioturbate increase during the recolonization process. Some polychaetes have hydrocarbon-metabolizing enzymes and others take up and metabolize various hydroxylated polycylic aromatic derivatives (Lee et al. 1977, 1979, 1980, Rossi and Anderson 1977). Thus, benthic biota other than the microbial community can enhance the degradation of subsurface petroleum hydrocarbons (Gardner et al. 1979, Gordon et al. 1978, Lee et al. 1979, 1980).

The influence of microbial degradation is detectable by changes in the ratios of n-heptodecane/pristane and n-octadecane/phytane, usually referred to as n-C17/Pr and n-C18/Ph (Blumer et al. 1973), since degradation by bacterial action leads to a higher consumption of normal alkanes than isoprenoid hydrocarbons. The n-alkane/ isoprenoid hydrocarbon ratio (Table 3) for the upper and lower portions of the core samples of each oil treatment reflect the same lack of difference in hydrocarbon degradation as in the total amounts of oil (Table 2). Table 3 shows that the n-C17/Pr and n-C 18/Ph ratios determined for samples from Days 0 and 28 for all oil treatments were not substantially less than to those in fresh Prudhoe Bay crude oil. Microbial modification of the n-alkanes is manifest

Table 3. n-alkane/isoprenoid hydrocarbon ratios for Prudhoe Bay
crude oil-contaminated experimental tray sediments.

Sample	n-C17/pristane	n-C18/phytane
Fresh Prudhoe Bay crude oil	1.7	2.2
I. Low oil concentration		
DOLO	1.1	2.4
D28LO top	1.4	2.0
D90LO top	1.3	1.3
D28LO bottom	1.7	1.2
D90LO bottom	1.1	1.1
II. Mid oil concentration		
DOMO	1.1	2.4
D28MO top	1.6	1.9
D90MO top	0.0	0.4
D28MO bottom	1.4	2.0
D90MO bottom	0.7	1.4
III. High oil concentration		
DOHO	1.7	2.2
D28HO top	1.5	2.4
D90HO top	1.7	2.3
D28HO bottom	1.7	1.9
D90HO bottom	0.9	1.2

only for samples from the final sampling date, suggesting that earlier
losses are due mainly to dissolution and other physical processes.

The aromatic fraction of the oil is represented as a group of six
peaks due to the relative lack of separability and difficulty of
identification by G.C. of aromatics (Table 4) as compared to aliphatic
compounds (Table 2). In addition, these six peaks represent a
substantial fraction of the toxic oil components and may represent
the most important with respect to the interpretation of hydrocarbon
effects on the biota.

As with the total oil concentration, the aromatics exhibit an
extreme range of variability for the reasons given above. Losses
were substantial for all aromatic groups, especially the lower
molecular weight compounds (C1 and C2-naphthalenes) in the low
and mid-oil concentrations. However, weathering of oil was equally
substantial for all compound types in the high-oil treatment, despite
the greater water solubility of the lower molecular weight aromatics
(naphthalenes) as compared to the higher molecular weight (HMW)
compounds (biphenyls, fluorenes, phenanthrenes). The percent loss
of aromatics was calculated based on the aromatic concentration in
a sample compared to the concentration of the particular aromatic
group at the initial target concentration. The samples which
apparently contain more oil than expected are again a result of
mixing inhomogeneity. Interestingly, however, most samples manifest
this apparent anomaly only in the concentrations of the HMW groups
(C2-phenanthrenes). This may tentatively be interpreted as a lessened
weathering of these compounds as compared to the more soluble LMW

Table 4. Concentrations (μg/kg dry sediment = ppb) and percent losses (in parentheses) of selected aromatic hydrocarbons from experimental tray and study site control sediments. Values for Prudhoe Bay crude oil-treated samples represent estimates above study site control levels.

Sample	C1-Naph.[1]	C2-Naph.[2]	C3-Naph.[3]	Phen.	C1-Phen.	C2-Phen.[4]
DO Study Site Control	31	31	518	32	106	93
D90 Study Site Control	40	33	476	18	12	76
DO Tray Control	21	48	380	37	253	75
D90 Tray Control	38	122	794	71	242	234
I. Low oil concentration						
DOLO	7(93)	10(95)	(100)	31(1)	254	48(11)
D28LO top	14(86)	119(35)	564	(100)	355	123
D90LO top	(100)	(100)	(100)	(100)	142	11(79)
D28LO bottom	(100)	(100)	(100)	(100)	65	
D90LO bottom	(100)	(100)	(100)	26(15)	23	40(26)
II. Mid oil concentration						
DOMO	(91)	527(88)	509(88)	360(53)	279(79)	645(55)
D28MO top	214(91)	635(86)	3201(27)	457(40)	2052	827(42)
D90MO top	81(97)	900(80)	2391(46)	633(17)	495(63)	345(76)
D28MO bottom	376(84)	2807(38)	12239	1229	5510	1569
D90MO bottom	87(96)	193(96)	2412(48)	365(52)	1807	610(57)
III. High oil concentration						
DOHO	7517(22)	32135	65615	5291	16069	9039
D28HO top	5291(45)	20025	30073	1238(59)	23248	4642(19)
D90HO top	1268(87)	2643(85)	14001(21)	698(77)	1863(65)	1484(74)
D28HO bottom	5268(45)	39466	25191	2871(6)	13705	8143(43)
D90HO bottom	5767(40)	8758(52)	41453	4873	15718	2978(48)

1 C1-Naphthalenes are the 1- and 2-methyl isomers.
2 C1-Naphthalenes include the ethyl and dimethyl-substituted naphthalenes and biphenyl.
3 C3-Naphthalenes include propyl-, methylerhyl-, trimethyl-substituted naphthalenes and methylbiphenyls and fluorene.
4 C2-Phenanthrenes include dimethyl- and ethyl-isomers.

aromatics (Cl-naphthalenes). After 90 days in situ, the range of concentrations of this more toxic fraction of the crude oil was still substantial, ranging from 65-1175 ppb, 2320-23730 ppb and 21957-94644 ppb in the low, mid and high oil concentrations, respectively.

Analysis of procedural blanks and study site and tray control sediments confirmed the presence of anthropogenic and autochthonous artifacts which interfered with the interpretation of the chromatograms. The aliphatic fraction of the control sediments exhibited minimal concentrations of the n-Cll to n-C32 paraffins, ranging from 0.9 to 2.1 ppm. The lack of odd/even predominance suggests that they are an allochthonous hydrocarbon assemblage, possibly derived from two past oil spills in this region of the river several years ago. The aromatics from control sediments range in concentration from 650 to 1500 ppb. These aromatic concentrations are not wholly unusual being well within the range of concentrations found in other urbanized areas (Hites et al. 1980). Aside from the two past oil spills, ship traffic and the presence of a nearby power plant and oil refinery may add pyrogenic and other anthropogenic contributions.

The amounts of Prudhoe Bay crude lost over the 90 day period were substantial for such a short time period as compared with other studies (Anderson et al. 1978, Smith and DeFur 1981). This factor, in consideration with the lack of significant differences in weathering between the oxidized and anoxic sediments and different concentrations, lends credence to the supposition that the losses were incurred primarily via the physical disruption of the fine-grained sediments

and associated oil by waves and tidal and wind-forced currents.

Abundance of Colonizing Meiobenthos

Faunal abundance varied substantially during the sampling period within and among the experimental treatments and surrounding natural community. All constituent phyla initially attained densities equivalent to the study site community within days (Mann-Whitney U-test, p > 0.167; Table 5) but continued to fluctuate greatly during the remainder of the experimental period. The population fluctuations may have accounted for the lack of a significant 'edge effect' as well as 'top' and 'bottom' core differences (2 x 2 contingency table, p > 0.05), although meiofaunal densities were generally concentrated in the upper two centimeters in agreement with prior studies (see review of Coull and Bell 1979).

Initial recovery of meiobenthos was generally earlier in the top portion than in the anoxic layer. This was especially true for the nematodes, which did not significantly (p > 0.167) recover in the anoxic portions of the mid- and high-oil treatments--probably due to greatly reduced abundance and/or absence of some of the less common species. Harpacticoid copepods, ostracods, and polychaetes apparently recovered more quickly than the nematodes in all of the treatments.

Nematodes (Figure 8) were the dominant taxon in all treatments and study site controls over the sampling period, comprising between 65% and 95% of total meiofaunal abundance. Copepods (Figure 9), ostracods (Figure 10), and polychaetes (Figure 11) were the next most abundant constituents but were far less abundant than nematodes.

Table 5. Initial recovery time (in days) of meiobenthos in top and bottom portions of experimental treatments. Based on lack of significant difference in population densities between the experimental treatments and study site control (Mann-Whitney U-Test, P > 0.167).

Phyla	Tray Control		Low Oil		Mid Oil		High Oil	
	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom
Total Nematoda	7	25	6	26	11	*	8	*
Neotonchus punctatus	8	3	5	3	5	7	8	7
Metalinhomoeus typicus	8	9	12	9	5	9	*	9
Sabatieria pulchra	11	9	7	7	5	10	10	25
Axonolaimus spinosus	5	5	5	9	9	8	8	8
Ptycholaimellus ponticus	5	5	5	5	5	9	5	5
Anticoma litoris	8	10	5	10	18	61	5	90
Theristus oxyuroides	8	10	13	10	31	10	31	10
Harpacticoida Copepoda	5	1	4	3	5	5	4	1
Ostracoda	3	2	3	3	4	5	3	2
Polychaeta	3	3	3	6	3	3	3	4
Other Phyla	5	3	2	1	2	1	7	1
Total Fauna	5	25	5	26	8	26	16	*

Treatment

* recovery not reached in 90 days.

35

Figure 8. Mean densities of Nematoda colonizing experimental treatments and study site control over the sampling period, May - August 1980. The four treatments and study site control values are nested into one bar for each sample date. Each component of a bar represents a sample area of 10 cm^{-2}. A. Top two cm. B. Bottom three cm.

NEMATODA

TIME (days)

NUMBER OF INDIVIDUALS · 10 cm⁻²

HIGH OIL
MID OIL
LOW OIL
TRAY CONTROL
STUDY SITE CONTROL

36

Figure 9. Mean densities of Harpacticoida Copepoda and Nauplii
colonizing experimental treatments and study site control
over the sampling period, May − August 1980. The four
treatments and study site control values are nested into
one bar for each sample date. Each component of a bar
represents a sample area of 10 cm^{-2}. A. Top two cm.
B. Bottom three cm.

HARPACTICOIDA COPEPODA + NAUPLII

NUMBER OF INDIVIDUALS · 10 cm⁻²

TIME (days)

HIGH OIL
MID OIL
LOW OIL
TRAY CONTROL
STUDY SITE CONTROL

37

Figure 10. Mean densities of Ostracoda colonizing experimental
            treatments and study site control over the sampling
            period, May – August 1980. The four treatments and
            study site control values are nested into one bar for
            each sample date. Each component of a bar represents
            a sample area of 10 cm^{-2}. A. Top two cm. B. Bottom
            three cm.

OSTRACODA

HIGH OIL
MID OIL
LOW OIL
TRAY CONTROL
STUDY SITE CONTROL

NUMBER OF INDIVIDUALS·10 cm⁻²

TIME (days)

A

B

Figure 11. Mean densities of Polychaeta colonizing experimental
treatments and study site control over the sampling
period, May – August 1980. The four treatments and
study site control values are nested into one bar for
each sample date. Each component of a bar represents
a sample area of 10 cm^{-2}. A. Top two cm. B. Bottom
three cm.

POLYCHAETA

HIGH OIL
MID OIL
LOW OIL
TRAY CONTROL
STUDY SITE CONTROL

A

B

NUMBER OF INDIVIDUALS · 10 cm^{-2}

TIME (days)

Other members of the meiofauna encountered were Bivalves, Foraminifera, Oligochaeta, Ciliata, Hydrozoa, Amphipoda, Isopoda, Archiannelida, Turbellaria, Kinorhyncha, Cumacea, Tardigrada and Gastrotricha (Figure 12).

Nematode Faunal Composition

Assemblages. Faunal similarity between the experimental treatments and natural community were examined by use of numerical classification. The hierarchical analysis of the 130 samples is presented in Figure 13. A detailed listing of samples in the selected collection groups is provided in Table 6.

The normal analysis of the abundances of nematodes showed high faunal similarity among samples with a poor separation on the basis of recolonization time and/or treatment. Only the natural community aggregated to form a distinct faunal unit, Group F. The experimental treatments were poorly grouped. A general trend was manifest in which the later date treatment samples (Groups C and H) were aggregated with the natural community (Group F); earlier date samples (Groups A, C, D and E) were generally clustered as a separate faunal unit. Group B consisted of two later date samples.

Reciprocal averaging ordination of the samples clarified the relationship between the experimental treatments and natural study site community (Figure 14). The centroids of the samples were linked on the basis of sampling date for the four treatments and natural community in order to better depict the progression of the colonizing fauna over time. The first axis explains 25%, and the first three, 50% of the total variance within the data set.

