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FACULTY OF GRADUATE STUDIES

The undersigned hereby certify that they have read and recommended to the Faculty of Graduate Studies for acceptance a thesis entitled " The Ecology of Meiobenthic Harpacticoids (Crustacea: Copepoda) in West Lawrencetown, Nova Scotia.

"

by Brian M. Marcotte

in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Dated September 1, 1977

External examiner
Research Supervisor
Examining Committee

[redacted]

Table of Contents

Table of Contents (cont'd)

ABSTRACT

Meiofauna were collected in 6 sets of 15 randomly distributed core tube samples taken bimonthly from sediments in an estuary in West Lawrencetown, Nova Scotia. Harpacticoid species were identified as to age, sex and reproductive state. 40 species were found. they were assembled into 3 groups according to the substrates they inhabited: sand, mud and mixed sediments. Video-tape observation of copepod feeding revealed 4 trophic groups defined by the geometry of the particles from which they get their food. 1) Point Feeders. Ameiria longipes and A. parvula were selective epistrate feeders, obtaining food from solitary points on large particles of sand and organic detritus. 2) Line Feeders. Heterolaophonte capillata and H. discophora lived and fed only on rectilinear edges and cylinders of blue green algae and worm tubes. 3) Plane feeders. Halectinosoma sp. 1 and Pseudobradya sp. 3 scraped food from the planar surfaces of sand. Dactylopodia sp. 1 swept food (diatoms) from the planar surfaces of algae and Zostera detritus. 4) Solid Feeders. Tisbe furcata fed on nematode prey and balls of detritus. Leima vaga, Amphiascus minutus and Amphiascoides debilis fed on balls of detritus. Microarthridion littorale and Enhydrosoma longifurcatum sorted food from tiny rubble. Stenhelia divergens ate diatoms.

Patterns of spatial and temporal distributions, morphometric changes and demographic structures are used to substantiate the hypothesis that competition can be an important factor structuring the ecology of meiobenthic communities.

Table of Abbreviations

The following abbreviations are used to designate oral and thoracic appendages.

A_1 = First Antenna, antennula

A_2 = Second Antenna, antenna

Md = mandible

Mx_1 = First Maxilla, maxillula

Mx_2 = Second Maxilla, maxilla

Mxp = Maxilliped

P_1 = First leg

The following abbreviations are used to designate species in the discriminant function analyses.

A = *Halectinosoma* sp. 1

B = *Pseudobradya* sp. 1

C = *Pseudobradya* sp. 2

D = *Tachidius* sp. 1

E = *Microarthridion littorale*

F = *Tisbe furcata*

G = *Dactylopodia* sp. 1

H = *Stenhelia divergens*

I = *Amphiascus minutus*

J = *Amphiascus propinquus*

K = *Amphiascoides debilis*

L = *Ameiria longipes*

Table of Abbreviations (Cont'd)

M = *Ameria parvula*

N = *Mesochra lilljeborgi*

O [illegible] *Mesochra pygmaea*

P = *Mesochra* sp. 1

Q = *Enhydrosoma longifurcatum*

R = *Heteropsyllus nunni*

S = *Leima vaga*

T = *Heterolaophonte capillatus*

The following abbreviations are used to designate physical variables in the discriminant function analyses.

1 = Temperature (°C)

2 = O_2 (PPM)

3 = Salinity (°/₀₀)

4 = pH

5 = Eh

6 = Porosity (% H_2O by weight)

7 = Organic Carbon (% C by weight)

8 = Percent Mud (sizes 2 µm to 101 µm)

9 = Percent fine sand (sizes 128 µm to 256 µm)

10 = Percent coarse sand (322 µm to 1024 µm)

11 = Grand Mode

12 = Mode of mud fraction

13 = Mode of fine sand fraction

14 = Median

15 = Percent standard deviation

16 = Percent skewness

17 = Percent kurtosis

18 = Mean

19 = Standard deviation

20 = Skewness

21 = Kurtosis

The following abbreviations are used to designate sediment particle sizes in the principle component analysis.

1 = 2.00 μm
2 = 2.52 μm
3 = 3.17 μm
4 = 4.00 μm
5 = 5.04 μm
6 = 6.34 μm
7 = 8.00 μm
8 =10.08 μm
9 =12.7 μm
10 =16.0 μm
11 =20.2 μm
12 =25.4 μm
13 =32.0 μm
14 =40.3 μm
15 =50.8 μm
16 = 64.0 μm
17 = 80.6 μm
18 =101.6 μm
19 =128. μm
20 =161. μm
21 =203. μm
22 =256. μm
23 =322. μm
24 =406. μm
25 = 512 μm
26 = 645. μm
27 = 812. μm
28 =1024. μm

Acknowledgements

I thank the people of Canada for financially supporting this research programme. I thank Kate Kranck and David Walker for use of their special facilities and knowledge at the Bedford Institute of Oceanography. I thank John Wright for assistance with the computer analyses and Alex Wilson and Mary Primrose for sharing their photographic expertise. Especially, I thank Eric Mills for giving me the space and time to grow both personally and professionally while at Dalhousie. To my parents, Roland and Eileen Marcotte and to John Lanci, C. S. C. I dedicate this thesis. They gave me life and love, helped me to grow, and showed me goodness and wisdom.

VOCATUS ATQUE NON VACATUS, DEUS ADERIT

Delphi

PREFACE

Truth is always sufficient but seldom necessary. Science, true understanding, is a very human form of knowing. It is not objective; knowing is not by confrontation. There is only intentional presence and this of two kinds: object to subject and subject to himself. Of the first type, insight, an act of understanding, stands between sensible data and the concepts whose true definition is sought. Of the second, one is present to oneself not as object being attended but as subject attending. Science proceeds methodically from empirical experience to intelligent inquiry and understanding to rational reflection and judgement. Its method ends in personal responsibility: deliberation, evaluation and action. Its compound issue is real and good. Science is honourable, a virtuous endeavour, its own reward.

I assert these fundamental notions to underscore both the personal intent of my method and the cognitive status of my results. What follows is an account of the ecology of bottom-dwelling, marine harpacticoids (Crustacea: Copepoda) in Nova Scotia. The world of these ancient argonauts is a thousand micron sea. It is a world of flake and stone, of crystalline herbs and truffled gardens, of thimble mountains and ever-shifting sand. It is not the pickled muds museums house, just as human society is not a city morgue. Rather, their world can only be understood as they would live in it: sense it, explore it, eat, rest, reproduce. Meiobenthic harpacticoids are not distributed in space and time; they are space and time. Their physiology, morphology and behaviour define the dimensional space in which they live and of which their evolutionary history can only hint. Meiofauna adapt not in time but embody it; size and community structure are the sensible beat of their clock. In short, their physics exists only in so far as they live and our understanding of them exists only in so far as we can take on their life. For this end, the present thesis begins.

INTRODUCTION

Marine meiofauna are small (< 0.5 mm), bottom-dwelling metazoans from most invertebrate phyla (Mare, 1942; McIntyre, 1964, 1969; Thorson, 1966). Numerically important among these are nematodes and crustacean copepods of the order Harpacticoida. Meiofauna outnumber and are energetically perhaps five times more active than their macrobenthic counterparts (Coull, 1970; Gerlach, 1971). Meiofauna biomass exceeds that of macrofauna in regions of high environmental stress, oligotrophic seas and in the deep sea (e.g. Guille and Soyer, 1968; McIntyre, 1971; Thiel, 1972a, 1972b). These small organisms contribute to production at higher trophic levels either directly as food or indirectly through nutrient recycling (Coull, 1970). For example, meiobenthic harpacticoids are a crucial food source for pink and chum salmon fry when they first enter the sea (Kacyznski, Feller and Clayton, 1973). Harpacticoids may also be important vectors of fish disease (McClelland, pers. comm.). Despite the substantial contribution of meiofauna to marine ecosystems, they are little studied.

The purpose of this study was to observe and understand the kinds of meiobenthic harpacticoids living in a Nova Scotian estuary and to construct hypotheses concerning those environmental factors which contribute most to the ecological distribution and longterm persistence of these copepods. The results are organized into three parts as suggested by the works of Humboldt (1807, 1847, 1850), Brown (1814); Lyell (1832), de Candolle (1855), Darwin (1859), Shelford (1911), Grinnell (1917), Gause (1934), Hutchinson (1957) and Pianka (1974). All populations live in some habitat at some time (seasonal or diel) and have some source of food. From these same studies it is clear that if more than one population attempts to live on the same, finite food source and habitat at the same time, competition can occur. This interaction may result in extinction or coexistence with associated adaptations involving habitat, temporal or trophic specialization.

The habitat and temporal distribution of meiobenthic harpacticoids have been described a number of times. For example, Noodt (1952) and Ivester and Coull (1977) have correlated species distributions with sediment grain size and other environmental variables. The seasonal succession of meiofauna has been studied by, for example, Noodt (1952), Coull (1968), and Elmgren (1976). Diel rhythms have been studied by Hauspie and Polk (1973).

The feeding of harpacticoids is practically unstudied. Lang (1946, 1948a, 1948b, 1965) has given some information on the architecture of harpacticoid oral appendages. Marcotte (1977) has provided the only precise analysis of oral kinematics in one species, Tisbe furcata. The gut contents of preserved specimens has been examined by, for example, Fraser (1936), Noodt (1957), Perkins (1958), Muus (1966), Gilat (1967), Coull (1968) and Fenchel (1969). These reports are usually of only limited value since harsh preservatives destroy delicate food items in the gut and they often promote egestion of food. Finally, feeding experiments have yielded some information on the metabolic success of some harpacticoids on diatom food (Sellner, 1973).

The present thesis will examine the architecture and kinematics of feeding in 12 species of harpacticoid. These data will provide information on what the copepods eat, how they feed and how the structure and function of oral appendages are related to behaviour both physical and appetitive.

METHODS AND MATERIALS

The study area is an estuary behind Conrad Beach in West Lawrencetown, Nova Scotia (Fig. 1). The bathymetry of the estuary was measured with a meter stick using the water level of higher-low tide on 11 January 1975 as an elevation datum. Diel changes of temperature, salinity and O_2 concentration in the sediment-seawater interface at subtidal station A (Fig. 3) were measured on 11 January, 8 February and 3 September 1975. Cyclic changes in the direction of water currents in and out of the estuary were observed on 11 January 1975.

Meiofauna were collected with 6 sets of 15 hand core samples taken bimonthly for one year. Subtidal sample stations were randomly located each month (Fig. 2) by rowing a boat or walking along a channel until a sound (car horn, cannon fire or bird call) was heard. Then, stopping, the core tube was lowered without visual guidance until it was just off the surface of the mud or sand. Then the sample was taken at that location in the usual manner as in Hulings and Gray (1971).

At each location, two coretube samples were taken, one for biological study, the other for measurement of physical variables. One tube had an inner diameter of 3.5 cm, a sample area of 9.621 cm^2. From it two subsamples were immediately taken. The flocculent layer at the surface was first removed using a large

Figure 1. Map of Nova Scotia and West Lawrencetown Marshes.