Figure 12. Mean densities of other faunal groups colonizing
experimental treatments and study site control over
the sampling period, May – August 1980. The four
treatments and study site control values are nested
into one bar for each sample date. Each component
of a bar represents a sample area of 10 cm^{-2}. A.
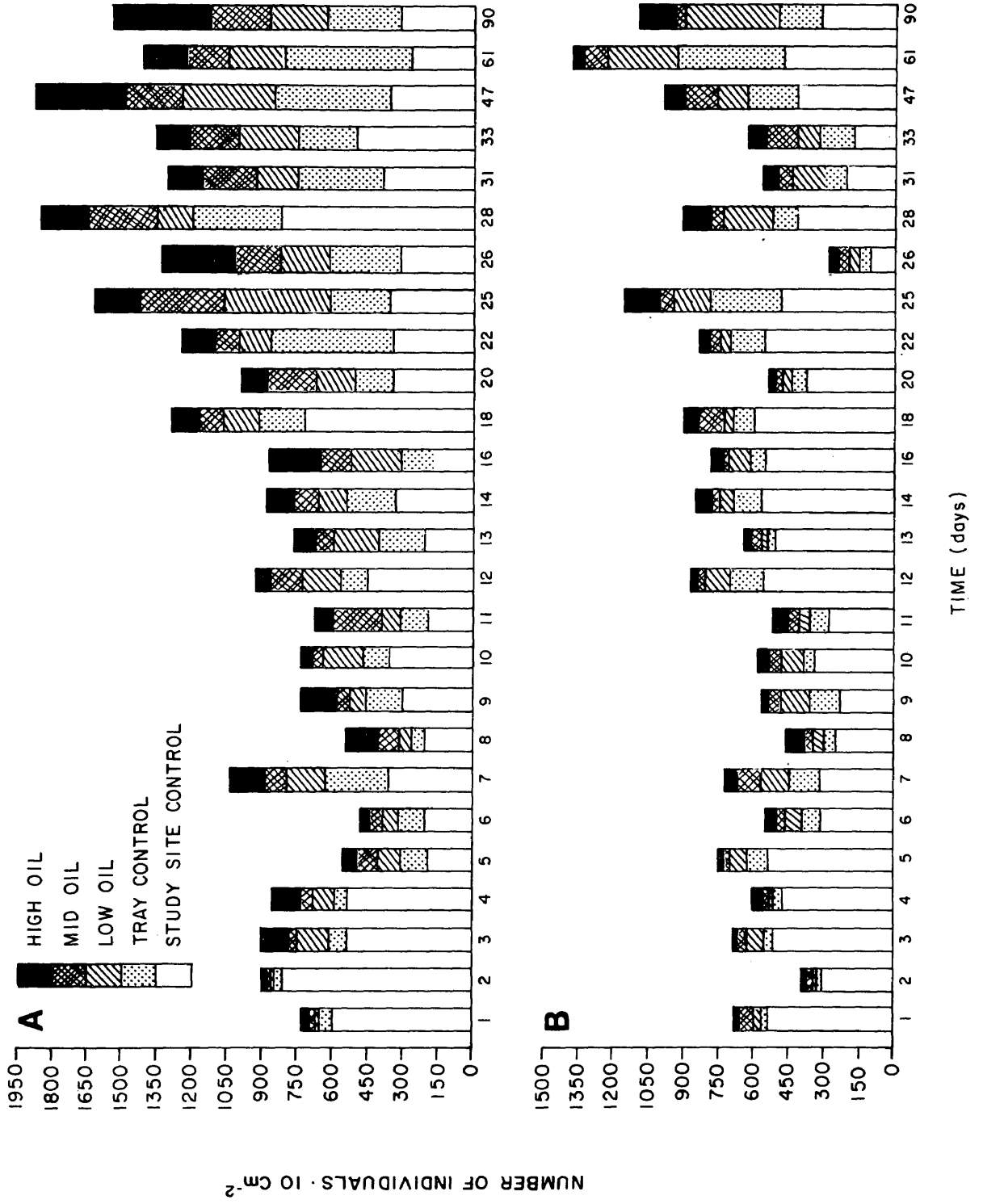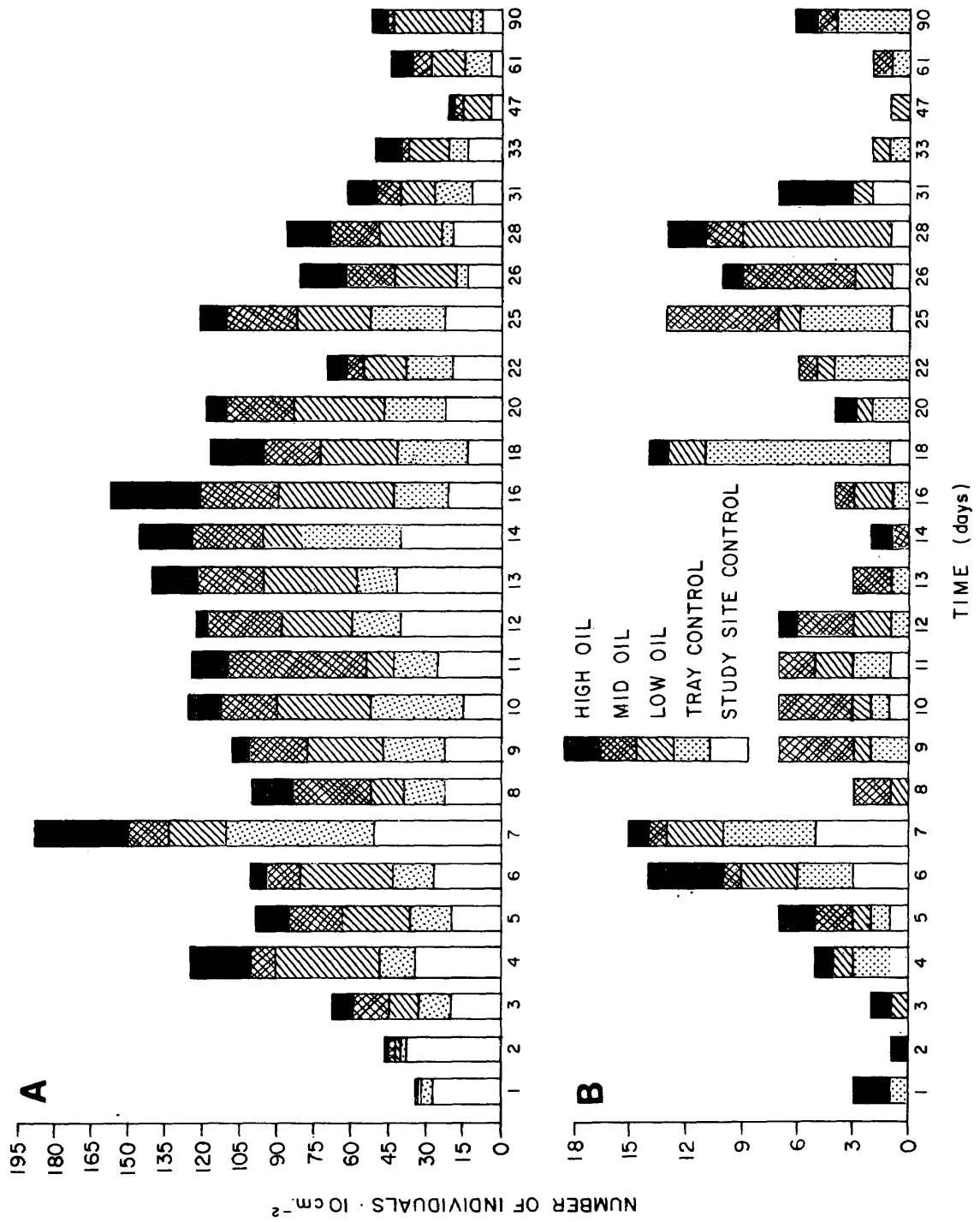top two cm. B. Bottom three cm.

OTHER PHYLA

41

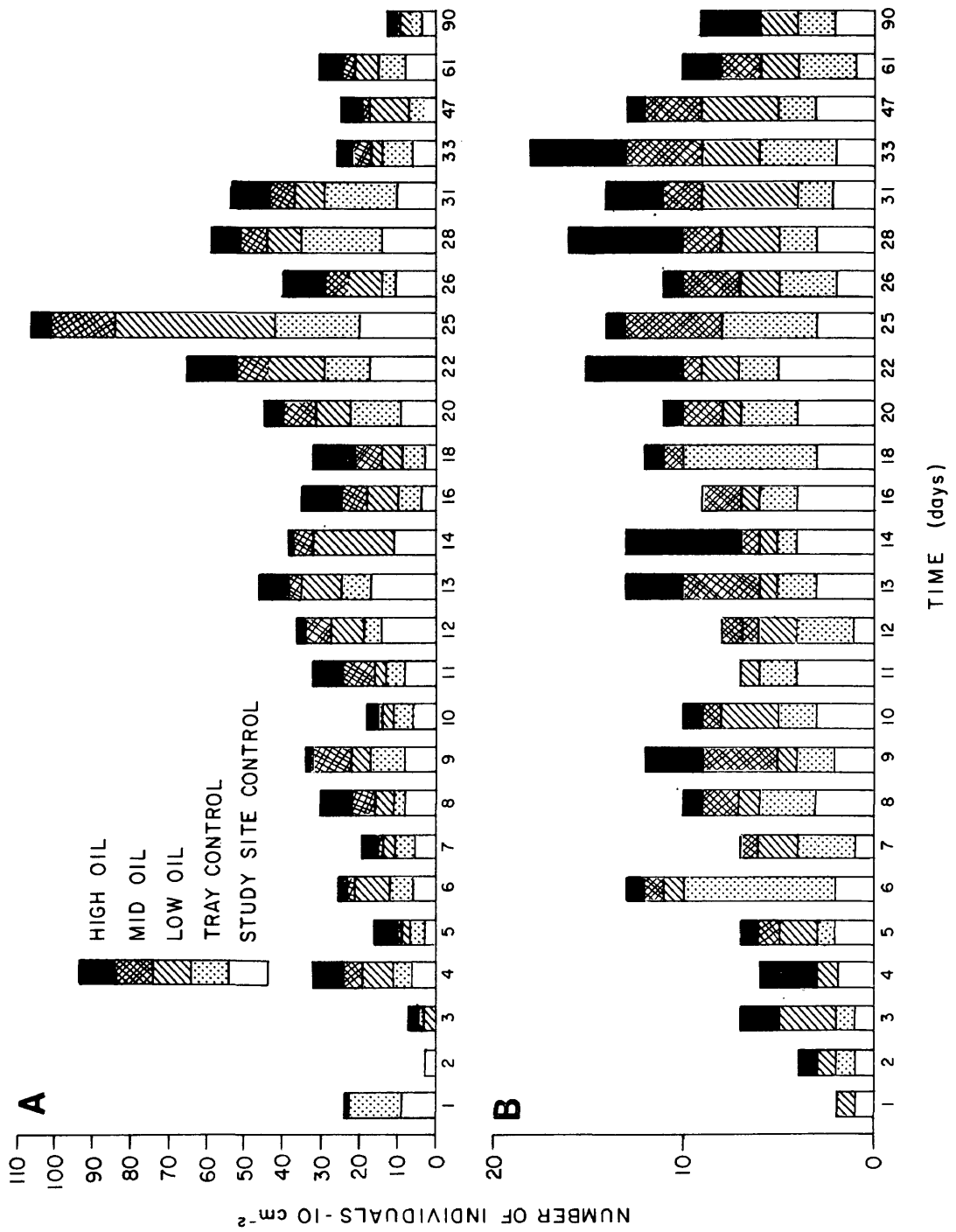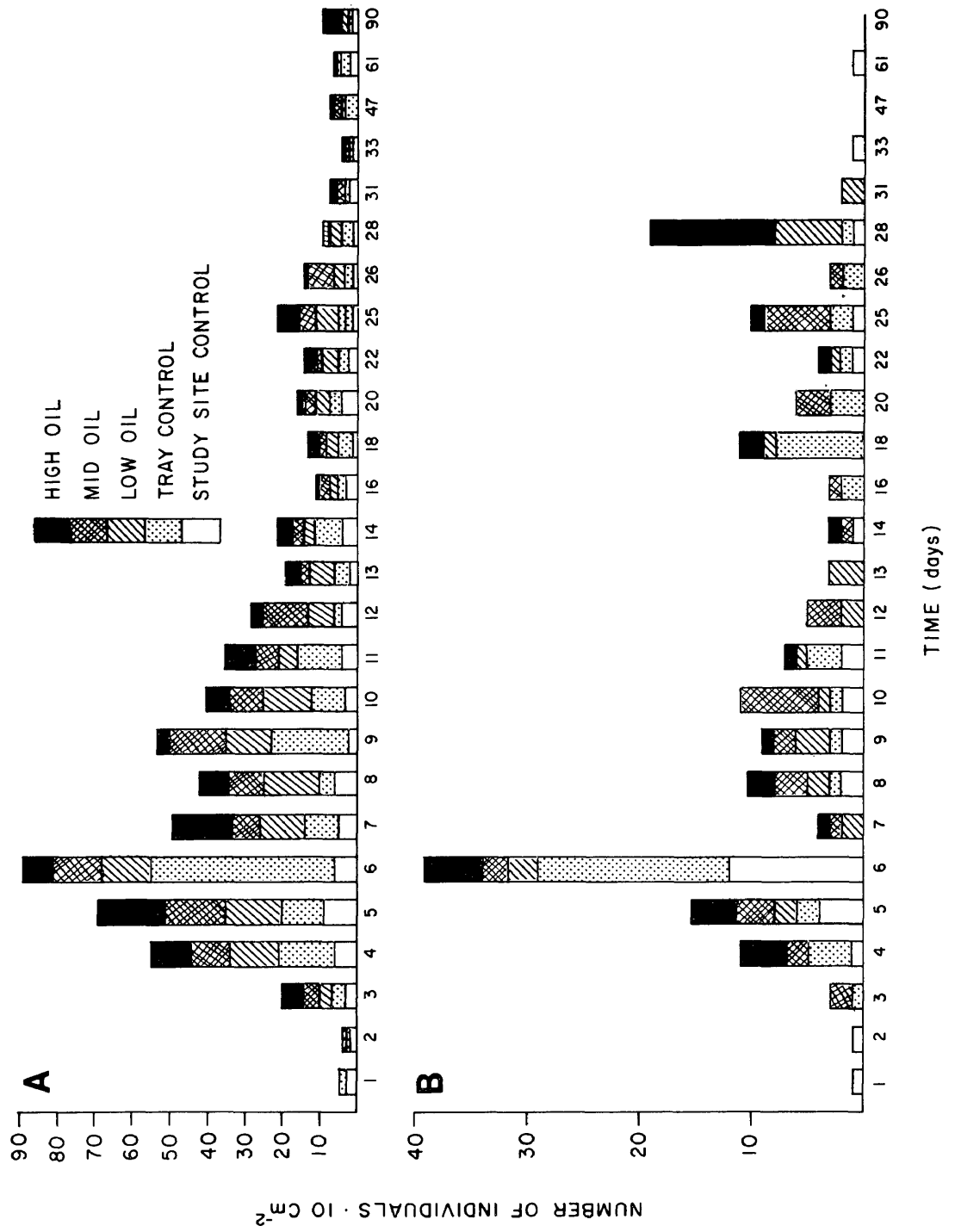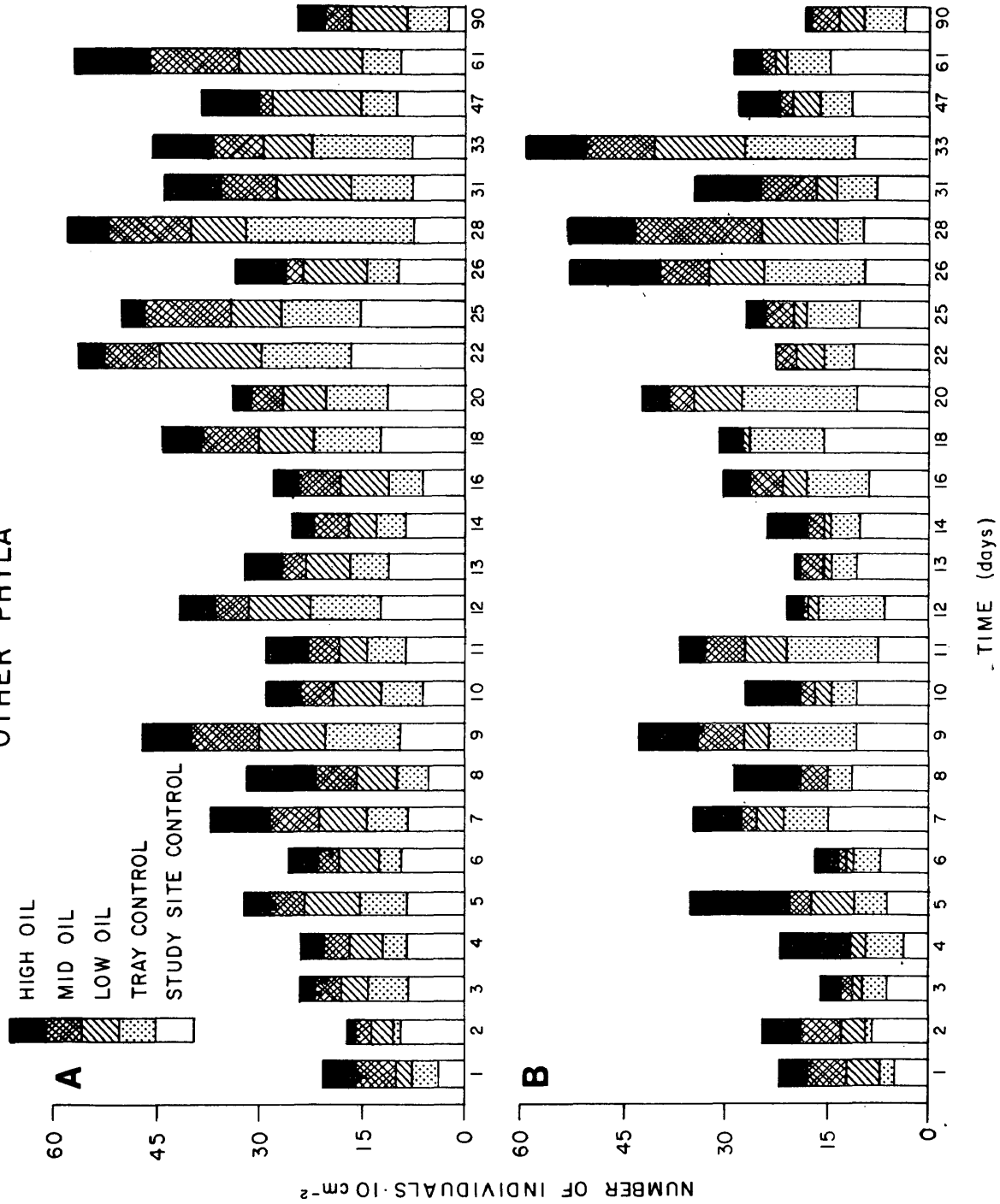Figure 13. Normal classification hierarchies and mean species

diversity values of samples of nematodes from experimental

treatments and study site control. Agglomeration of

samples into eight groups is indicated.
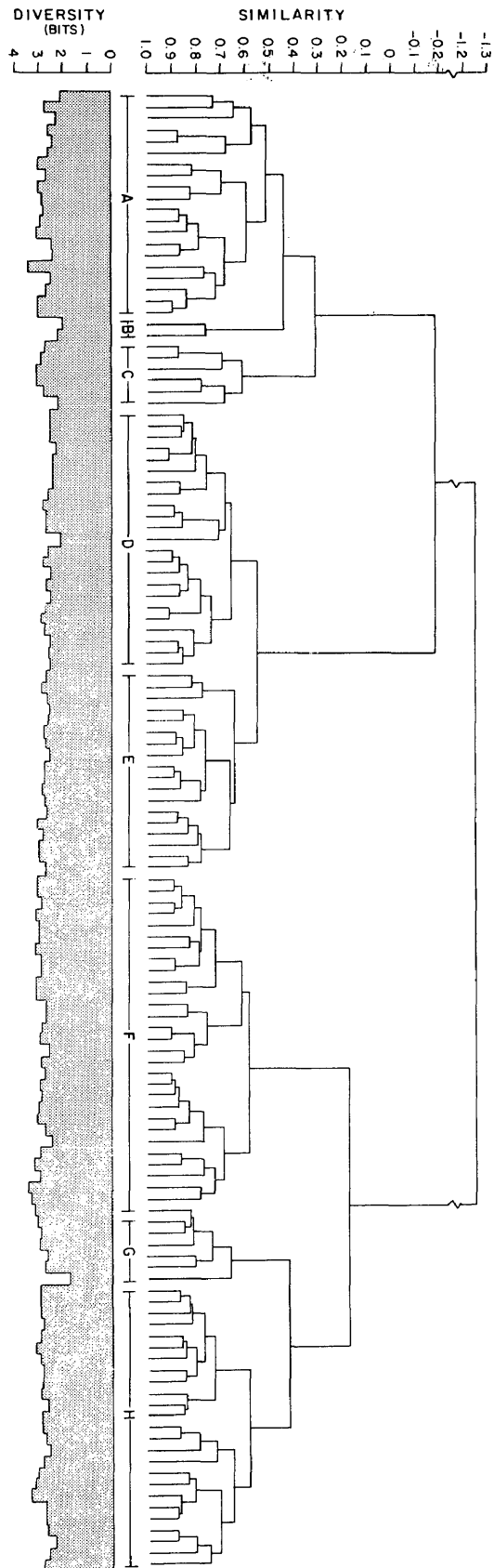
Table 6. Sample groups selected from numerical classification of
nematodes from experimental treatments and study site
controls of all sampling dates. Samples are abbreviated
to two-letter designations. (First letter denotes sampling
date: Day 1=A, Day 2=B, Day 90=Z, etc; second letter
denotes treatment type: C=Tray control, L=low oil,
M=mid oil, H=high oil; study site controls are denoted
by first letter designations only.)

Sample Group	Samples
A	AC, CH, AM, AH, DM, HC, CC, MC, OC, PH, DC, HC, DL, KL, MM, FH, LH, IM, JM, KH
B	VH, ZM
C	AL, BC, BL, BH, CM, BM
D	CL, DH, QL, EC, OH, HH, JH, LM, FL, ML, CH, RH, EH, EM, IH, FM, HM, OM, RM, FC, MH, QH, NM
E	EL, RL, CC, GL, PL, KM, QC, QM, IL, JL, TL, NL, GM, JC, LC, KC, NH, TM
F (includes all study site controls)	A, N, B, D, Q, C, P, E, L, U, YC, H, Z, RC, Y, SC, XC, G, M, S, O, W, X, R, I, K, T, J, V, F
G	YL, ZC, XL, XH, ZH, ZL
H	YM, TH, VC, IC, SH, TC, UH, NC, PC, WM, OL, WH, UC, YH, XM, WC, LC, WL, PM, SM, SL, VM, UL, UM, VL

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Figure 14. Reciprocal averaging ordination of samples of nematodes

from experimental treatments and study site control.

AXIS 2

AXIS I

AXIS 3

AXIS I
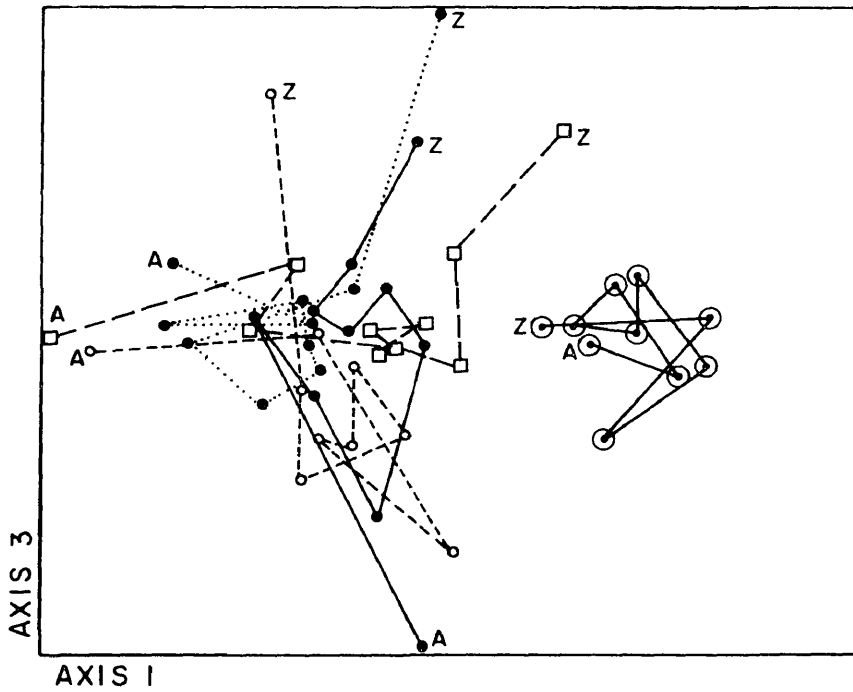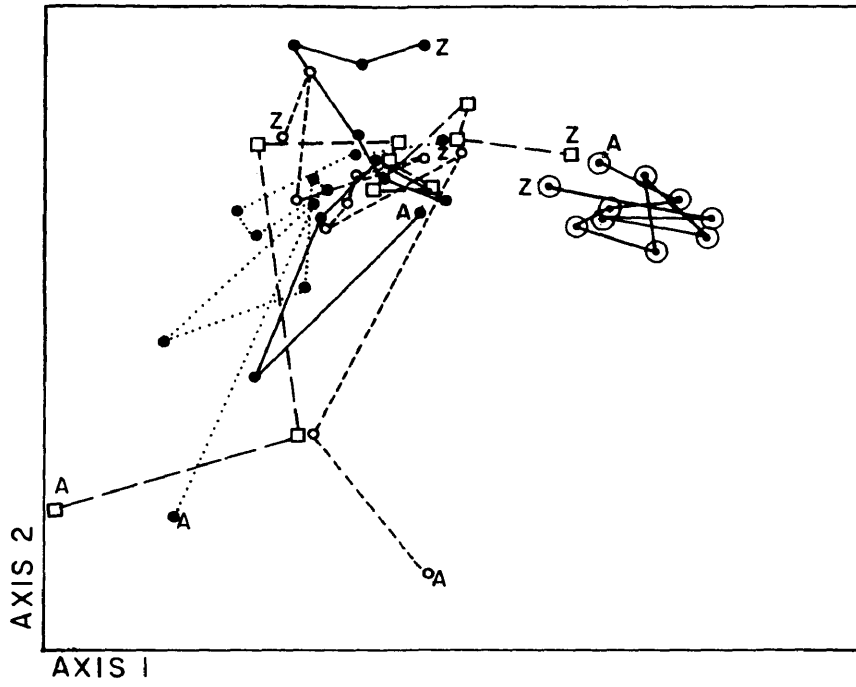
⊙————⊙ SITE CONTROL   ●·········● LOW OIL

□————□ TRAY CONTROL   ○----○ MID OIL

●————● HIGH OIL

The natural community was cast separately from the treatments with a high cluster of scores along axes 1 and 2 and mid-range values along axis 3. A temporal continuum of the linked treatment centroids is evident along axes 2 and 3. Early date samples have generally low to mid-range scores along these axes; as the recolonization progressed over time, scores for the samples were cast over a wide range along these two axes. The result is a continuum from early date, low to mid-scores to later date samples with higher scores on axes 2 and 3. A clearer depiction of the relationship among samples on the basis of treatment is provided by the ordination along axes 1 and 3. Examining the Day 90 samples (designated 'Z'), the oil and tray control treatments are all positioned with high scores along the third axis with a good differentiation between oil and control treatments depicted along axis 1. The tray control sample is positioned within the ordination space of the Day 90 study site control sample along all three axes. It is of interest to note the closer position of the high oil sample to the natural community as compared to its lower oil counterparts along axis 1. The non-overlapping of the oiled treatments with the natural community may provide some visual evidence for the supposition that the colonization process was not completed at the end of the sampling period, although all oiled treatments periodically attained abundances comparable to the study site controls.

The ordination of species cast along the first three extracted axes (Figure 15) help to clarify the observed spatial relationships between treatments and natural community. A continuum of species aligned with axis 1 resulted. Species with the lowest scores on the

Figure 15. Reciprocal averaging ordination of nematode species from
experimental treatments and study site controls.

AXIS 2

T. setosus

P. ponticus ▲

Steineria sp.●

▲ N. punctatus

M. retrosetosus

P. brevamphida ●

● S. pulchra

Oncholaimus sp. ■

Paracanthonchus sp. ▲

A. spinosus ●

M. typicus ●

T. oxyuroides

● Thalassoalaimus sp.

A. litoris ●

● M. parasitifera

AXIS I

AXIS 3

S. pulchra ●

Steineria sp. ●

● M. retrosetosus

● M. typicus

● T. oxyuroides

● M. parasitifera

N. punctatus

A. litoris ●

Parodontophora sp. ●

▲ ■ Oncholaimus sp.

P. ponticus ▲

● A. spinosus

● Thalassoalaimus sp.

● T. setosus

Paracanthonchus sp. ▲

AXIS I

TROPHIC TYPE

● SELECTIVE OR NONSELECTIVE DEPOSIT FEEDER

▲ EPIGROWTH FEEDER

■ OMNIVORE / PREDATOR

46

first axis, such as <u>Theristus</u> <u>setosus</u> and <u>Metachromadora</u> <u>parasitifera</u>, were found primarily in the experimental treatments. Mid-range scores were characteristic of those species found in nearly equal abundance in all treatments and the natural community. <u>Neotonchus</u> <u>punctatus</u>, <u>Sabatieria</u> <u>pulchra</u>, <u>Axonolaimus</u> <u>spinosus</u>, <u>Ptycholaimellus</u> <u>ponticus</u>, <u>Parodontophora</u> <u>brevamphida</u> and <u>Oncholaimus</u> sp. were among those cast in this mid-range region. High scores on axis 1 are indicative of species such as <u>Steineria</u> sp., <u>M</u>. <u>retrosetosus</u>, <u>M</u>. <u>typicus</u>, <u>T</u>. <u>oxyuroides</u> and <u>Thalassoalaimus</u> sp. which had higher abundances in the natural community than any of the treatments. <u>Anticoma</u> <u>litoris</u> and <u>Paracanthonchus</u> sp., which were relatively poor colonizers of the experimental trays, had the highest scores on axis 1. Although not as clearly defined as the gradient along axis 1, the second extractable axis separates the worms on a temporal basis in which early colonizers exhibited low scores and species which did not exhibit any conspicuous colonizing patterns and/or were generally poor colonizers were positioned in the mid- to high score region. For example, <u>Metachromadora</u> <u>parasitifera</u> was cast alone with a low score on axis 2 due to its presence primarily in the early treatment samples. Mid-range scores on the third axis indicate a species such as <u>Theristus</u> <u>setosus</u> which appeared during the latter week of the sampling period. <u>Paracanthonchus</u> sp. possessed a low score on the third axis, being present mainly in the natural community in low abundance.