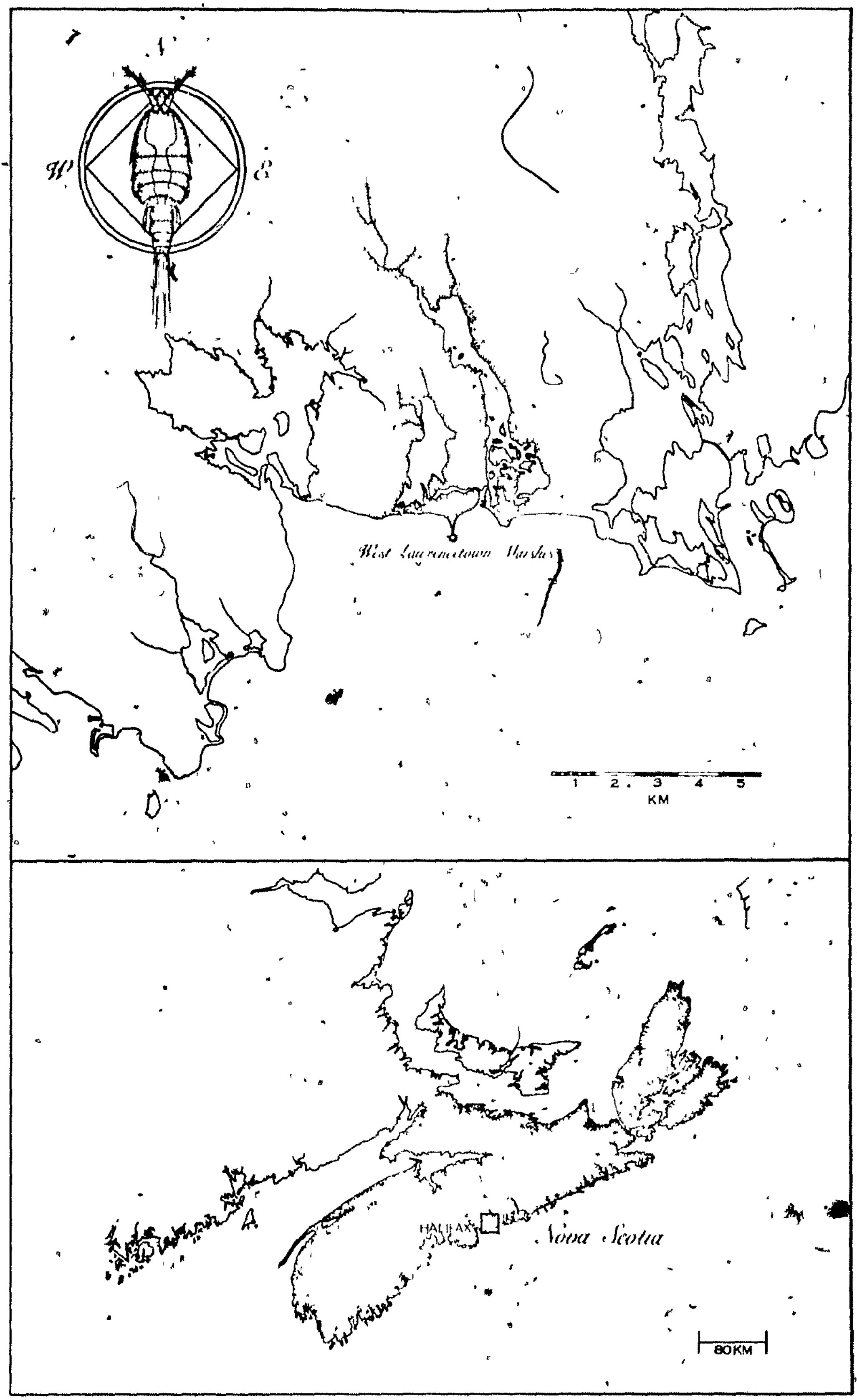
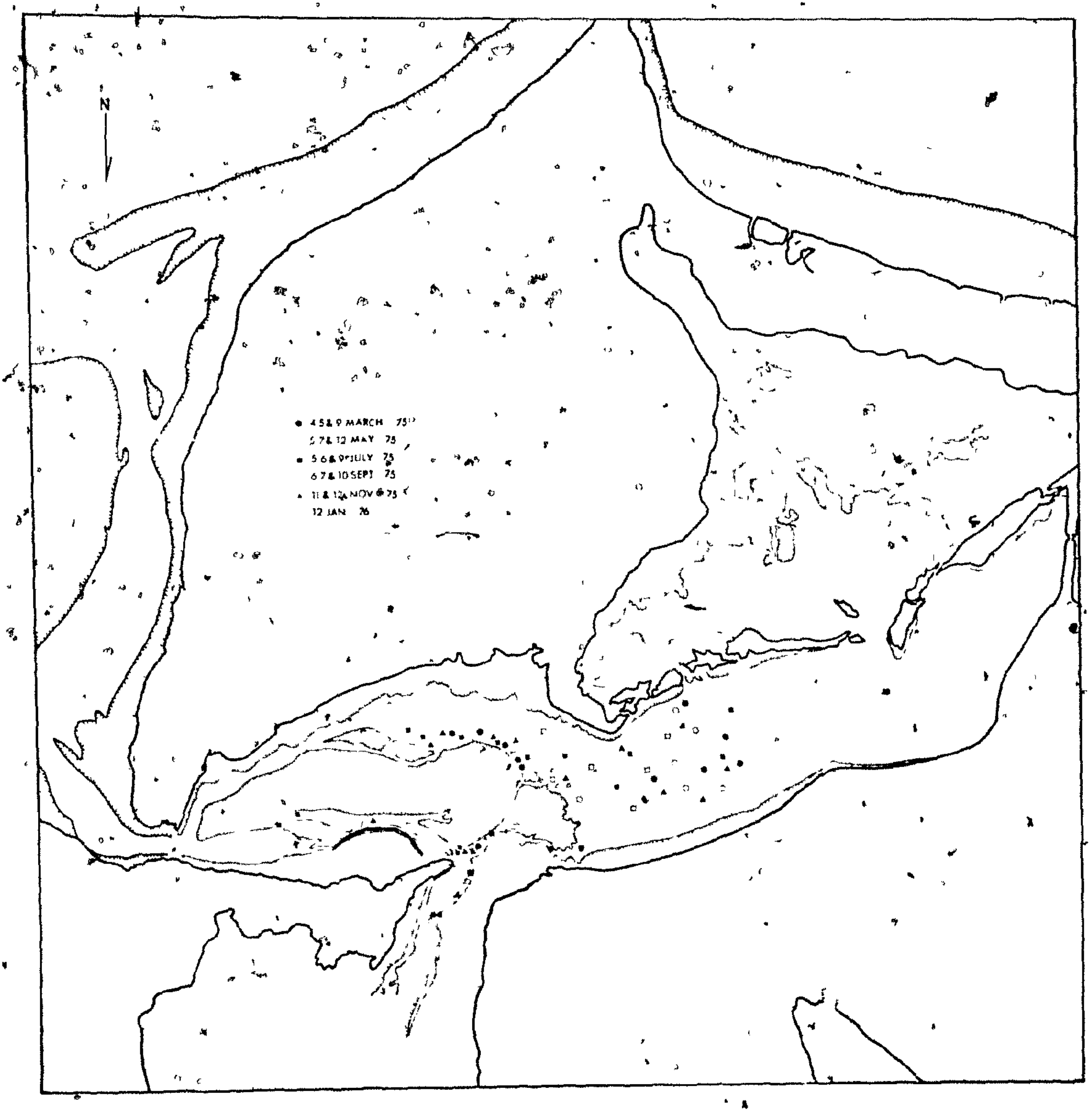

W
E
West Lawrencetown Marsh
1
2
3
4
5
KM
HALIFAX
Nova Scotia
80KM

Figure 2. Map of estuary behind Conrad Beach in West Lawrencetown, Nova Scotia with all sample sites marked.


N
● 4 5 & 9 MARCH 75
5 7 & 12 MAY 75
■ 5 6 & 9 JULY 75
6 7 & 10 SEPT 75
▲ 11 & 12 NOV 75
12 JAN 76

bulb pipette. Then the compact layers below were removed to a depth of 5 cm. These subsamples were placed in separate jars. The contents were fixed and stored in 5% glutaraldehyde solution in seawater until sorted. Each subsample was subsequently washed with seawater through a 500 μm, 125 μm and a 63 μm sieve. From the fractions retained on the sieves less than 500 μm, all harpacticoids were removed, counted and identified as to species, sex, age and fecundity. All nematodes were counted and the first 100 individuals were removed. All other meiofauna were removed, counted and identified to major taxon.

The second core sample was taken from sediment adjacent and similar to that in the first core sample. This second core tube had an inner diameter of 5.6 cm. From this sample the following variables were immediately measured: temperature, O_2 concentration and salinity. Eh and pH in both the flocculent and compact zones were also measured. (See Appendix A for a list of all instruments used). This core was then placed in ice and returned to the laboratory. It was then frozen at -21°C. Later, the frozen sediment was extruded. The flocculent and compact layers were successively sawed from the sample. One half of each of the resulting frozen wafers was weighed, dried at 40°C and weighed again. The loss of water was taken as an index of sediment porosity. This dried sample was then crushed to a fine powder. Approximately 0.5 gms of the resulting powder were weighed, oxidized in a low temperature asher for at least 12 hours and weighed again. The difference in weight was taken as a measure of organic carbon present in the sediment. A small portion of the second half of the frozen wafer was suspended in a glycerin-electrolyte solution. The size distribution of the sediment particles in the suspension was measured at 27 intervals (2 - 1024 μm) using a specially equipped Coulter Counter (Krank, unpublished technique). The frequency distribution of particle sizes was finally expressed as a percentage of the total sample volume. The following statistical measures were calculated: percent mud (2-100 μm), percent fine sand (128-256 μm), percent coarse sand (322-1024 μm), mode of mud, mode of fine sand, mode of coarse sand, median, percent standard deviation, percent skewness, percent kurtosis, mean, standard deviation, skewness, and kurtosis.

The kinematics of feeding and locomotion in the 12 numerically dominant species of harpacticoid were studied. Live copepods were collected from sediments and algal scrapings. Populations were separated to species and kept overnight in food-free sea water at 10°C. The following morning, active individuals were placed in depression slides containing one of the following substrates.

1. Pure sea water
2. Sea water and methyl-cellulose
3. Sea water and a culture of the diatom <u>Thalassiosira fluviatilis</u>
4. Sea water, methyl-cellulose and the diatom <u>T. fluviatilis</u>

The copepods were observed by means of a Zeis Universal Microscope fitted with a mercury vapour light source and a darkfield epi-illuminator. The feeding and locomotor behaviour of the copepods was video-taped by means of a Sony television camera mounted atop the microscope. The image was recorded at a rate of fifty frames per second on a Sony videotape recorder. These tapes were later viewed in slow motion with repeated stop-motion examination of individual appendages.

In situ observations were also made of individuals living in laboratory mud, sand and mixed sediment cultures and feeding on large detritus particles, rubble, diatoms and nematode prey. The swimming behaviours of the species were timed using a stop-watch. For this purpose, animals were placed in fingerbowls in which at least 5 cm of seawater lay over the sediment covered bottom. These observations further clarified the function of oral movements observed in the video-tape studies.

Anatomical results presented in this essay were obtained from the same individuals as were the video-tape studies. After the video-taping session, individuals were fixed in 4% formalin and examined with phase contrast microscopy. The oral region of these specimens was divided between the first and second maxillae and mounted on a glass slide with the posterior surface upward. Individual appendages were then drawn with the aid of a camera lucida. If details were obscured in these mounts, further dissection followed, but only after the proper position and general shape of the individual mouth parts had been recorded. Examination of at least twenty additional individuals confirmed that the oral anatomy of the single specimens studied in this manner was usual for the West Lawrencetown populations.