The distributional characteristics of the species in the eight collection groups are expressed in the nodal analysis represented in Figure 16.

Figure 16. Inverse classification hierarchies of nematode species and
            their nodal statistics in sample groups. See text for key
            to species numbers and Table 6 for sample groups
            identifications.

COLLECTION GROUPS

ABUNDANCE CONCENTRATION

FIDELITY

PERCENT CONSTANCY

SIMILARITY

SPECIES

48
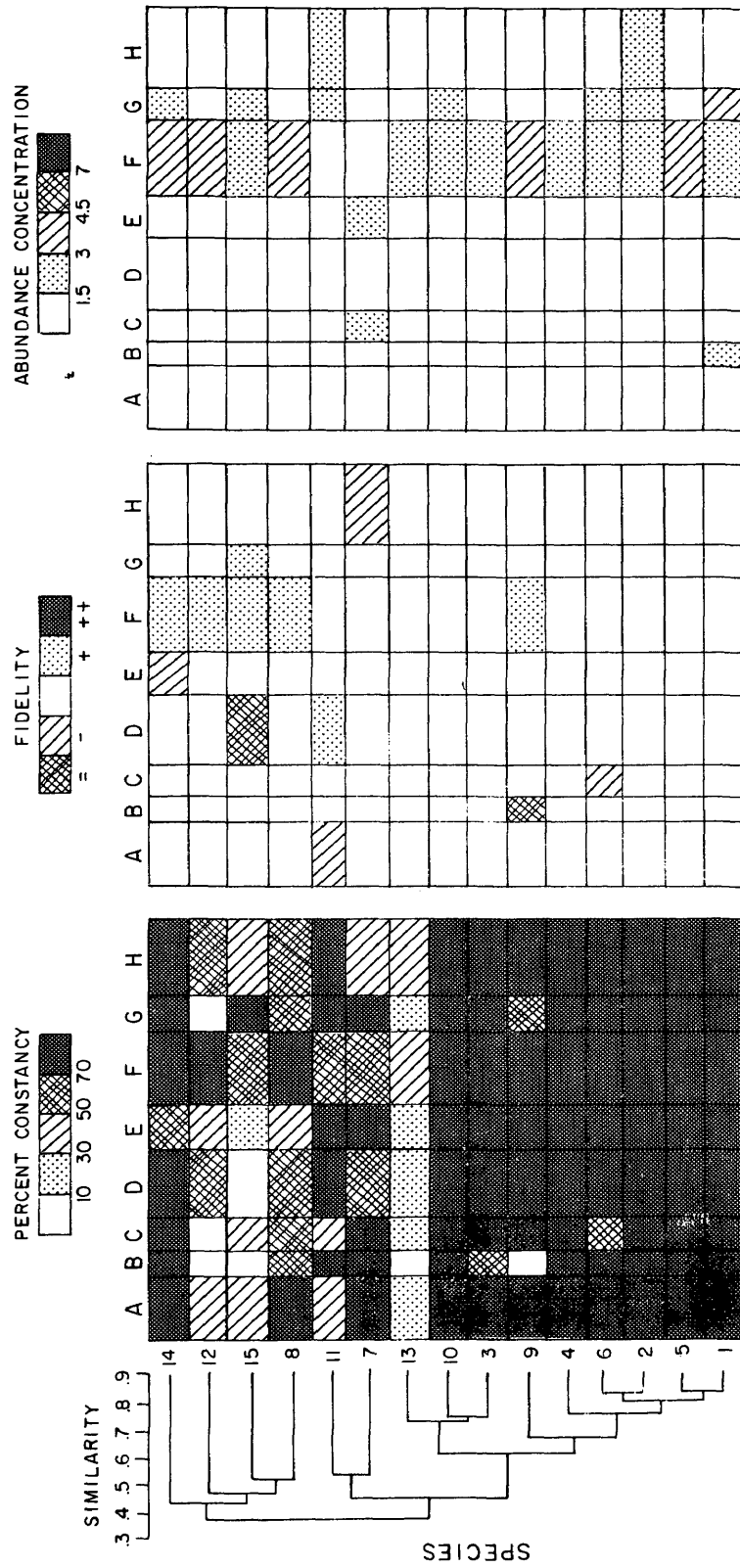
Sabatieria pulchra (1), Theristus oxyuroides (5), Ptycholaimellus

ponticus (2), Neotonchus punctatus (6), Axonolaimus spinosus (4),

Oncholaimus sp. (3), Parodontophora brevamphida (10) and Metalinhomoeus

typicus (13) were most ubiquitous showing no significant fidelity but

exhibiting greater abundance concentrations in the natural community

than in the treatment collection groups. Anticoma litoris (9) and

Metalinhomoeus retrosetosus (14) were widely distributed but

significantly faithful to the natural community. Though less

widespread in their distribution, Paracanthonchus sp. (12), Steineria

sp. (15) and Thalassoalaimus sp. (8) also exhibited significant

fidelity to the study site controls. Theristus setosus (11) and

Metachromadora parasitifera (17) were generally highly constant and

more abundant in several of the collection groups than in the natural

community. T. setosus was highly faithful to Group D, which includes

a wide array of samples from the oiled treatments.

Individual Species Patterns. Several patterns of nematode species

abundance were discernible in the contaminated and untreated sediments.

A list of all nematode species collected from the natural community and

the suite of experimental treatments is provided in Table 7.

All species collected from the natural community were established

in the distributed sediments with the exception of the rare species

Euchromadora sp. and Desmodora sp. which were not found in the high

oil samples. Species were generally of greater abundance and

fluctuation and exhibited quicker response in the top oxidized

layer than in the anoxic region of the boxes (Table 5). The species

were characterized by generally decreased levels of abundance with

Table 7. List of nematode species in the study site control
          community and colonization experiments. Ranked within
          treatment by total abundance.

Treatment	Species	Rank	Mean Density (No. ·10 cm^{-2})
Study Site	Axonolaimus spinosus	1	318
Control	Theristus oxyuroides	2	294
	Anticoma litoris	3	285
	Sabatieria pulchra	4	195
	Ptycholaimellus ponticus	5	145
	Neotonchus punctatus	6	111
	Metalinhomoeus typicus	7	72
	Parodontophora brevamphida	8	59
	Oncholaimus sp.	9	34
	Thalassoalaimus sp.	10	24
	Paracanthonchus sp.	11	23
	Steineria sp.	12	14
	Theristus setosus	13	10
	Metachromadora parasitifera	14.5	8
	Metalinhomoeus retrosetosus	14.5	8
	Pomponema sp.	16	2
	Paramonhystera proteus	17	1
	Euchromadora sp.	19	<1
	Sphaerolaimus balticus	19	<1
	Desmodora sp.	19	<1
		Total	1606

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Table 7 (continued)

Treatment	Species	Rank	Mean Density (No. ·10 cm^{-2})
Tray Control	Axonolaimus spinosus	1	142
	Ptycholaimellus ponticus	2	122
	Sabatieria pulchra	3	101
	Theristus oxyuroides	4	75
	Neotonchus punctatus	5	57
	Oncholaimus sp.	6.5	26
	Parodontophora brevamphida	6.5	26
	Anticoma litoris	8	19
	Metalinhomoeus typicus	9	12
	Steineria sp.	10	9
	Metachromadora parasitifera	11	6
	Thalassoalaimus sp.	12	5
	Paramonhystera proteus	14	3
	Theristus setosus	14	3
	Paracanthonchus sp.	14	3
	Pomponema sp.	16.5	2
	Metalinhomoeus retrosetosus	16.5	2
	Euchromadora sp.	19	<1
	Sphaerolaimus balticus	19	<1
	Desmodora sp.	19	<1
		Total	616

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Table 7 (continued)

Treatment	Species	Rank	Mean Density (No. $\cdot 10 \ cm^{-2}$)
Low Oil	Axonolaimus spinosus	1	135
	Ptycholaimellus ponticus	2	94
	Sabatieria pulchra	3	90
	Theristus oxyuroides	4	47
	Neotonchus punctatus	5	43
	Parodontophora brevamphida	6	27
	Anticoma litoris	7	19
	Metachromadora parasitifera	8	17
	Theristus setosus	9	14
	Oncholaimus sp.	10.5	10
	Metalinhomoeus typicus	10.5	10
	Thalassoalaimus sp.	12	3
	Paramonhystera proteus	13.5	2
	Steineria sp.	13.5	2
	Metalinhomoeus retrosetosus	15	1
	Paracanthonchus sp.	18	<1
	Pomponema sp.	18	<1
	Euchromadora sp.	18	<1
	Sphaerolaimus balticus	18	<1
	Desmodora sp.	18	<1
	Total		589

Table 7 (continued)

Treatment	Species	Rank	Mean Density (No. $\cdot 10$ cm^{-2})
Mid Oil	Axonolaimus spinosus	1	115
	Ptycholaimellus ponticus	2	79
	Sabatieria pulchra	3	45
	Neotonchus punctatus	4	36
	Parodontophora brevamphida	5	22
	Theristus oxyuroides	6	20
	Anticoma litoris	7	12
	Oncholaimus sp.	8	10
	Theristus setosus	9	8
	Metachromadora parasitifera	10.5	7
	Metalinhomoeus typicus	10.5	7
	Paracanthonchus sp.	12.5	3
	Paramonhystera proteus	12.5	3
	Metalinhomoeus retrosetosus	14.5	2
	Thalassoalaimus sp.	14.5	2
	Pomponema sp.	18	<1
	Steineria sp.	18	<1
	Euchromadora sp.	18	<1
	Sphaerolaimus balticus	18	<1
	Desmodora sp.	18	<1
		Total	376

Table 7 (concluded)

Treatment	Species	Rank	Mean Density (No. ·10 cm^{-2})
High Oil	Axonolaimus spinosus	1	96
	Ptycholaimellus ponticus	2	72
	Sabatieria pulchra	3	63
	Neotonchus punctatus	4	33
	Theristus oxyuroides	5	30
	Parodontophora brevamphida	6	17
	Metalinhomoeus typicus	7	10
	Theristus setosus	8	9
	Oncholaimus sp.	9	8
	Metachromadora parasitifera	10.5	6
	Anticoma litoris	10.5	6
	Metalinhomoeus retrosetosus	12	4
	Steineria sp.	13.5	3
	Thalassoalaimus sp.	13.5	3
	Paracanthonchus sp.	15.5	2
	Paramonhystera proteus	15.5	2
	Pomponema sp.	17	1
	Sphaerolaimus balticus	18	<1
		Total	366

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increasing hydrocarbon concentration (Table 7).

Two dominant species in the natural community, the deposit feeder Anticoma litoris (Figure 17) and the omnivore/predator Metalinhomoeus typicus (Figure 18), were poor colonizers of all treatments. With the exception of these two species, those ranked among the eight most abundant in the natural community retained their dominance in the experimental boxes.

Several of those dominants displayed rather distinct colonizing response patterns. The most significant was the response by Sabatieria pulchra (Figure 19) which arrived early during colonization, exhibited moderate population growth and became dominant by the end of the samping period in all of the experimental boxes. A bimodal response distribution was characteristic of the epigrowth feeder Ptycholaimellus ponticus (Figure 20) which attained peak densities after approximately 25 and 61 days, respectively. Theristus oxyuroides (Figure 21) and Neotonchus punctatus (Figure 22) exhibited bimodal responses over the colonization period in the tray control boxes. These two species recruited gradually in the oiled treatments, attaining peak densities after approximately 20 days and declining during the remainder of the sampling period. Ranked first in the natural community and disturbed treatments on the basis of total abundance, Axonolaimus spinosus (Figure 23) colonized rapidly, especially in the tray control boxes and attained peak abundance by the third week of colonization. During the remainder of the sampling period, this species experienced a substantial decline in abundance.

Figure 17. Population densities of <u>Anticoma litoris</u> colonizing
experimental treatments and study site control over
the sampling period, May - August 1980. The four
treatments and study site control values are nested
into one bar for each sample date. Each component
of a bar represents a sample area of 10 cm^{-2}. A. Top
two cm. B. Bottom three cm.

Anticoma litoris

NUMBER OF INDIVIDUALS · 10 cm^{-2}

TIME (days)

HIGH OIL
MID OIL
LOW OIL
TRAY CONTROL
STUDY SITE CONTROL

Figure 18. Population densities of <u>Metalinhomoeus typicus</u>
colonizing experimental treatments and study site
control over the sampling period, May – August 1980.
The four treatments and study site control values
are nested into one bar for each sample date.
Each component of a bar represents a sample area
of 10 cm^{-2}. A. Top two cm. B. Bottom three cm.

Metalinhomoeus typicus

57
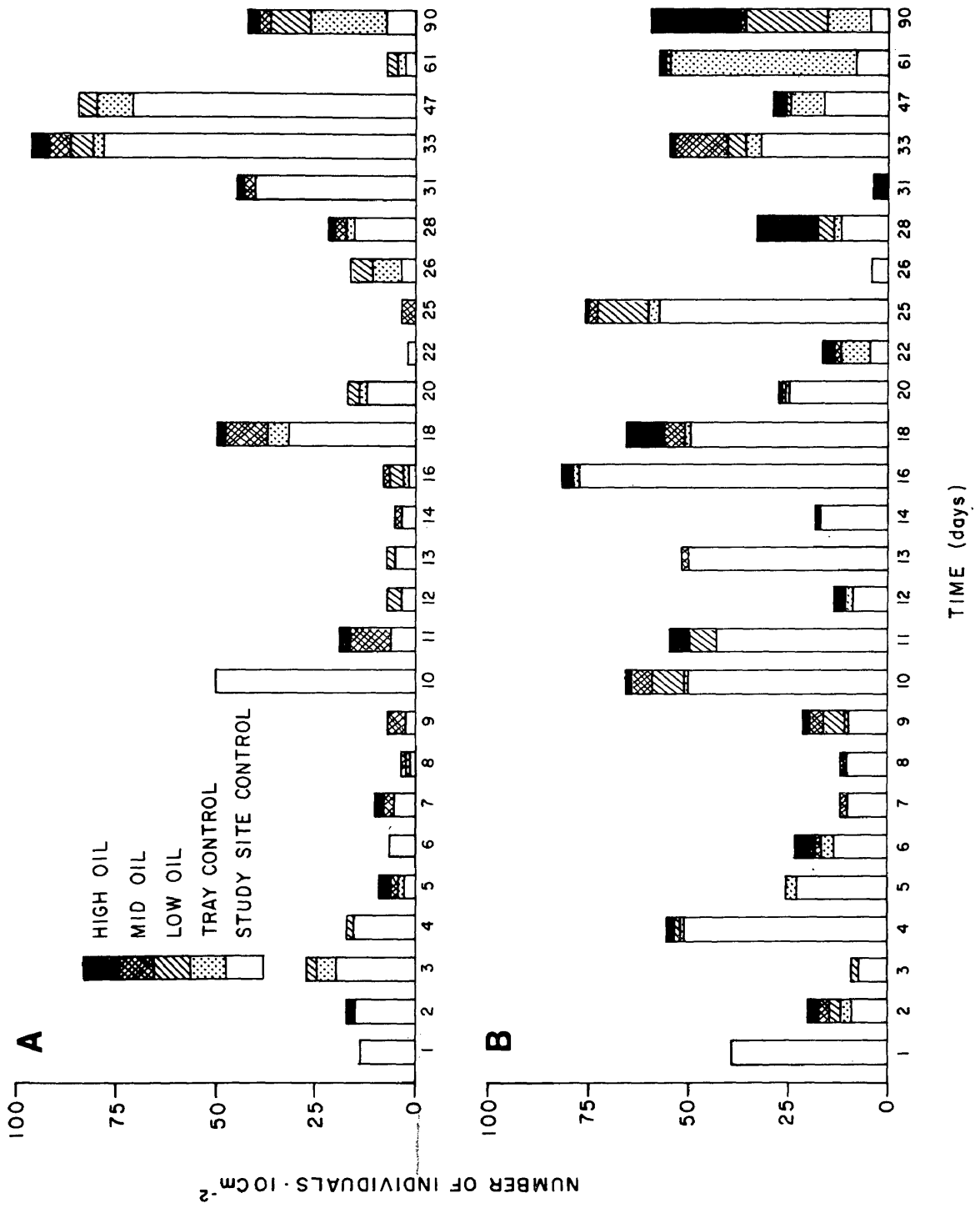
Figure 19. Population densities of <u>Sabatieria</u> <u>pulchra</u> colonizing
experimental treatments and study site control over the
sampling period, May – August 1980. The four treatments
and study site control values are nested into one bar
for each sample date. Each component of a bar represents
a sample area of 10 cm^{-2}. A. Top two cm. B. Bottom
three cm.

Sabatieria pulchra
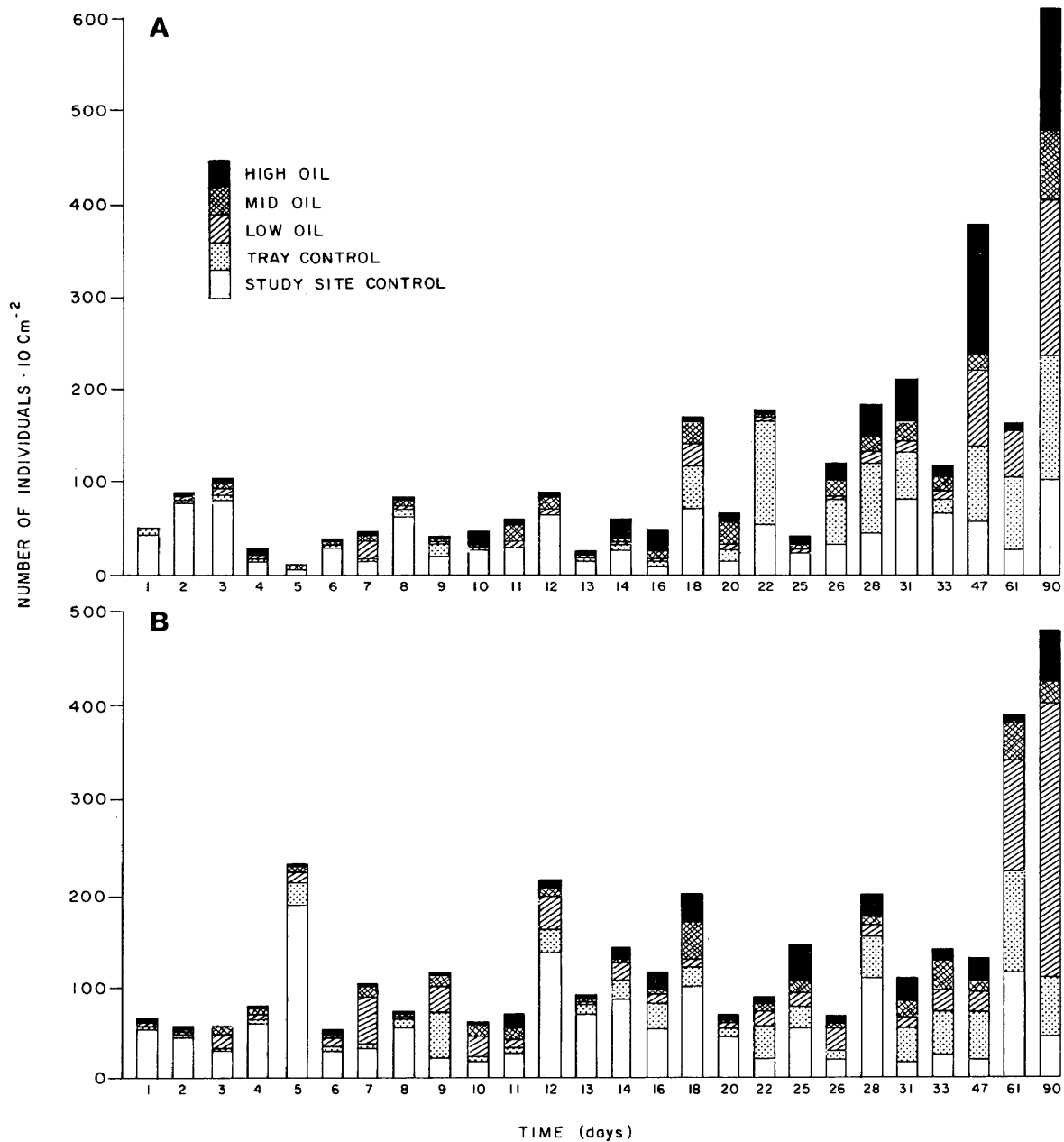
Figure 20. Population densities of <u>Ptycholaimellus</u> <u>ponticus</u>
colonizing experimental treatments and study site
control over the sampling period, May – August 1980.
The four treatments and study site control values are
nested into one bar for each sample date. Each component
of a bar represents a sample area of 10 cm^{-2}. A. Top
two cm. B. Bottom three cm.

Ptycholaimellus ponticus

59
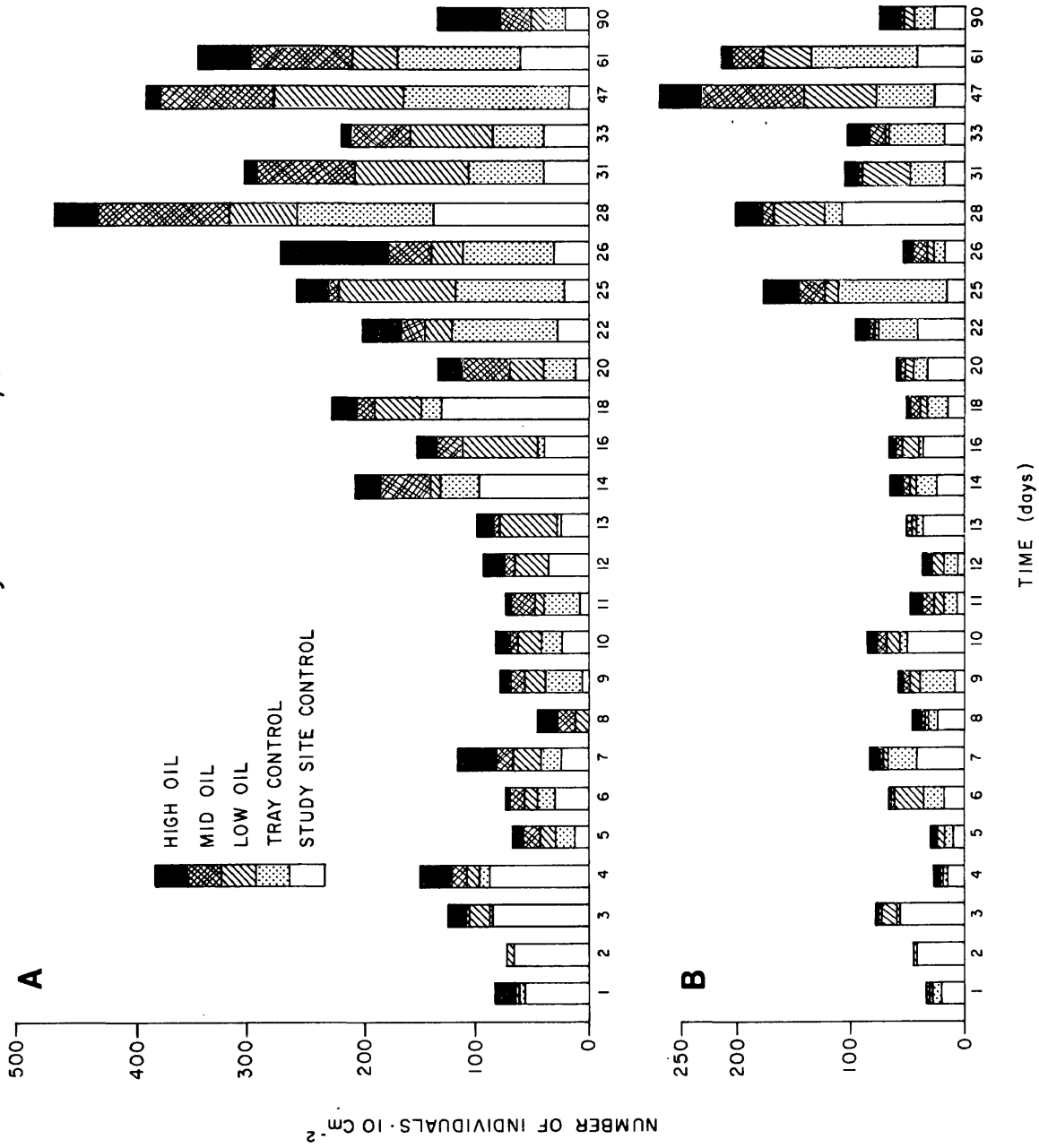
Figure 21. Population densities of Theristus oxyuroides colonizing
experimental treatments and study site control over the
sampling period, May – August 1980. The four treatments
and study site control values are nested into one bar
for each sample date. Each component of a bar represents
a sample area of 10 cm^{-2}. A. Top two cm. B. Bottom three
cm.

Theristus oxyuroides
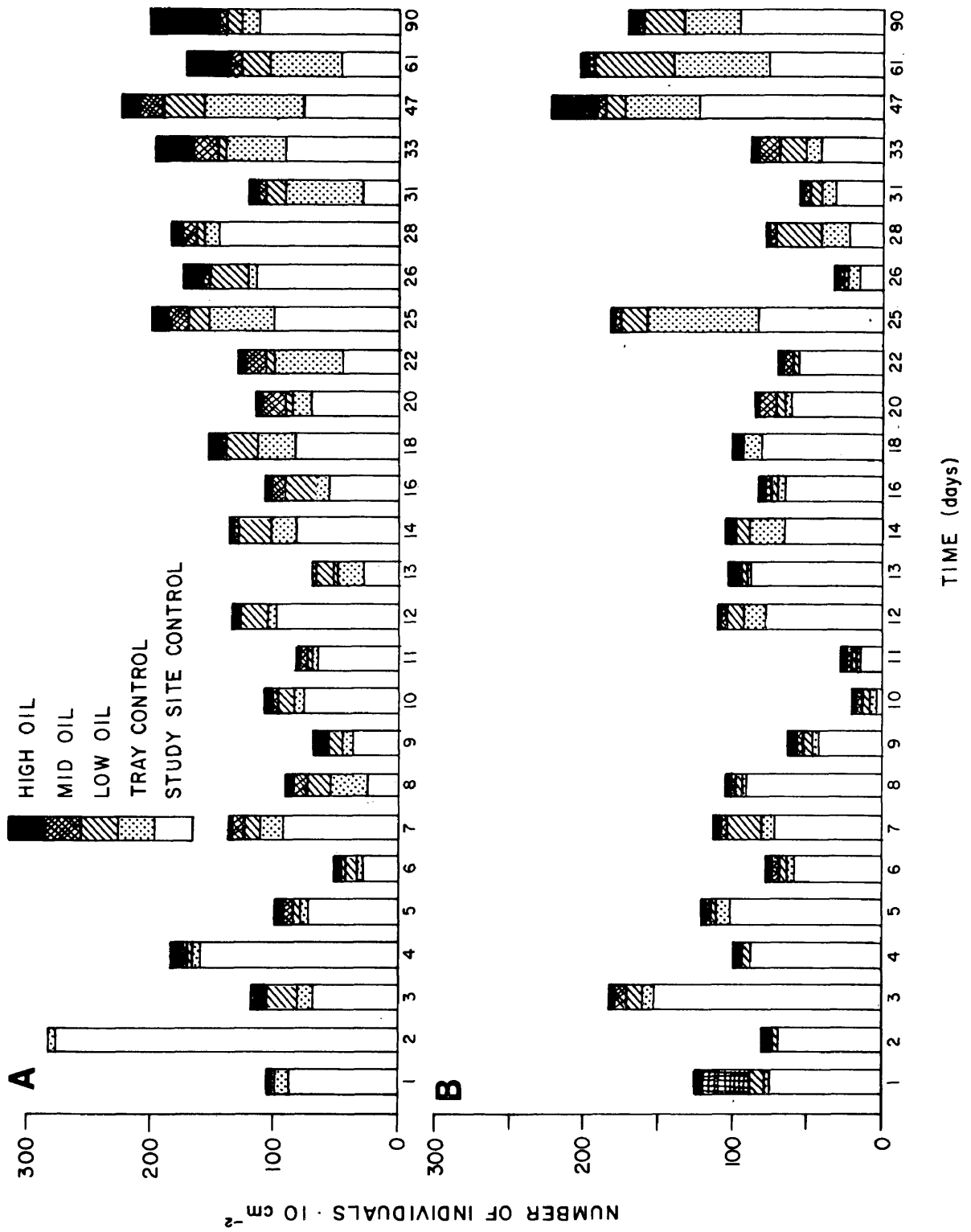
Figure 22. Population densities of <u>Neotonchus</u> <u>punctatus</u> colonizing experimental treatments and study site control over the sampling period, May – August 1980. The four treatments and study site control values are nested into one bar for each sample date. Each component of a bar represents a sample area of 10 cm^{-2}. A. Top two cm. B. Bottom three cm.