The architecture of feeding appendages was also examined using scanning electron microscopy (SEM). Specimens for SEM were fixed in a 4% glutaraldehyde-seawater solution. They were washed in distilled water to remove salt and air dried. Skeletal shrinkage occurred but was usually minimal. This technique avoided collapse of setae and setules which was found to be a common result of other drying techniques. The dried specimens were coated in gold-platinum (Edwards Evapourator) and observed using a Cambridge S180 microscope (Accelerating voltage - 20 Kv, Beam Current = 250-500 Amps). Polaroid black and white film and Ektachrome X colour film were used.

Computer programmes in the Statistical Package for the Social Sciences (SPSS) were used for all numerical analyses. All data were tested for normality (Kolmogorov-Smirnov Goodness of Fit Test) using the untransformed values and 13 transformations. Data distributions of best fit were used in all subsequent principle component and discriminant function analyses. For biological data the transformation, $[\ln (X_i + 1)]$, where X_i is the number of individuals of species i, was used. For all data expressed as a percentage, the transformation $[\arcsin\sqrt{P}]$, where P is the percentage, was used.

It should be noted again that the purpose of this thesis was understanding: hypothesis making, not testing. As Pielou (1972) (quoting Goodall, 1970) has correctly observed, "... the development of hypotheses and their testing are entirely separate enterprises. The rules that must be obeyed when tests are done do not apply when hypotheses are sought; indeed artificial constraints are more apt to stultify the development of new theory than to promote it." This is especially true of rules governing sampling regimens when working with tiny, heterogeneously distributed animals like meiofauna. In this study all requirements of randomness have been satisfied but demands of large sample numbers (> 40 samples per month) have been relaxed.

RESULTS AND DISCUSSION

Description of Study Area

Water depth in the sample area is homogeneously shallow (Fig. 3). Water enters the marsh through its east and west ends. On a falling tide, currents flow west to east. On a rising tide, water flows into the marsh through both ends. Only at high tide is there a net westward movement of water.

Tidal changes in temperature, salinity and O_2 concentration for station A (Fig. 3) in winter and late summer are given in Figures 4 and 5. Temperature was highest at low tide in both seasons. Salinity was highest at high tide. It reached its lowest point on the rising tide in winter (probably due to the effects of shore ice) and at low tide in summer. O_2 concentrations were highest generally around high tide and lowest at low tide. The shape of the water depth curve measured during each tidal cycle should be noted. The water fell for 8 hours out of every 12 hour cycle. Low tide was 4½ hours later than that of Halifax. High tide was less than 2 hours later than that of Halifax.

The plant life of these wet lands was typical for a north temperate estuary. Spartina spp. lived in the intertidal zone. Photographic observations showed that they grew from mid-May until early autumn. In winter their leaves were torn from the ground by ice. Zostera spp. filled the subtidal regions except for a channel

Figure 3. Map of estuary behind Conrad Beach in West Lawrencetown, Nova Scotia with subtidal bathymetry indicated. Triangles indicate measurement locations.


N
100
90
80
70
60
50
40
30 cm
20
A
DEPTH IN CENTIMETERS

Figure 4. Changes in water depth, temperature, salinity and oxygen concentration during a tidal cycle in the winter of 1975.

8 FEBRUARY 1977

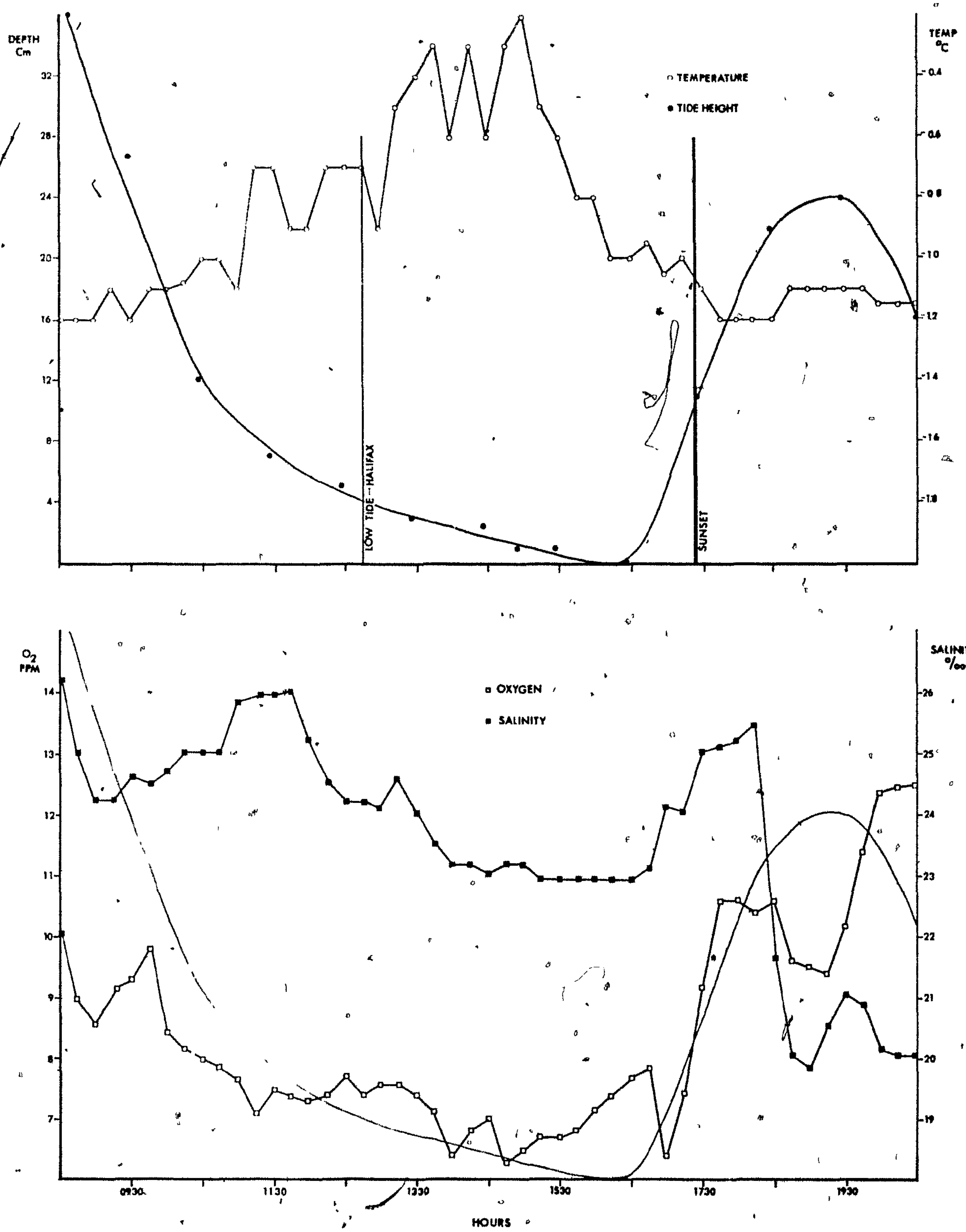
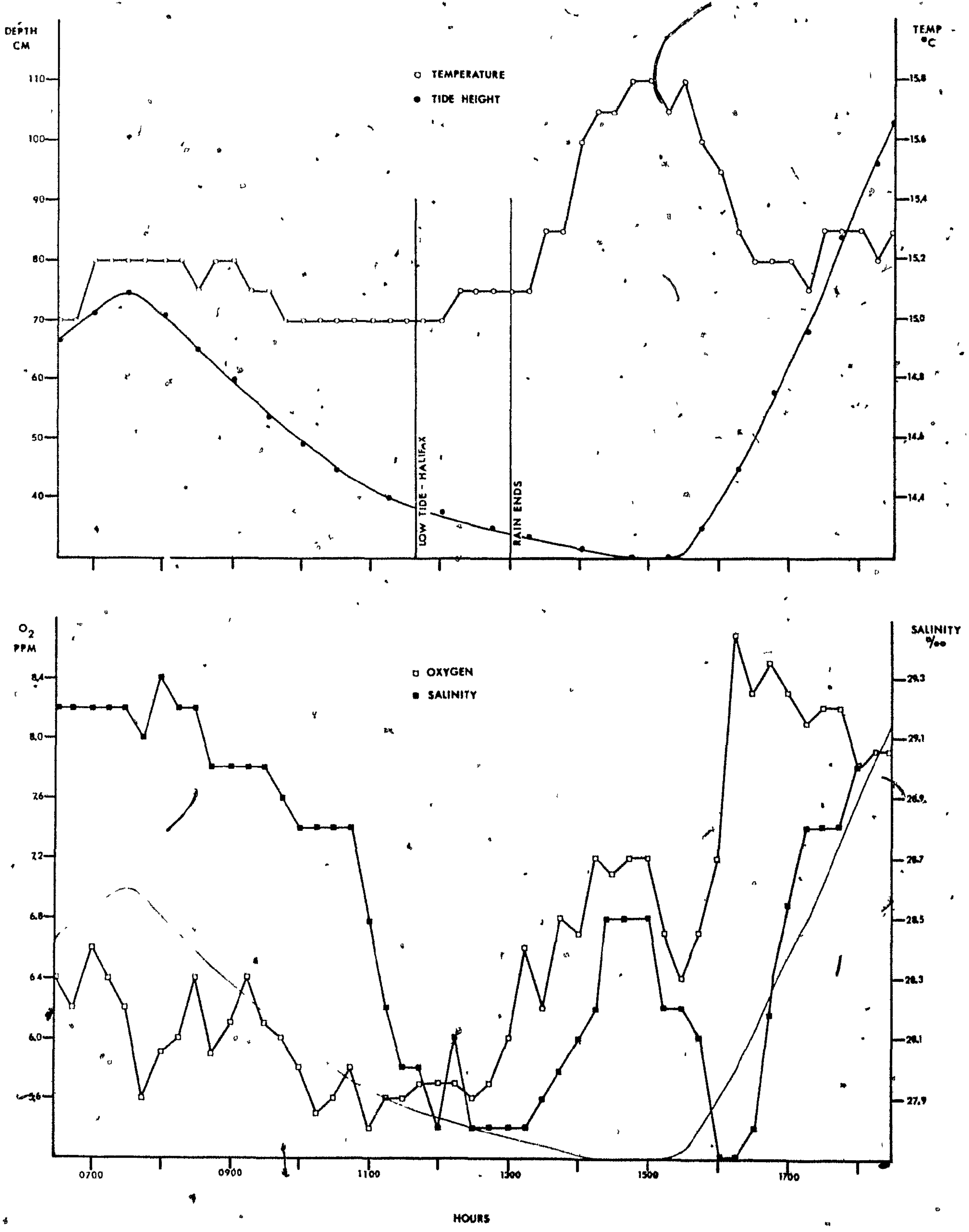


Figure 5. Changes in water depth, temperature, salinity and oxygen concentration during a tidal cycle in late summer, 1975.

3 SEPTEMBER 1975



which swept across the centre of the estuary. Algae also grew there, starting with Ulva spp. in the early spring. In summer, Ptilota sp., a red alga, grew abundantly. Kelp, Laminaria spp. and Agarum sp., and fucoid algae were transported into the estuary especially after a storm. Bluegreen algae bloomed at the surface of the water from late spring to late autumn, forming thick mats in the quiet waters along the north and south shores of the estuary. As the summer progressed, these mats became laden with juvenile Mytilus edulis and snails. Eventually they sank, covering beds of Zostera. Their filamentous mass reduced water movements near the bottom, suffocating animals in the sediments below. In the winter these submerged mats were covered with sediment. In the following spring, fresh Zostera returned.

Sedimentary Environment

The sediment in the estuary was a product of physical forces (deposition and erosion), seasonal plant growth and biological reworking. Sand entered the estuary on tidal currents and was deposited in a delta at the eastern entrance. With each tide, these sands were resuspended and light debris was winnowed out. As a result, this sediment was well sorted and poorly consolidated. Silt and clay seemed to originate from freshly innundated land in the southwestern corner of the estuary. These fine particles fell from waters calmed by beds of Zostera. Mytilus promoted the deposition of these particles in swifter moving waters by filtering them from suspension. Once on the bottom they were mixed with organic detritus, especially Zostera and Spartina leaves in winter, to form a poorly sorted mud. Where mud and sand facies met, mixed sediments occurred. There, along the edge of the delta, Ptilota grew best and Arenicola excavated tubes, depositing once buried organic debris at the surface.

Thus there were three sedimentary facies: sand, mud and mixed sediments (Fig. 6). Sand had a particle size frequency spike in the 161 - 203 μm range. Mud had a platykurtic frequency distribution in the 20 - 125 μm range. Mixed sediments were bimodal for these characters. In general, mud was more porous than sand (Table 1). Mud had more organic carbon and less oxygen than did sand. Redox potentials were generally lowest in mud. The organic carbon content of all sediments was generally highest in summer when O_2 concentrations were low.

The amount of organic carbon in the sediments probably reflected the growth of bacteria and diatoms. It was clear from even casual observation that the surface of sand substrates was yellow with diatoms in summer and not in winter. The quantity and especially the micro-pattern of the growth of these micro-organisms were important for understanding the ecology of meiofauna.

Figure 6. Representative particle size spectra for the three sediment types of the estuary.

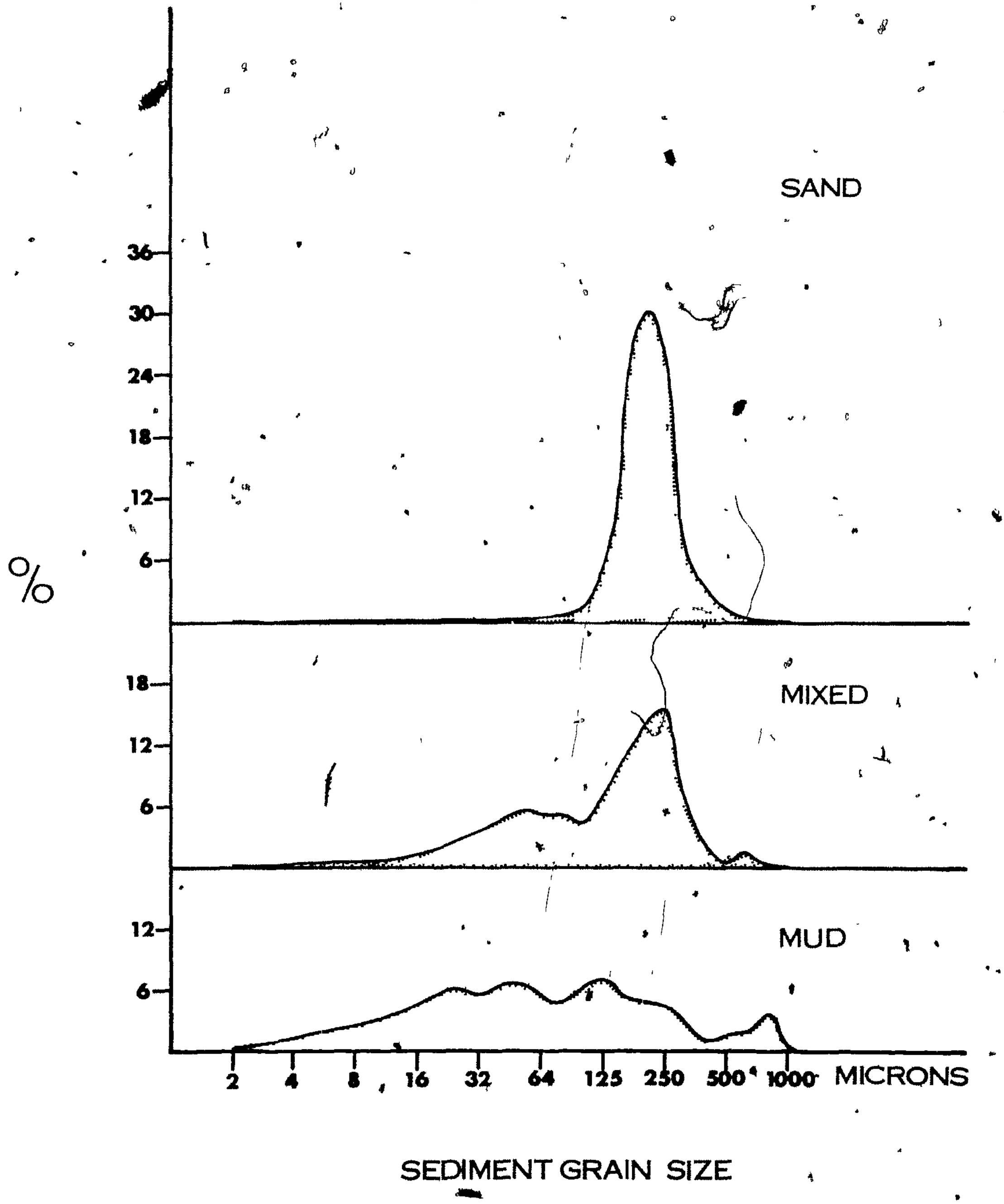

SAND
MIXED
MUD
%
36
30
24
18
12
6
18
12
6
12
6
2
4
8
16
32
64
125
250
500
1000
MICRONS
SEDIMENT GRAIN SIZE

Table 1. Changes in physical variables, abundance of meiofauna and the number of harpacticoid species in three sediment types during three representative months of the sample year.

Table 1

Month		March			July			November		
Sediment type		Sand	Mixed	Mud	Sand	Mixed	Mud	Sand	Mixed	Mud
Temperature range (°C)		1.0 - 2.8	0.8 - 2.8	7.0-7.1	17.0 - 17.8	19.0 - 20.2	20.5 - 23.0	12.8 -13.5	10.7 - 12.0	8.6 - 11.9
O_2 concentration range (PPM)		9.8 - 10.6	10.2-10.6	9.0-9.8	7.0 - 8.1	9.2 - 10.1	2.1 - 5.0	8.9 - 9.8	9.4 - 12.0	10.2 - 11.2
Salinity range (°/₀₀)		22.1 - 27.0	21.5-26.1	22.2-24.0	28.0 - 28.5	27.8 - 29.2	27.0 - 28.8	27.6 -28.8	25.5 - 28.2	24.4 - 27.0
Eh range	flocculent	+130 to-30	0 to -20	+110to-60	0 to -30	-20 to -70	-80 to -235	+50 to -20	+50 to -50	+20 to -320
	compact	+30 to -110	-40 to-110	-20 to -260	-80 to-320	-70 to-270	-180 to-350	+90 to-290	-180 to-330	-200 to-340
H_2O range	flocculent	23.6 -34.5	32.0-66.6	61.3-85.0	16.9- 39.1	40.0 -71.4	60.0-83.6	39.5-54.3	41.7 - 72.6	32.2 - 84.3
	compact	18.9 -43.1	18.9-49.0	54.4-71.4	19.5 -27.8	25.3 - 38.4	53.8-67.6	20.0-32.7	33.5 - 54.3	56.8 - 72.2
% organic carbon range	flocculent	0.00-0.90	0.74-3.01	2.70-6.20	0.57 - 1.26	0.38 - 2.85	1.97-14.32	0.00-0.94	0.00 - 5.26	4.82 - 9.30
	compact	0.00-1.30	0.47-2.39	0.95-4.40	0.00 - 1.38	0.00 -1.39	0.94-4.62	0.00-0.81	0.48 - 3.60	5.32 -15.38
Total Abundance of Meiofauna per $10cm^2$	flocculent	55 - 967	403 -1567	164 -1040	248 - 1515	402 - 1018	591 - 5861	164 -1833	175 - 1197	212 - 734
	compact	385 -2021	514 -2817	72 - 811	165 - 528	561 - 840	236 - 2976	141 - 1484	278 - 1350	277 - 570
Number of Harpacticoid species		8	20	20	18	21	22	12	13	15

Organic detritus occurred in a variety of shapes and sizes. Large pieces (> 2mm) were richly covered with diatoms (Fig. 7). The flat surfaces and edges of these particles had different physical textures and different species of epiflora (Fig. 8). Smaller pieces of organic debris, about 100 - 200 μm in diameter, were generally spherical. They had the texture of cotton balls and appeared to be organic-mineral aggregates. Rubble was still smaller material (< 50 μm), composed of organic detritus, freeliving diatoms, mica chips, shell fragments and floccules of silt, clay and bacteria.

SEM observations showed that on quartz sand, growth of epiflora was generally confined to pits and faults. The occurence of these structures and hence the occurrence of the food they contained, was inversely related to particle diameter (Fig.11). For example, on large particles, freshly sheared, polished surfaces were common (Fig. 9). Diatoms and bacteria grew only sporadically and in discrete clumps. On smaller particles (Fig. 10) pits were more common and in them many diatoms and bacteria grew. The region of overlap in the size distributions of sheared and pitted sands was about 150 - 350 μm.