Neotonchus punctatus

A

B

NUMBER OF INDIVIDUALS · 10 CM⁻²

TIME (days)

HIGH OIL
MID OIL
LOW OIL
TRAY CONTROL
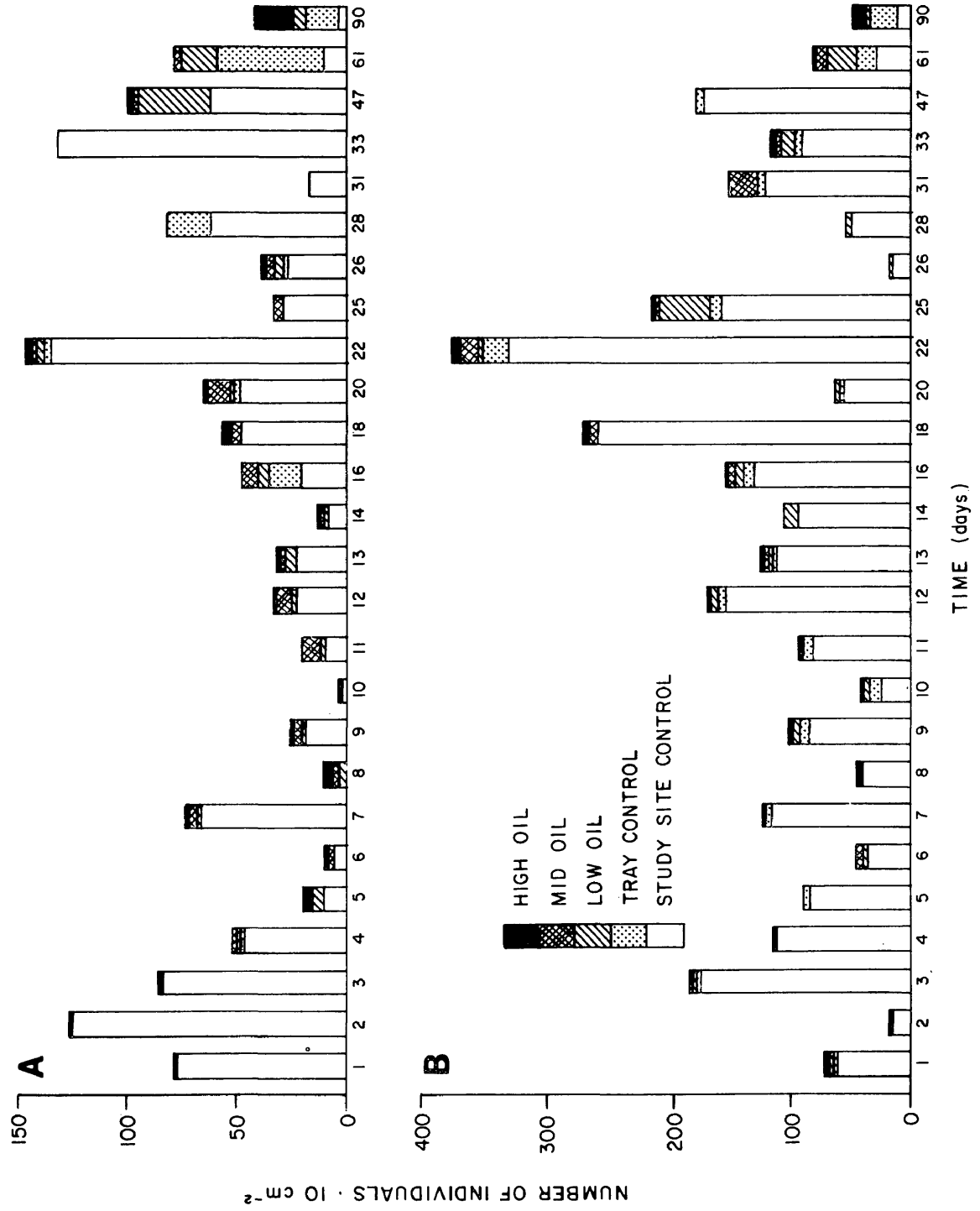STUDY SITE CONTROL
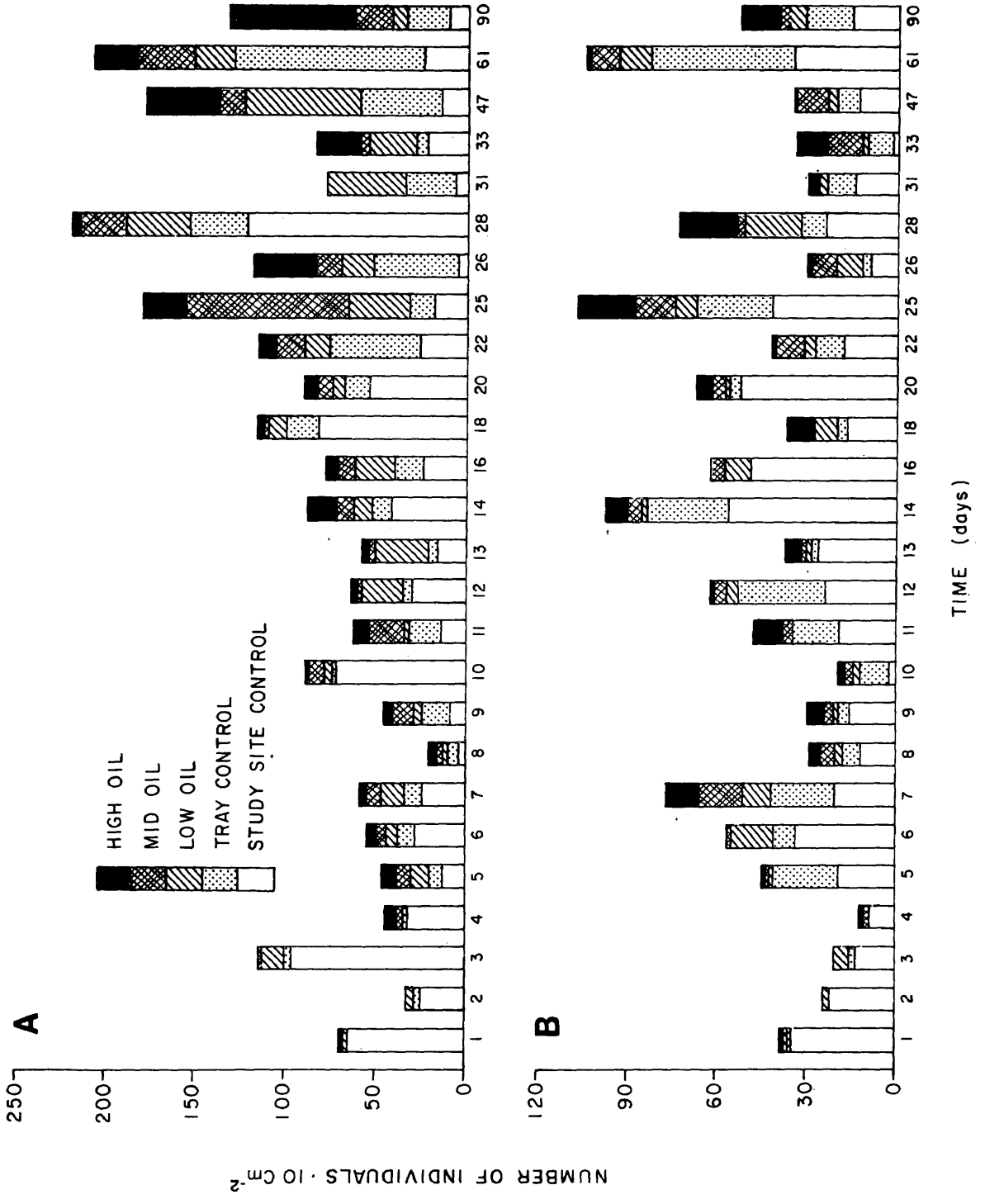
Figure 23.   Population densities of <u>Axonolaimus</u> <u>spinosus</u> colonizing
            experimental treatments and study site control over the
            sampling period, May – August 1980. The four treatments
            and study site control values are nested into one bar
            for each sample date. Each component of a bar represents
            a sample area of 10 cm^{-2}. A. Top two cm. B. Bottom
   three cm.

Axonolaimus spinosus

HIGH OIL
MID OIL
LOW OIL
TRAY CONTROL
STUDY SITE CONTROL

A

B

NUMBER OF INDIVIDUALS · 10 cm^{-2}

TIME (days)

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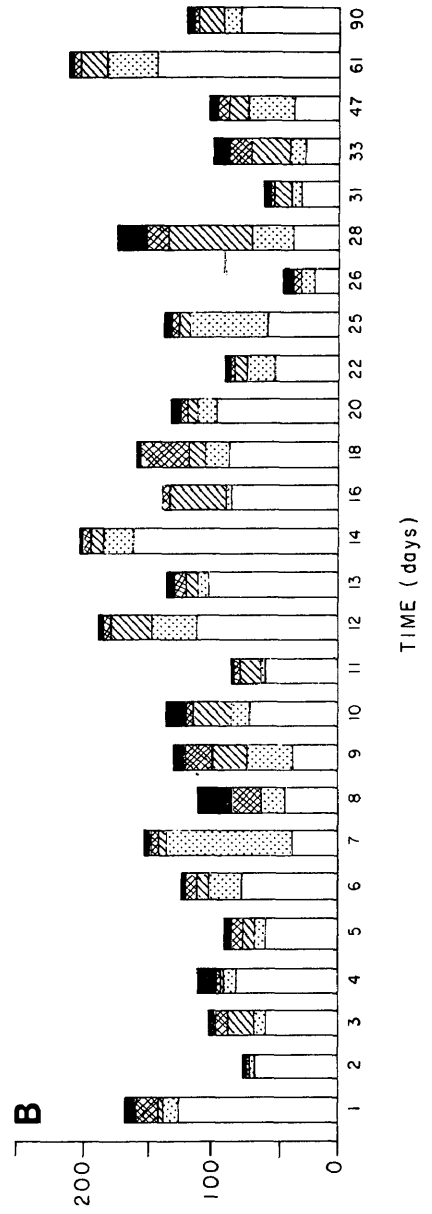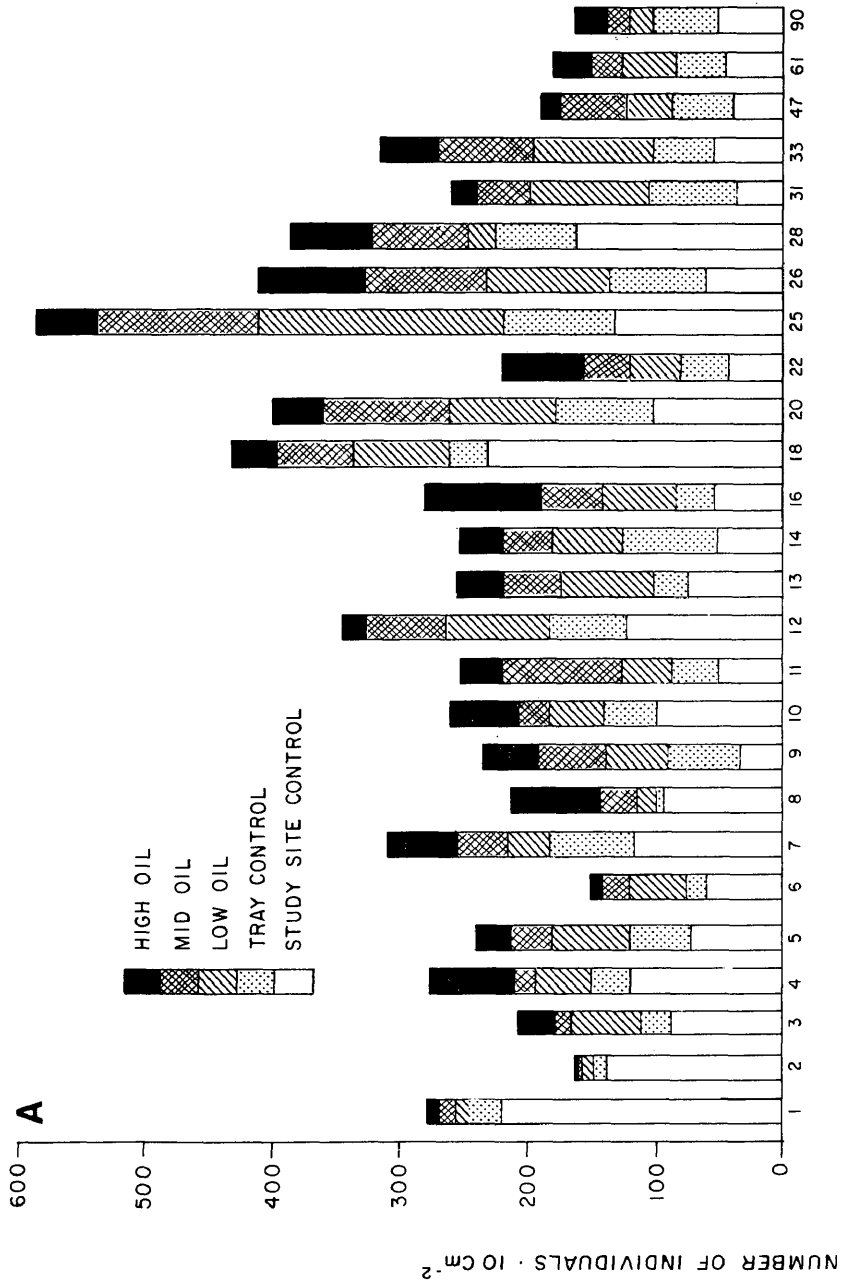
The delineation of response patterns for six species was hindered by their depressed abundance in the oiled treatments (Table 7). These species may perhaps be described as generally poor colonizers. Included in this group are Paracanthonchus sp., M. retrosetosus, P. proteus, Thalassoalaimus sp., Steineria sp. and Oncholaimus sp.

One interesting species pattern was the early occurrence of the epigrowth feeder M. parasitifera in the experimental boxes (sample groups C and E, Figure 16). This species exhibited a greater mean density in the low oil boxes (17/10 cm^2) than in the natural community (8/10 cm^2). Similarly, T. setosus attained a higher mean density in the low oil samples (14/10 cm^2) than the study site controls (10/10 cm^2), although it occurred comparatively late in the sampling period.

Species Diversity. The mean values of species diversity (H') for the experimental treatments and study site control samples are shown with the cluster diagram in Figure 13.

Diversity was a significant (p < 0.01) function of evenness and positively correlated with species richness. Kendall's coefficient of rank correlation (τ) was +0.65 for evenness and +0.14 for richness, respectively.