These data are important for understanding the character of sandy environments and the origin of interstitial faunas. Dale 1974 has studied, by direct count, the distribution of bacteria on intertidal sand at Petpeswick Inlet, Nova Scotia. He found that total bacterial numbers were two orders of magnitude lower

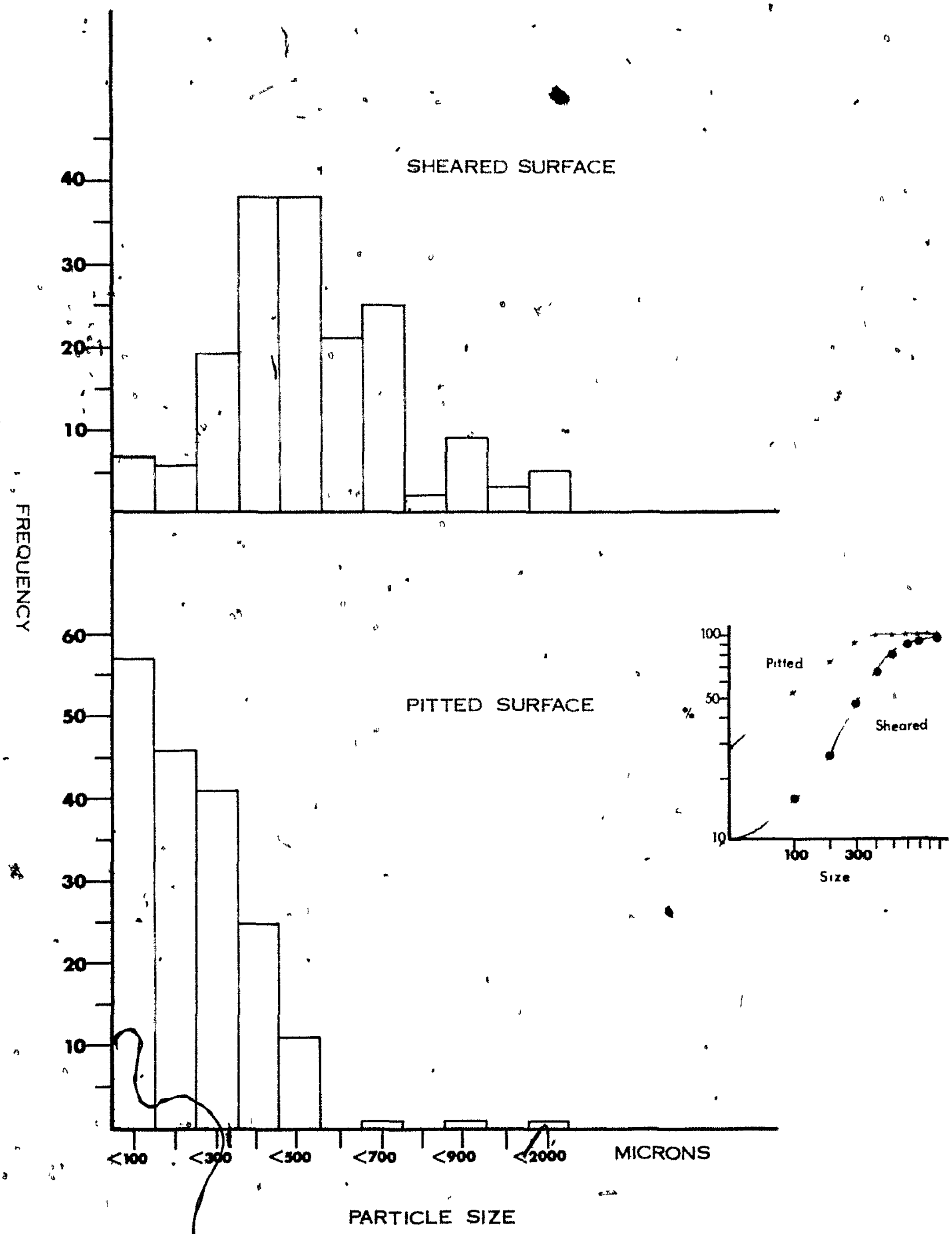
Figure 7. (upper left) Epiflora on the planar surface of a piece of Spartina detritus. Distance between adjacent white tick marks is 30 µm.

Figure 8. (upper right) Epiflora on the edge of a piece of Spartina detritus. Distance between adjacent white tick marks is 30 µm.

Figure 9. (lower left) Epiflora on the sheared surface of a large quartz particle. Distance between adjacent white tick marks is 100 µm.

Figure 10. (lower right) Epiflora on a pitted quartz particle. Distance between adjacent white tick marks is 30 µm.

Figure 11. Frequency distributions of quartz particle sizes partitioned into two categories: those with sheared surfaces and those with pitted surfaces. Inset: cumulative frequency curves for these same data.


SHEARED SURFACE
40
30
20
10
FREQUENCY
PITTED SURFACE
60
50
40
30
20
10
100
Pitted
50
%
Sheared
10
100
300
Size
<100
<300
<500
<700
<900
<2000
MICRONS
PARTICLE SIZE

on 200 μm particles than on 20 μm grains. This bacteria/particle size curve follows the slope of the pitted particle distribution given in Fig.11 .

Wieser (1959) has indicated that interstitial faunas develop best in sands with a mean diameter of about 200 μm. Below this size, interstitial spaces are too small for interstitial locomotion and burrowers become numerically important. Very much above this size the interstitial spaces fill up with fine material. Further, he points out that some epistrate feeders feed only on sand in the 150 - 350 μm range.

Hjulström (1939) has diagrammed the effect of particle diameter on the velocity of water required to deposit and erode sediment. Sands larger than 200 μm are easily deposited even in swift waters and require high water velocities to be eroded presumably because of their large mass. Muds and silts can only be deposited in quiet waters and require large water velocities to be eroded presumably because of electrostatic and other particle-particle binding forces. Particles with a mean diameter of 200 μm need quiet waters for deposition and are easily resuspended. Thus where a well sorted sediment with a mean size of 200 μm occurs, the environment must be dynamically stable. A slackening in water velocity would cause the deposition of finer, less-erodable particles. A substantial increase in water velocity would remove the 200 μm fraction altogether. This interpretation of three types of sediment/water velocity relationships is substantiated by a principle component analysis of the 180 sediment size determinations done in the present study (Fig. 12). Three size assemblages covaried: Muds, sizes 2 - 101 µm, fine sands, sizes 128 - 256 µm, and large sands, sizes 322 - 1024 µm.

From these accounts and from the data in figure 9, a 200 µm sand has the following characteristics. It is dynamically stable. It has a well developed network of interstitial spaces and is thus well flushed with water. On about half of the sand particles, food is distributed as a spatially fine grained resource, and on the other half food occurs only in isolated patches, i.e. as a coarse grained resource.

This unique set of circumstances probably contributes to the consistently high diversity of faunas inhabiting these intermediate-sized sediments (see Gray, 1974, for a review of these diversity data).

Harpacticoid Habitat and Temporal Distributions, I.

The abundance per 10 cm^2 of all meiofauna (Table 1) was lowest in January and highest in May and July. In any one month, abundance was usually highest in the mixed sediments and lowest in the sand.

40 harpacticoid species were found in the estuary over the entire year (Table 2). The number of harpacticoid species in all sediments was greatest in March (28 species) and lowest in November (22 species). Mud and mixed sediments harboured the largest number of species and sand the least (Table 1).

Figure 12. Principle component analysis of sediment particle sizes. Particle sizes are abbreviated as indicated in the table of abbreviations.

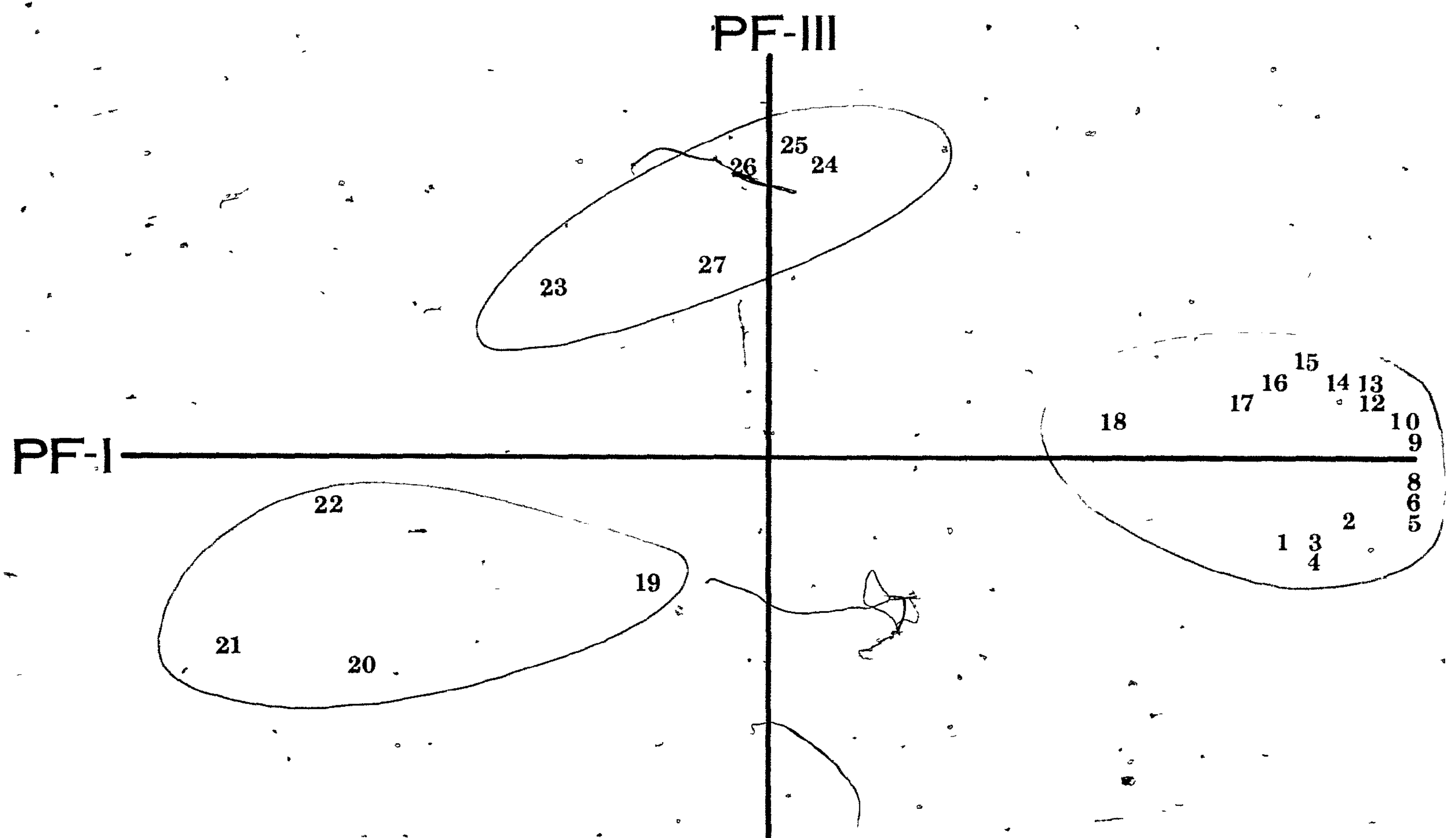

PF-III
PF-I
25
24
26
27
23
15
16
14
13
17
12
18
10
9
8
6
5
2
1
3
4
22
19
21
20

Table 2. Number of occurrences and abundances of harpacticoid species, their habitats, month (s) of greatest abundance and feeding type (if studied).