In the natural community, Shannon diversity values ranged from 2.43 to 3.43 bits/individual. Evenness and species richness ranged from 0.68 to 0.88 and from 1.31 to 1.95, respectively. All three community structure indices were not significantly (p < 0.01) different between the natural community and the colonizing communities. Index values for the communities from the oiled and untreated samples

ranged from 2.07 to 3.41 (diversity), 0.50 to 0.93 (evenness) and 1.29 to 3.13 (species richness).

Diversity was significantly (τ = -0.38, p < 0.05) inversely related to percent total organic carbon as was evenness (τ = -0.67) and species richness (τ = -0.35). A negative relationship also existed between the indices and percent silt and clay. The correlation was significant only for the evenness component (τ = -0.29). Conversely, a slightly positive correlation was established between percent sand and all three community measurements.

The relationship between these indices and petroleum hydrocarbon concentration was unclear. Diversity (τ = +0.35), evenness (τ = +0.29) and species richness (τ = +0.26) were positively correlated with total hydrocarbons; none of these correlations were significant at the 0.05 level. The correlations between the concentrations of selected aromatics (C1-, C2, and C3-naphthalenes, phenanthene, C1- and C2-phenanthenes) and diversity and evenness were positive (p > 0.05); species richness exhibited a negative relationship (p > 0.05) with these groups.

DISCUSSION

Colonization of oiled and untreated azoic muddy sands by meiofauna
was rapid at this shallow subtidal site, and generally greater than the
recovery times observed in prior recolonization studies (Table 8).
The colonizing meiofauna community periodically attained densities
similar to the natural community, but never progressed to an
equilibrium state. The linked ordination revealed that by Day 90
the untreated tray community overlapped the ordination space of
the natural community, suggesting complete recovery for the nematodes
in the unoiled trays.

Although the work of previous researchers had lead to the
tentative conclusion that meiobenthos disperse primarily by means
of resuspension, the examination of colonization rates and their
subsequent differentiation in both oxidized and reduced layers in
this study offer some additional and more substantive insights into
the resilience of meiobenthos. The entry of individuals into the
trays may be explained in the following manner. As tidal and wind-
forced currents and waves resuspend the thin surface layer of
aggregated fine sediment, the meiobenthos associated with the
surficial deposits is transported in the water column and settles
out, carpeting the tray surfaces along with the heavier detrital
aggregates. Those organisms capable of significant locomotion and
most tolerant to hypoxia are able to invade and move gradually to

Table 8. Compilation of previous studies investigating meiobenthic recolonization.

Locality	Depth	Nature of Disturbance	Recovery Time	Source
Sandy beach, North Wales, U.K.	intertidal	Artificial	within 20 days	Boaden, 1962
Western Baltic Sea	19m	Artificial	3 days	Scheibel, 1974
Sandy beach, Long Island, U.S.A.	1m	Artificial	within 90 days	Conrad, 1976
Long Island Sound, U.S.A.	15-20m	Dredge Spoil	one month	Rhoads et al., 1977
seagrass meadow, St. George Sound, Florida, U.S.A.	1.4-1.8m	Natural	1 day	Thistle, 1980
Mudbar, North Inlet Estuary, South Carolina, U.S.A.	intertidal	Artificial	1/2 day (1 tidal cycle)	Sherman and Coull, 1980
Meriadyed Terrace, Bay of Biscay, France	2160m	Artificial	within 6 months	Desbruyeres et al., 1980
Ythan estuary, Scotland	intertidal	Artificial	one month	Hockin & Ollason, 1981

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the lowest layers of the trays, perhaps during slack high and low tide. Palmer and Brandt (1981) found higher copepod densities in the sediments during slack water than during flood or ebb tides. Active migration via swimming and/or burrowing thru the interstices of the sands is a laborious process compared to passive dispersal, thus necessitating a longer period of time for colonization to occur below the redox potential discontinuity (RPD). The possibility of active habitat selection by meiofauna cannot be summarily dismissed since colonization may also occur by surrounding fauna via lateral migration through the puncture holes in the boxes. Gerlach (1977), Lee et al. (1977), Warwick (1977) and Jensen (1981) have shown nematodes and other meiobenthos, capable of selecting a habitat on the basis of food quality and/or physio-chemical stimuli.

Assuming such a scenario, doubt must be cast upon whether the meiobenthos colonized below the RPD in these prior studies. Since none of these workers subdivided samples into surface and subsurface fractions their conclusions of complete colonization may be premature; without fractionation, total abundance may account only for organisms initially deposited, and not a complete return to ambient conditions. These densities may be statistically equivalent to the natural community but provide no account of vertical distribution. Colonization can be considered complete only when the vertical distribution profile is reestablished. In addition, none of these studies utilized multivariate methods to analyze for the progression of the colonizing community - a possibly subtle sequence which may not be elicitable by univariate statistics.

The lack of a significant edge effect during colonization can be
interpreted in light of the small-scale nature of this disturbance –
the trays are only 0.1 m² in surface area. One can easily envision
resuspended sediment capable of carpeting the entire surface area of
the trays with a single pulse of suspended sediment.

Effects of petroleum hydrocarbon contamination

The presence of Prudhoe Bay crude oil in the disturbed sediments
was expressed by decreased levels of nematode abundance with no clear
relationship of species or community response to the hydrocarbon
concentrations. With the exception of the rare species, _Euchromadora_
sp. and _Desmodora_ sp., all species found in the natural community were
present in the oiled treatments. No other apparent changes were
discernible in nematode species composition in the oiled sediments
compared to the tray control assemblage. The linked reciprocal
averaging ordinations subtly reveal that the nematode taxocene which
colonized the oiled trays did not progress as far as the nematodes
in the untreated trays to the natural community. Such a result can
only be interpreted as incomplete recovery of the nematodes within
the oil treated experimental boxes. Also, the addition of crude oil
did not result in significantly decreased densities of meiobenthic
crustaceans, which are generally more sensitive than the other taxa
to the presence of hydrocarbons (Dalla Veneyia and Fossato 1977,
Elmgren et al. 1979). The apparent lack of demonstrable toxicity
for crustaceans is not surprising in view of Prudhoe Bay crude oil's
comparatively narrow suite of toxic aromatic components as compared to
other crudes, and especially, refined oils (Robert G. Riley, personal

communication, Smith 1981). Previous studies utilizing Prudhoe Bay

crude oil (Feder et al. 1976, Naidu et al. 1978) showed that meiofauna,

especially the crustaceans, were never adversely affected by oil at

the concentrations used.

In contrast to present ecological wisdom, the nematode community

structure indices of species diversity, evenness and species richness

were positively correlated with hydrocarbon concentration. Macro- and

meiobenthic communities in other polluted habitats have generally

exhibited lower values for these indices in comparison to relatively

pristine environments (Sanders et al. 1980, Marcotte and Coull 1974,

Tietjen 1980). Benthic researchers have usually ascribed this

occurrence to the toxic effects of the pollutant (s) and subsequent

diminution of favorable microhabitats. In this study, the phenomenon

may reflect the initial open habitat availability of the azoic oiled

sediments.

As a low diversity estuarine assemblage, the nematodes, like the

macrobenthos, may be adapted to absorb the stressful conditions of low

dissolved oxygen concentrations and high organic content coincident

with hydrocarbon contamination. Examining Table 4, the gradual

buildup of such a moderate concentration of aromatics in the natural

environment may have resulted in the gradual replacement of the more

fragile species by more suitable eurytolerant organisms. Though an

ecologically valid tenet, it does not actually explain how nematodes

and other meiofauna, can actively and/or passively invade a habitat

inundated with crude oil and maintain their normal functions (feeding,

respiring, reproducing). The mechanical and/or physiological

interference with reproductive processes by petroleum may partly account for the observed decreased levels of nematode abundance (see Table 7).

The nematodes may counter the toxic effect of the aromatic compounds by various physical, physiological and behavioral adaptive mechanisms. Examination of the dominant species by scanning electron microscopy revealed that none of these species possess cuticle pores which may facilitate the entry of hydrocarbons into the body proper (Alongi, unpublished ms.). Nematodes possess a three layered cuticle consisting of cortical, median and basal layers (Bird 1971, Lee and Atkinson 1977). The cuticle is semipermeable, capable of being penetrated by neutral non-polar lipophilic molecules, but not particularly permeable to dissolved water soluble organics (Chia and Warwick 1969, Tietjen and Lee 1975). Since the lower molecular weight aromatics such as benzene and toluene, are small, of relatively low polarity and are lipophilic, it is reasonable to suppose their entry and absorption into the hypodermis, the chief lipid reserve in free-living nematodes (Atkinson 1977). The absorptive nature of the hypodermis should be capable of effectively negating the toxicological effects of aromatics as well as further progression into the body proper.

As an alternative adaptation, nematodes may possess hydrocarbon-metabolizing enzymes enabling the worms to metabolize aromatic hydrocarbons to numerous hydroxylated derivatives, as discovered by Lee et al. (1977, 1979, 1980) in the polychaetes Capitella capitata and Nereis virens. As for the n-alkanes, viable hydrocarbon-degrading

bacteria ingested during feeding and residing within the esophageal lumen, may assist in rapid degradation of the n-alkanes.

Crawling throughout the interstices during their life cycle, the worms cannot overtly avoid exposure to the petroleum. The oil within the substrate is retained by the dissolution of the water soluble fraction (LMW aliphatics and aromatics) in the pore waters, and the sorption of the heavier compounds (especially n-alkanes) to organic particulates.

Nematodes at this muddy sand site are predominantly detritivores which feed by picking bacteria attached to extremely small (<3 μm) particles and/or unattached within the interstitial pore waters. Since the less soluble aliphatics sorb onto sediment particles, nematodes possessing any of the suite of adaptations mentioned above may be tolerant to the more toxic water soluble fraction and thus relatively immune to the effects of oil. Competitively superior nematodes will feed on the more abundant bacteria attached to the particulates and be exposed primarily to the less toxic and more readily degradable n-alkanes. Those species competitively excluded from this microhabit are restricted to feed on pore water bacteria, exposing themselves to the more toxic hydrocarbon components. Such limited niche separation has been postulated for competitive nematode species in mixed laboratory culture (Alongi and Tietjen 1980).

The few studies designed to investigate the uptake and bioaccumulation of hydrocarbons by macrobenthic deposit feeders indicate greater availability of hydrocarbons from organic particulates than from pore waters (Anderson et al. 1977, Rossi 1977, Roesijadi

et al. 1978). Regardless of which hydrocarbon reservoir is utilized, the very presence of nematodes indicates an intrinsic capacity to tolerate the available toxicants.

The deleterious effects of oil contamination may be manifest in the long-term, leading to an eventual modification of nematode community composition, although it is impossible to predict such an occurrence at this point in time. A particularly pertinent example lending credence as to the possibility of such a phenomenon is the study by Boucher (1981) investigating the long-term effects of the Amoco Cadiz oil spill off Morlaix Bay, English channel. Monitoring the affected nematode community during the year after the spill, the effects of the oil were especially evident between nine and twelve months after the accident.

Conclusions reached on the basis of long-term evidence are still subjective and tentative at best. Nothing is known concerning nematode behavioral and physiological modifications when subjected to a pollutant. The total lack of laboratory studies designed to assess the sublethal effects of petroleum on nematodes, and other meiobenthos, should result in a considerable amount of skepticism with regard to sanguine conclusions based only on field data.

Adaptive strategies and succession

The initial colonization and subsequent recruitment sequence of nematodes following a perturbation is not as stochastic a process as previously conjectured (Sherman and Coull 1980, Bell and Sherman 1980). A successional sequence of nematode colonization was found in the

experimental treatments; similar successional patterns were discernible in all four treatment types (Figure 24).

The successional pattern agrees most closely with McCall's (1975) model of macrobenthic colonization of azoic substrates describing the adaptive response of the benthic infauna as three successive 'pulse waves' of propagules. The first group termed first wave dominants (Fredette 1980), initializes the colonization sequence. Members of this group are ascribed as being opportunistic in their life strategies, and thus susceptible to catastrophic population decline after initial invasion. Axonolaimus spinosus apparently falls within the first group generally exhibiting early colonization and gradual decline. The less common epigrowth feeder Metachromadora parasitifera was also an early inhabitant of the treatments and can be listed as a Group I member.

During the decline of members of the first group, a second wave of dominants (Group II, McCall 1975) begins to colonize the habitat, slowly attaining peak abundance and then declining to the end of the successional process. These colonizers are probably intermediate along the r-K continuum (Pianka 1970, 1974) in terms of life history tactics. Members of this group II are Ptycholaimellus ponticus, Theristus oxyuroides, Neotonchus punctatus. Metalinhomoeus typicus and Anticoma litoris exhibit such a pattern and may be readily ascribed to this group, although depauperate densities obscures their patterns of colonization. The third group of recruits, termed stable point dominants by Fredette (1980), initially colonize at low densities and gradually become dominant after the preceding groups have declined. The group is persistent over the long term, and may best

Figure 24. Schematic plot of colonization curves of most abundant
nematode species in natural community from tray control
and oiled treatments.