Table 2

Species	Number of occurrences of all females, gravid females, males and juveniles	Total abundance of all females, gravid females, males and juveniles.	Micro-habitat			Microhabitat					Month of Abundance Maximum (a)	Feeding Type & Notes on Microhabitat (1) point feeder (2) line feeder (3) plane feeder (4) solid feeder
			Sand	Mixed	Mud	Deep Burrower	Shallow Burrower	Epibenthic	Natant	Epiphytic		
Halectinosoma sp. 1	431	4577		x	x			x	x		Jan	(3) Sand filer
Psuedobradya sp. 1	122	812		x			x	x			March	(3) Sand filer
Pseudobradya sp. 2	64	249		x			x	x			Nov.	(3) Sand filer
Pseudobradya sp. 3	39	108		x			x				Jul.& Sept.	
Phyllothalestris sp. 1	1	1			x			x		x	Jan.	
Tachidius sp. 1	89	260	x	x				x	x		Jul. to Nov.	
Microarthridion littorale	295	2554		x	x			x	x		May	(4) rubble sorter
Thompsonula hyaenae	5	10	x				x				Nov.	
Harpacticus chelifer	22	50		x	x					x	March	
Harpacticus sp. 1	35	66		x	x					x	Jul.	
Zaus abbreviatus	19	35			x					x	Mar. & Nov.	
Tisbe furcata	155	1575			x			x	x	x	May	(4) sphere cleaner & predator
Tisbe sp. 1	29	512			x			x	x	x	March	
Parategastes sphaericus	1	1			x			x		x	March	
Dactylopodia sp. 1	93	483			x					x	July	(3) plane sweeper
Parastenhelia sp. 1	2	143		x	x			x?			Jan.	
Stenhelia divergens	282	1643	x	x		x	x				Sept.& Nov.	(4) diatom feeder
Amphiascus minutus	83	412			x		x	x			Jul.&, Jan.	(4) sphere cleaner
Amphiascus propingvus	67	241			x		x	x			Nov.	(4) sphere cleaner
Amphiascoides debilis	229	1525			x		x	x			July	(4) sphere cleaner

Table 2 (cont'd)

Species	Number of occurrences of all females, gravid females, males and juveniles	Total abundance of all females, gravid females, males and juveniles	Macrohabitat: Sand	Macrohabitat: Mixed	Macrohabitat: Mud	Microhabitat: Deep Burrower	Microhabitat: Shallow Burrower	Microhabitat: Epibenthic	Microhabitat: Natant	Microhabitat: Epiphytic	Month of Abundance Maximum (a)	Feeding Type & Notes on Microhabitat (1) point feeder (2) line feeder (3) plane feeder (4) solid feeder
Ameiria longipes	89	395		x	x		x	x			March	(1) selective epistrate feeder
Ameiria parvula	73	246		x	x		x	x			Sept.	(1) selective epistrate feeder
Nitocra affinis	2	2			x					x	March	(3) plane sweeper
Nitocra pusilla	1	1			x					x	Nov.	
Mesochra lilljeborgi	72	343		x	x		x				Nov.& Jan.	(4) sphere cleaner
Mesochra pygmaea	27	226	x				x				Sept.	(4) sphere cleaner
Mesochra sp. 1	36	106			x	x					Sept.	
Orthopsyllus sp. 1	1	2	x			x	x				July	
Arenocaris sp. 1	2	2	x			x	x				March	
Enhydrosoma buchholtzi	7	7	x	x		x	x				Mar. & Jan.	(4) rubble sorter
Enhydrosoma longifurcatum	175	869		x	x	x	x				Sept.& Nov.	(4) rubble sorter
Rhizothrix minuta	3	11					x				Sept.	
Heteropsyllus nunni	138	749	x			x	x				Mar.& May	(3) sand filer
Leima vaga	197	891			x			x	x		May & July	(4) sphere cleaner
Pseudonychocamptus proximus	5	7	x	x				x?			March	
Heterolaophante discophora	18	34			x			x		x	July	(2) rectilinear edge gleaner
Heterolaophante capillata	227	1632	x	x				x		x	Jan.	(2) cylinder and edge gleaner

Table 2 (cont'd)

Species	Number of occurrences of all females, gravid females, males and juveniles	Total abundance of all females, gravid females, males and juveniles	Macrohabitat			Microhabitat					Month of Abundance Maximum (a)	Feeding Type & Notes on Microhabitat (1) point feeder (2) line feeder (3) plane feeder (4) solid feeder
			Sand	Mixed	Mud	Deep Burrower	Shallow Burrower	Epibenthic	Natant	Epiphytic		
Paralaophonte macera	1	1	x	x				x?			May	
Platychelipus sp. 1	11	17	x	x				x?			Jan.	
Pilifera gracilis	5	6	x	x				x?			July	

The habitat distributions of the 28 most abundant species at three points in the sample period are plotted in figures 13 to 16. Included in these figures are the number of stations in which each species appeared, their density in both the flocculent and compact subsamples and the sediment facies of the station. From these data four species-habitat groups can be defined (Table 2). Within each of these gross categories each species occupied a specific micro-habitat. Some harpacticoids are natant, others live on the surface of the sediment, some burrow into the flocculent layer, some are truly interstitial and still others live clutching to cylindrical tubes and algal debris (see also functional anatomy to follow). These habitat-time occurrences are summarized in table 2 .

In addition to this semi-quantitative classification, 19 species, each representing more than 2% of the annual sum of species occurrences, were classified using discriminant function analysis with all environmental factors as discriminating variables. A stepwise solution method was chosen. It should be noted that the species included in this analysis over-represent the mixed sediment facies where species abundances were greatest. Mud and sand assemblages were characterized by many specialist species with densities too low for inclusion in this analysis. Thus the true number and composition of species groups in the estuary cannot be discerned by this technique. Nevertheless, the information obtained is instructive.

Figure 13. Semi-quantitative classification of copepod assemblages based on their gross habitat distributions: sand assemblage with minor distributions in mixed sediments. KEY at bottom indicates tabular construction.

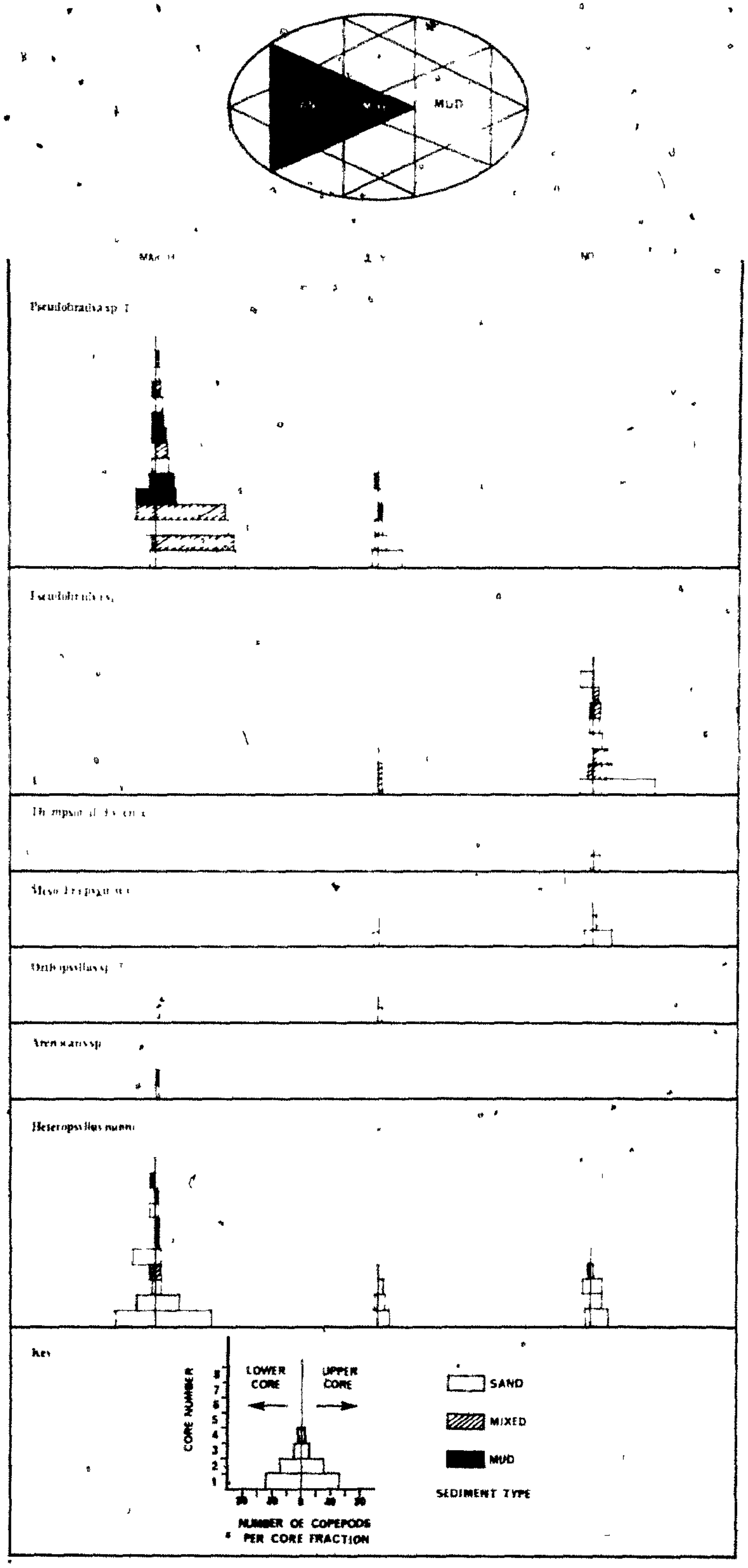

MUD
MARCH
JULY
NO
Pseudobradya sp. I
Pseudobradya
Thompsonula
Mesochra pygmaea
Orthopsyllus sp.
Arenosetella sp.
Heteropsyllus nunni
Key
CORE NUMBER
LOWER CORE
UPPER CORE
NUMBER OF COPEPODS PER CORE FRACTION
SAND
MIXED
MUD
SEDIMENT TYPE

Figure 14. Semi-quantitative classification of copepod assemblages based on their gross habitat distributions: mixed sediment assemblage with minor distributions in sand.

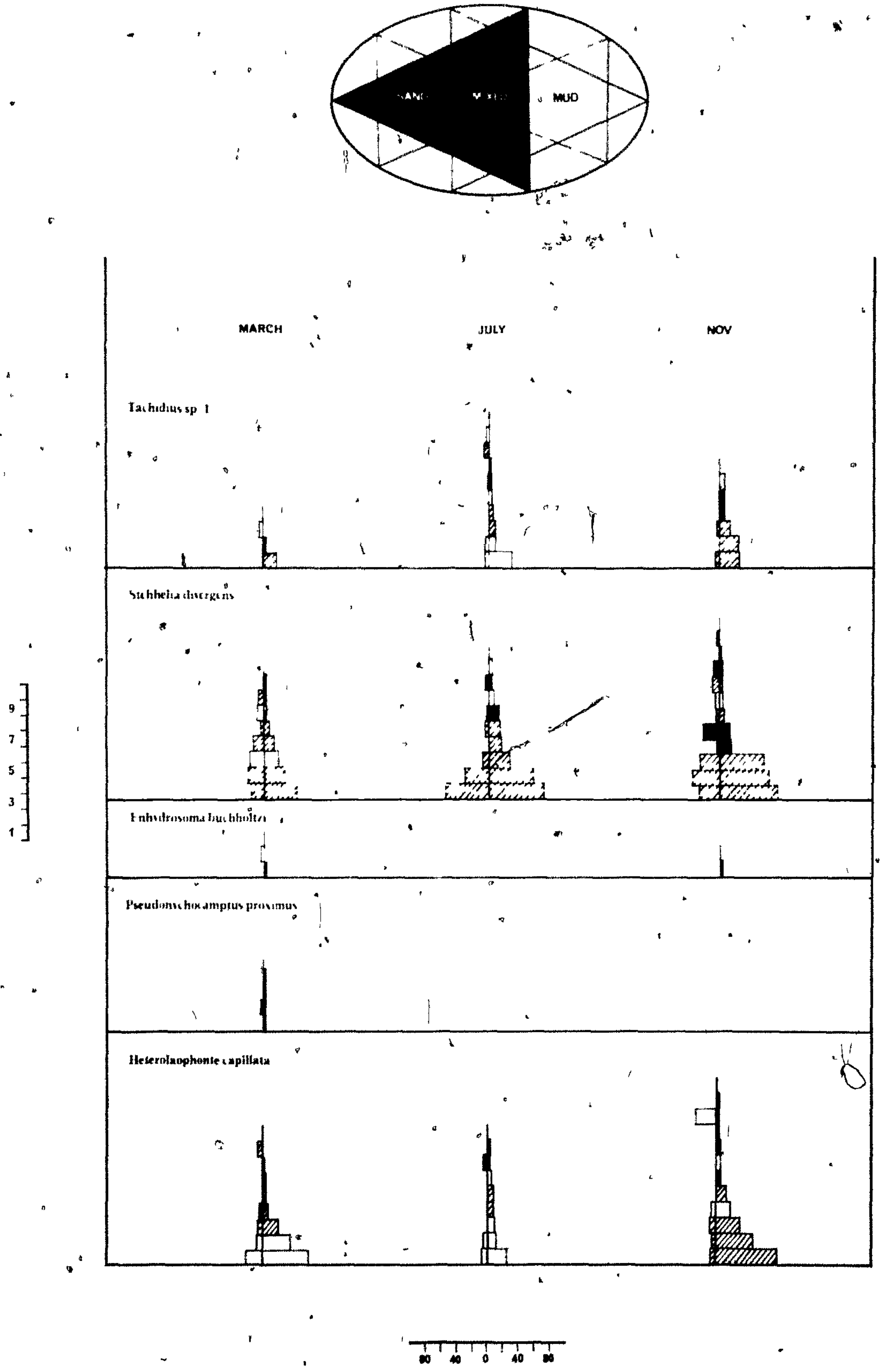

SAND
MIXED
MUD
MARCH
JULY
NOV
Tachidius sp. 1
Stenhelia divergens
Enhydrosoma buchholtzi
Pseudonychocamptus proximus
Heterolaophonte capillata
9
7
5
3
1
80
40
0
40
80

Figure 15. Semi-quantitative classification of copepod asseblages based on their gross habitat distributions: mixed sediment assemblage with minor distributions in mud.

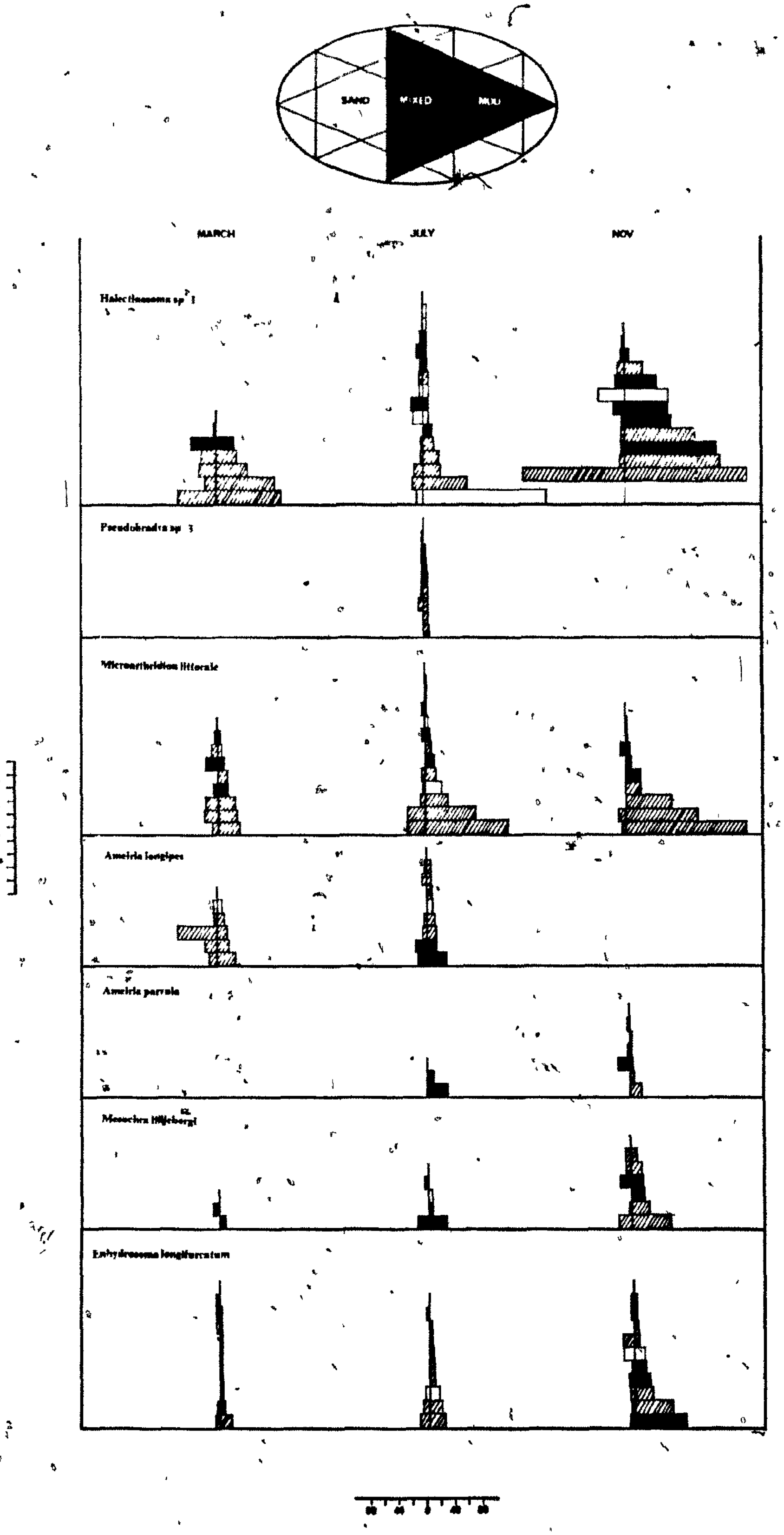
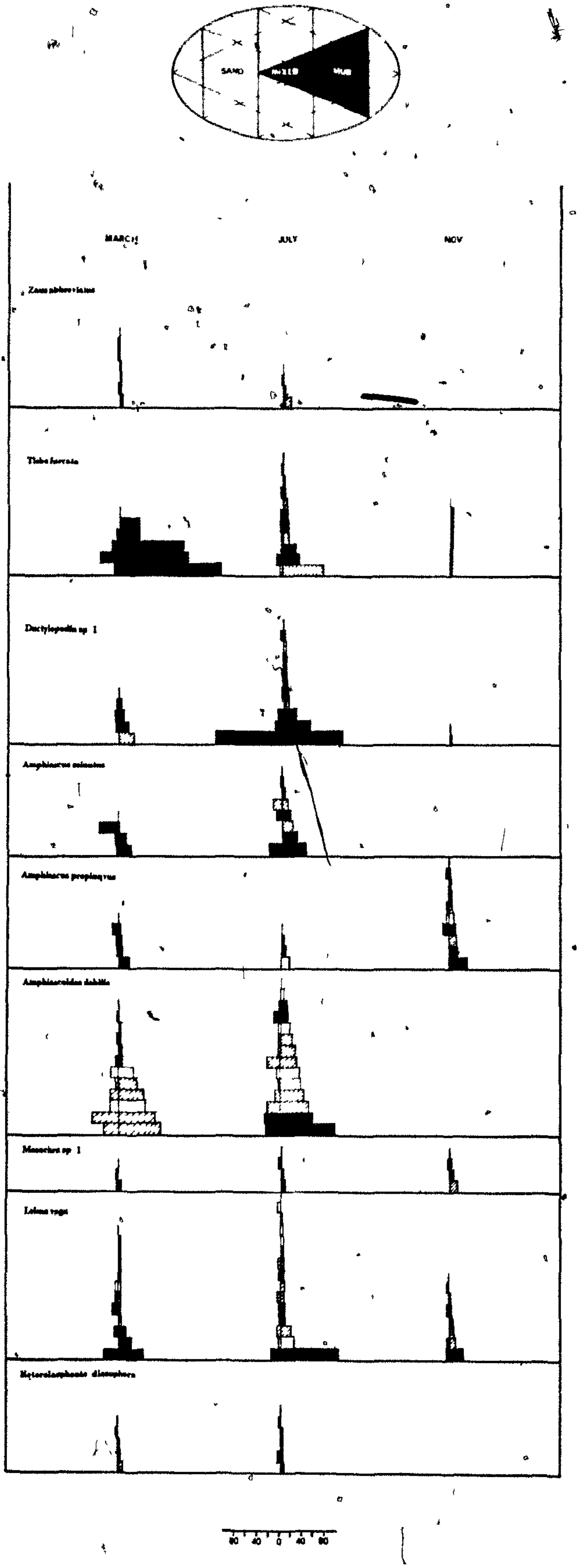

SAND
MIXED
MUD
MARCH
JULY
NOV
Halectinosoma sp? 1
Pseudobradya sp 3
Microarthridion littorale
Ameiria longipes
Ameiria parvula
Mesochra lilljeborgi
Enhydrosoma longifurcatum
9
7
5
3
1
80
40
0
40
80

Figure 16. Semi-quantitative classification of copepod assemblages based on their gross habitat distributions: mud assemblage with minor distributions in mixed sediments.


SAND
MUD
MARCH
JULY
NOV
Zaus abbreviatus
Tisbe furcata
Dactylopodia sp. 1
Amphiascus minutus
Amphiascus propinquus
Amphiascoides debilis
Mesochra sp. 1
Leimia vaga
Heterolaophonte discophora
9
7
5
3
1
80
40
0
40
80

Analysis of all species over all months, stations, physical factors and, of the granulometric statistics, using only percent mud, percent fine sand, percent coarse sand and grand mode as discriminating variables revealed a coherent bifurcation of the species assemblage (Fig. 17). Granulometry was most important in discriminating the species. The nature of these assemblages will be made clear later.

The results of this analysis for each month are given in Figures 17 to 23. Three points are immediately important. 1) Sediment properties dependent on grain size usually contribute most to the discriminant functions. 2) Two assemblages of species (sand and mixed-mud) can be clearly recognized only in July. 3) Some species change their places relative to other species during the year. For example, Amphiascus minutus, A. propinquus and Amphiascoides debilis, all closely related members of the family Diosaccidae are grouped together when all months are considered at once. However, when each month is considered separately, A. minutus and A. propinquus are seen to alternate in time (See also Figs. 13-16). A. minutus and Am. debilis change habitats relative to each other. First they are grouped apart (March and May) and then together (July). The meaning of these changes cannot be clear without reference to the trophic ecology of these species.

Harpacticoid Trophic Analysis

Complementing the habitat and seasonal distribution of

Figure 17. Discriminant function analysis of 19 harpacticoid species over all months and stations with all physical factors considered. Abbreviations are as in Table of Abbreviations. Lines around centroids are visual aids indicating directions of covariance.