TRAY CONTROL LOW OIL

MID OIL HIGH OIL

ABUNDANCE

TIME →
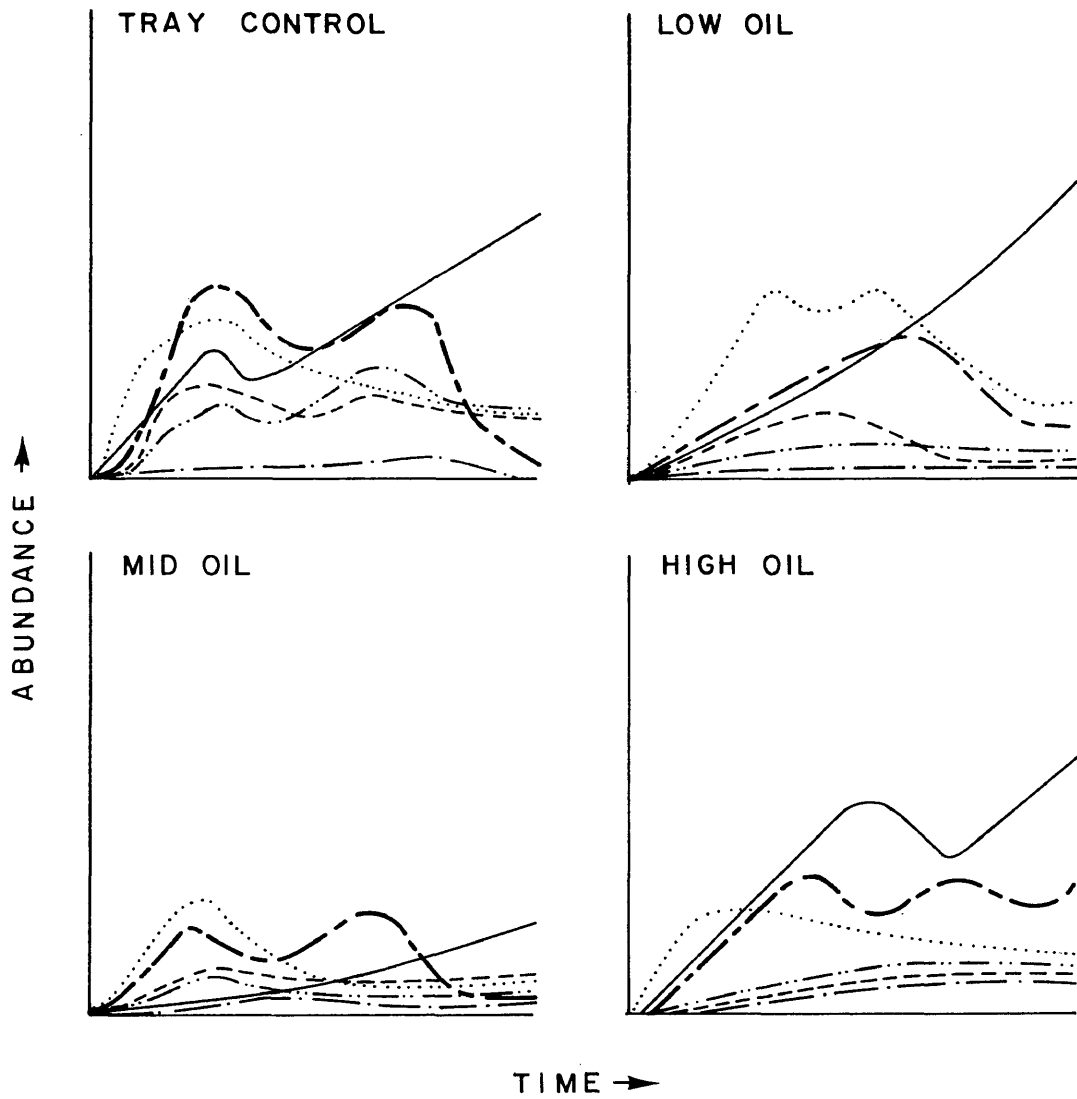
——————— Sabatieria pulchra   ——··——Theristus oxyuroides

············ Axonolaimus spinosus   — — — — Neotonchus punctatus

——·——Ptycholaimellus   ——·——Metalinohomoeus typicus
               ponticus   and Anticoma litoris

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be characterized as maintenance-process species. Only the detritivore
Sabatieria pulchra which became the dominant nematode by the end of
the successional sequence, fits such a recruitment pattern. The close
fit of this successional sequence to McCall's (1975) model suggests a
universality of benthic response to disturbance, although lack of
knowledge concerning life histories of individual nematode species
renders further conjecture unwise.

The three succession models developed by Connell and Slatyer (1977)
(Figure 25) may be applied to the nematode recruitment tactics. In the
facilitation model (Model 1), they propose that early-succession
species such as *A. spinosus* and *M. parasitifera*, modify the environment
to create a more suitable condition for the invasion of late
successors. Modification by meiofauna would include bioturbation
since sufficient evidence for the phenomenon exists (Cullen 1973,
Rhoads *et al*. 1977, Yingst and Rhoads 1978). Meiofaunal bioturbation
may also contribute to further habitat modification by depression of
the RPD layer (Rhoads *et al*. 1977). However, in this study, continual
measurement revealed no substantial change in the RPD within any of
the experimental treatments.

By the very nature of this model, one must then envisage early
colonizing species as being greater opportunists than the later
successors. Unfortunately, only two prior studies (Sherman and Coull
1980, Thistle 1980) have identified meiobenthic taxa to species level
in order to examine whether a change in species composition occurred
during recruitment. Based on previous fragmentary data, one would
speculate that all nematodes (and perhaps other meiobenthos) are

Figure 25. Three successional models hypothesized by Connell and

Slatyer (1977). (Modified from Connell and Slatyer 1977).

Catastrophic Disturbance

Stochastic Survivors established

Suitable Early Colonizers established

Habitat modification by initial colonizers results in less suitability for recruitment of subsequent early and late succession species.

Individuals of initial colonizers persist, excluding or supporting subsequent colonists.

Habitat modification by early colonizers resulting in less suitability for additional early colonists, but little or no effect on recruitment of late succession species.

Maturation of late succession species in presence of early successors. Later, early colonizers are eliminated.

Habitat modification by early colonizers resulting in less suitability for additional early colonists, but more suitability for late succession species.

Maturation of late succession species. Earlier colonizers are eliminated.

Late successors dominate, concluding successional sequence.

Renewed Catastrophic Disturbance

opportunistic, with no distinction with regard to early-or late-
succession species. However, as evidenced in Figure 24, the
nematodes in the present study exhibited differential opportunism.

The second model (tolerance model) proposes neither increase nor
reduction in the recruitment rates and growth of late colonists brought
upon by the habitat modifications produced by the early colonists.
This initial modification results in less suitability for recruitment
of early colonizers. If meiofauna behaved in such a fashion, one
would probably observe a fluctuation in meiofauna recruitment. As
early colonists modify (bioturbate) the environment, the habitat
becomes more unfavorable for their growth which leads to a decline
in their abundance. The subsequent invasion of the late colonizers
would begin. Evidence for such a scenario is supplied by Rhoads et al.
(1977). They observed a decrease in meiofauna abundance after initial
recruitment and attributed the decline to partial destruction of the
fecal pellet layer by grazing meiofauna. The meiofauna colonizing the
York River boxes did fluctuate greatly, but to ascribe such fluctuation
to partial destruction of the fecal pellets was beyond the scope of
this project.

Finally, the inhibition model (Model 3) states that the very first
recruits interfere with further invasion by habitat modification,
preventing colonization by late-succession species. Connell and
Slatyer (1977) claim no species necessarily has competitive superiority
over another. Consequently, all species are capable of resisting
invasion of competitors. Evidence exists demonstrating that
competition does indeed occur among nematodes of the same trophic

type (Alongi and Tietjen 1980). Though a valid explanation for the patterns of colonization observed in this study, it is difficult to conceive how evidence to suggest interference by initial recruits with subsequent invaders can be ascertained.

The colonizing capability of nematodes may be a function of a suite of factors such as their susceptibility to dislodgement via physical disruption, ability to withstand stress, and their behavioral patterns. A species inhabiting the deeper, anoxic layers would probably not colonize as quickly as a species restricted to oxidized regions, where it would be susceptible to the effects of sediment turbation. The fact that Anticoma litoris was a poor colonizer and inhabitor of the deeper substrata bodes well for this caveat. As a facultative anaerobe, A. litoris should be well adapted to tolerate the anaerobic conditions enhanced by oil addition. Wieser and Kanwisher (1961) found A. litoris capable of living anaerobically for at least 50-60 days in laboratory culture. However, other poor colonizers such as M. typicus were found mainly within the top centimeters but may perhaps be more obligately anaerobic than A. litoris and/or less habitat restricted.

It is reasonable that recruitability is not a function of a single variable but of several. For example, although A. litoris is a facultative anaerobe it may be too restricted in its habitat requirement or locomotory abilities to colonize within the period sampled. Wieser and Kanwisher (1961) often observed this species lying motionless or coiled within their culture dishes suggesting that it is a relatively quiescent organism. Sabatieria pulchra, like A. litoris, is a

facultative anaerobe, but was homogeneously distributed with depth and was an excellent colonizer. Undoubtedly, the other nematode species also express variability with regard to these factors, making generalizations and/or predictions of recruitment capability incongruous.

Meiobenthic opportunism and the concept of r and K selection

Empirical evidence has been presented to support the hypothesis that nematodes are differentially opportunistic at least in inconstant environments, and can exhibit a successional sequence upon recruitment. The designation of certain nematode species such as A. spinosus and M. parasitifera as opportunists, and S. pulchra as a stable point dominant, leads to several interesting observations concerning the applicability of the established concepts of opportunism and r-K selection to meiobenthic organisms.

Ecological theory postulates that following a disturbance, species whose life histories and dispersal abilities adapt them for rapid arrival and dominance in a perturbed habit are termed 'opportunistic' (Grassle and Grassle 1974), and possess correlates attributable to r-strategists (Pianka 1970). The subsequent decline of such species after abatement of pollution which permits other less eurytolerant species to colonize, has lent credence to the hypothesis that opportunistic species are poor competitors.

Based on the definition of an opportunistic species, one would have expected A. spinosus to maintain its dominance in the oiled sediments since although a considerable amount of oil was lost, the

toxic aromatics were still present in substantial concentrations at the end of the sampling period, especially in the high oil treatment, to supposedly limit the number of species capable of colonizing. Wieser and Kanwisher (1961) observed A. spinosus' intolerance to anaerobic conditions. The past and present evidence form a basis for an apparent contradiction. A spinosus exhibited a colonization pattern typical of an opportunist, but is not eurytolerant -- a primary attribute of an opportunistic species.

Another paradox is presented by Sabatieria pulchra. Like its macrobenthic counterpart Capitella capitata, S. pulchra and other congeners have been consistent in their dominance under polluted conditions (Tietjen 1977, 1980; Bowman 1978, Giere 1979, Boucher 1980; Alongi, unpublished data). It has been conjectured that species of this genus are opportunistic on the basis of this empirical evidence (Preben Jensen and John H. Tietjen, personal communications). However, the colonization pattern of S. pulchra was reminiscent of a stable point dominant strategy in all of the experimental treatments – a recruitment strategy characteristic of species with K-selected life history characteristics. A subdominant in the natural community, S. pulchra was the dominant species in all treatments by the end of the sampling period, having attained considerably higher abundances in all treatments than in the natural community. Can S. pulchra be described as a K-selected, maintenance-process species with low resilience (compared to the other species) and good competitive ability, and yet be an opportunistic species?

Warwick (1980) presents substantial evidence to account for the conservative reproductive behavior of meiofauna, describing the life history characteristics of these phyla as typical of K-strategists. A comparison of attributes between a 'typical' meiobenthic species and r- and K-strategists reveals the apparent dichotomy between ecological theory and meiobenthic population biology (Table 9). Although the concept of r and K-selection has no absolute criteria for the classification of a species, S. pulchra's conservative colonizing strategy and its possession of attributes characterizing opportunists forces one to realize the limitations of certain ecological theories as applied to the lesser studied phyla.

If we conclude on the basis of the conflicting attributes summarized in Table 9, that S. pulchra is not an opportunistic species, especially since it did not colonize as such, one is lead to the conjecture that nematodes dominating in polluted sediments are not necessarily opportunistic but on the contrary, may in fact be more eurytolerant, efficient species possessing greater competitive ability within the nematode taxocene. Such an a posteriori concept is contrary to present dogma but a logical explanation of the observed colonization patterns and the dominance of Sabatieria pulchra in other polluted habitats. Evidence for this species' competitive capabilities may be gleaned from its dominance in the untreated samples. Although both oiled and untreated trays represent types of disturbance, they differ in the presumed residual effect caused by petroleum hydrocarbons. In addition, S. pulchra has been found to be a relatively quiescent organism in laboratory culture (Preben

Table 9. Comparison of attributes between a 'typical' meiobenthic species

and r and K strategists.

meiobenthic species	r strategist	K-strategist
high intrinsic rate of natural increase, r	high r; low competitive ability	low r; high competitive ability
delayed reproduction	early reproduction	delayed reproduction
small body size	small body size	large body size
repeated reproduction	single reproduction	repeated reproduction
high recruitment	high recruitment	low recruitment
few small offspring	many small offspring	few large offspring
short lifespan	short lifespan	long lifespan
variable population over time, at or near carrying capacity, K	variable population over time, below K	fairly constant population over time, at or near K

Jensen, personal communication). Such behavior is not in accordance with our stereotyped view of an opportunist as being a rather dynamic organism.

Although the meio- and macrobenthos are separated only arbitrarily on the basis of sieve size, this artificial division isolates components of an assemblage which differ not only in their behavioral, metabolic and physiological requirements, but reproductive strategies and ecological niche as well. Thus, the meiofauna provide a fine contrast to larger benthic organisms in the testing of recolonization-disturbance theory formulated primarily on the basis of the life histories of larger (>1 mm) organisms (terrestrial and aquatic). The ubiquitous nature of marine nematodes in concert with our lack of knowledge concerning their life history tactics, renders the application of such models to meiobenthic communities problematic.

Community Stability

Estuarine meiobenthic communities can be characterized by their low constancy, but are stable to disturbance due to their high resistance and resiliency. Boesch (1974) concluded that such attributes are typical of estuarine benthos. The short-term fluctuations observed for the meiobenthos at this site and others (Rhode Island, Tietjen 1969; Bermuda platform, Coull 1970; Helgoland Bay, Stripp 1969) as well as the long-term meiofaunal variability in North Inlet estuary, South Carolina (Coull and Bell 1979) suggest their low persistence. However, the capacity of meiobenthos to recover rapidly from catastrophic disturbance attests to their high

resilience and resistance (sensu Boesch 1974) in an estuarine

ecosystem.

The results of this study tend to support the stress tolerance

model of Boesch and Rosenberg (1981) which predicts the greater

resistance to stress by estuarine communities because they are

composed of more eurytolerant resistant species by virtue of their

natural adaptability to an inconstant environment than communities

inhabiting more constant environments. Their hypothesis further

states that following a perturbation in a less constant environment,

initial colonizers will consist, for the most part, of natural

community dominants. In this study, one of the less common species,

M. parasitifera was an initial colonist, whereas A. litoris - a

dominant species in the natural community - was a poor colonizer.

Stress tolerance is manifest and effective at the individual or

population level (Boesch and Rosenberg 1981). However, such

generalization ignores the fact that not every species of an

estuarine community may be equally tolerant to various forms of

stress. For example, A. litoris is a dominant especially below

the RPD in the York River. By virtue of its distribution, such a

species must be capable of withstanding the continual stress of

inhabiting a low oxygen environment. However, its inability to

colonize following a disturbance suggests the importance of

considering the type of stress to which such species are exposed.

In other words, a given species may not react similarly to different

forms of induced stress because each type of stress may test different

physiological and behavioral capacities of an organism. A. litoris

may be tolerant of depleted oxygen conditions and toxic sulfides, but intolerant of petroleum hydrocarbons. Undoubtedly, its extremely poor competitive abilities partly account for its inability to invade the experimental treatments.

Judgment in support of the Boesch and Rosenberg (1981) model must be tempered by a total lack of knowledge concerning the stability of meiobenthic communities in quiescent environments (deep sea, etc.). A true characterization of meiobenthic community stability can only be explicated by further analysis of life history strategies, productivity, competition, and physiological limitations of these organisms.

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