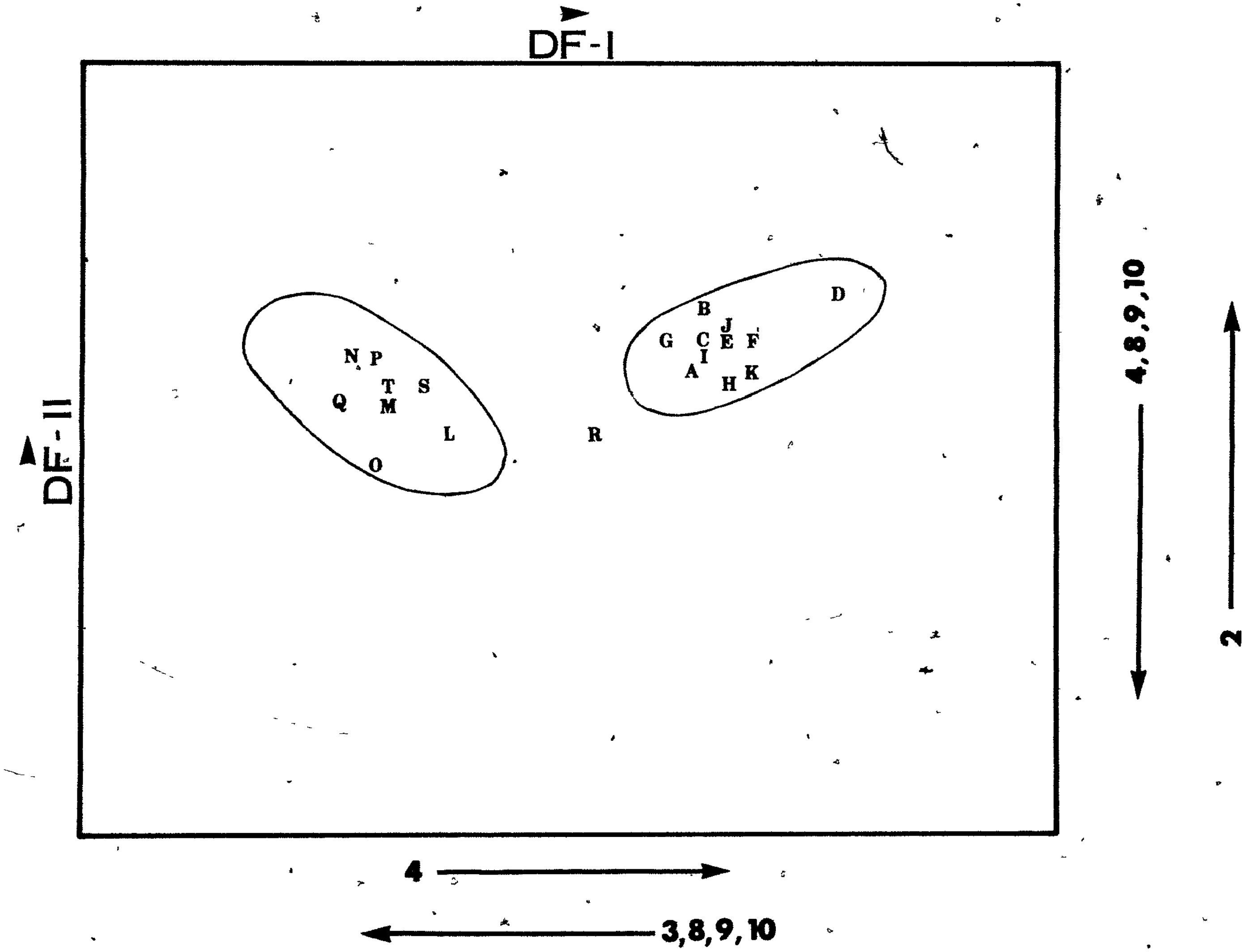

DF-I
DF-II
D
B
J
G C E F
I
A H K
N P
T S
Q M
L
O
R
4,8,9,10
2
4
3,8,9,10

Figure 18. Discriminant function analysis of 19 harpacticoid species in March 1975 at all stations with all physical factors considered. Abbreviations are as in Table of Abbreviations. Lines around centroids are visual aids indicating directions of covariance.

MARCH

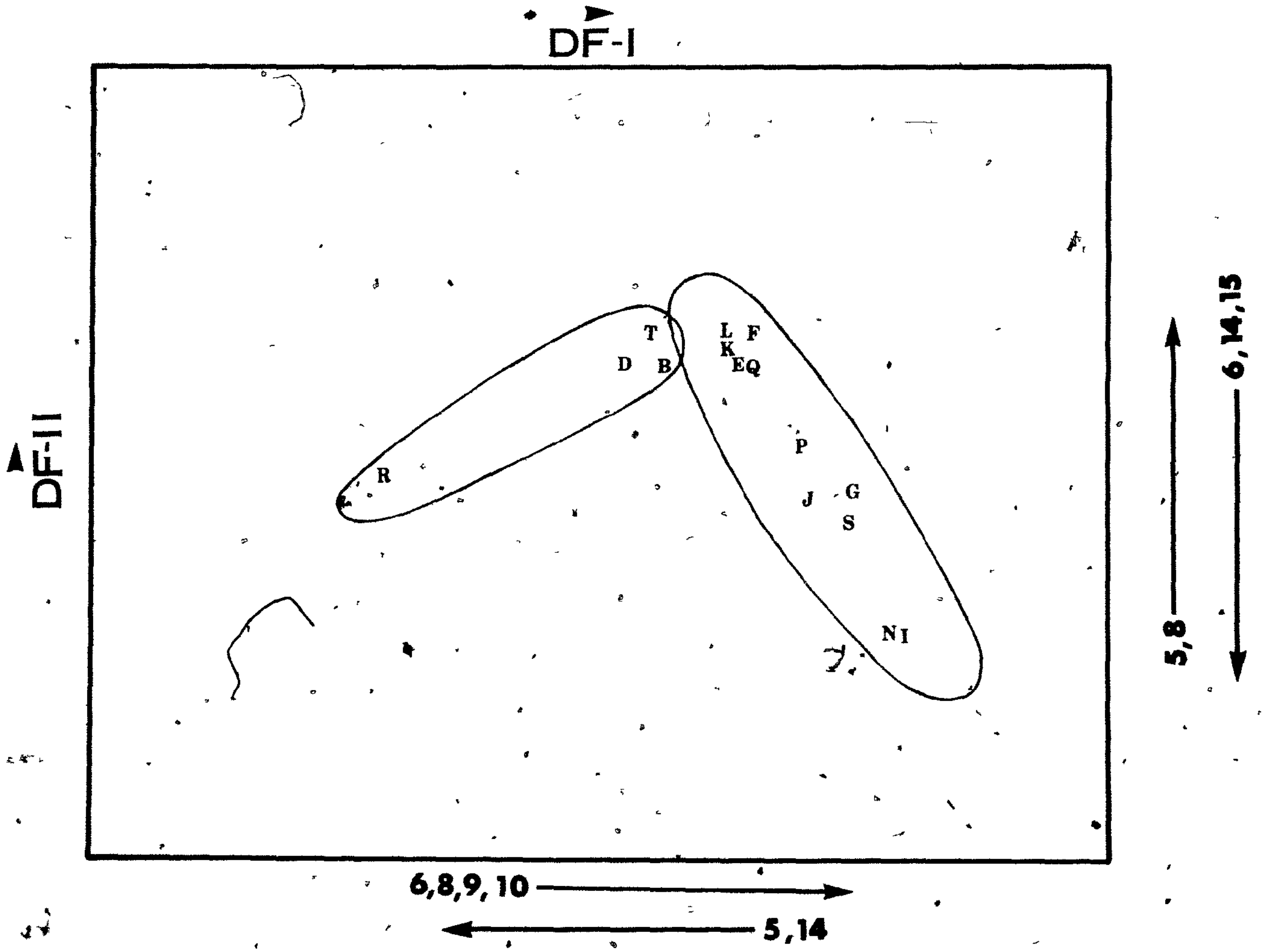


Figure 19. Discriminant function analysis of 19 harpacticoid species in May 1975 at all stations with all physical factors considered. Abbreviations are as in Table of Abbreviations. Lines around centroids are visual aids indicating directions of covariance.

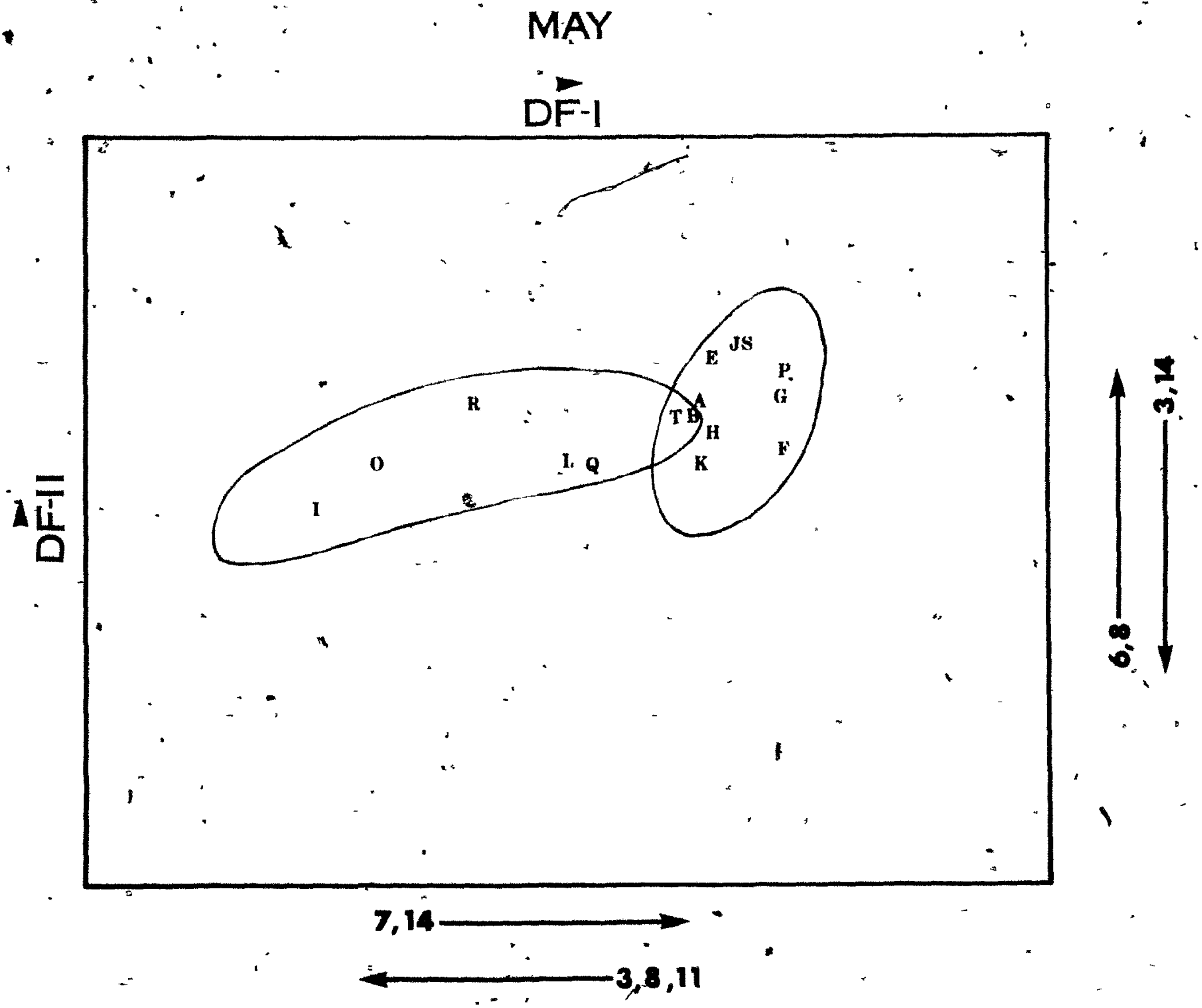

MAY
DF-I
DF-II
E
JS
P
G
A
T B
H
F
K
R
O
L Q
I
3,14
6,8
7,14
3,8,11

Figure 20. Discriminant function analysis of 19 harpacticoid species in July 1975 at all stations with all physical factors considered. Abbreviations are as in Table of Abbreviations. Lines around centroids are visual aids indicating directions of covariance.

JULY

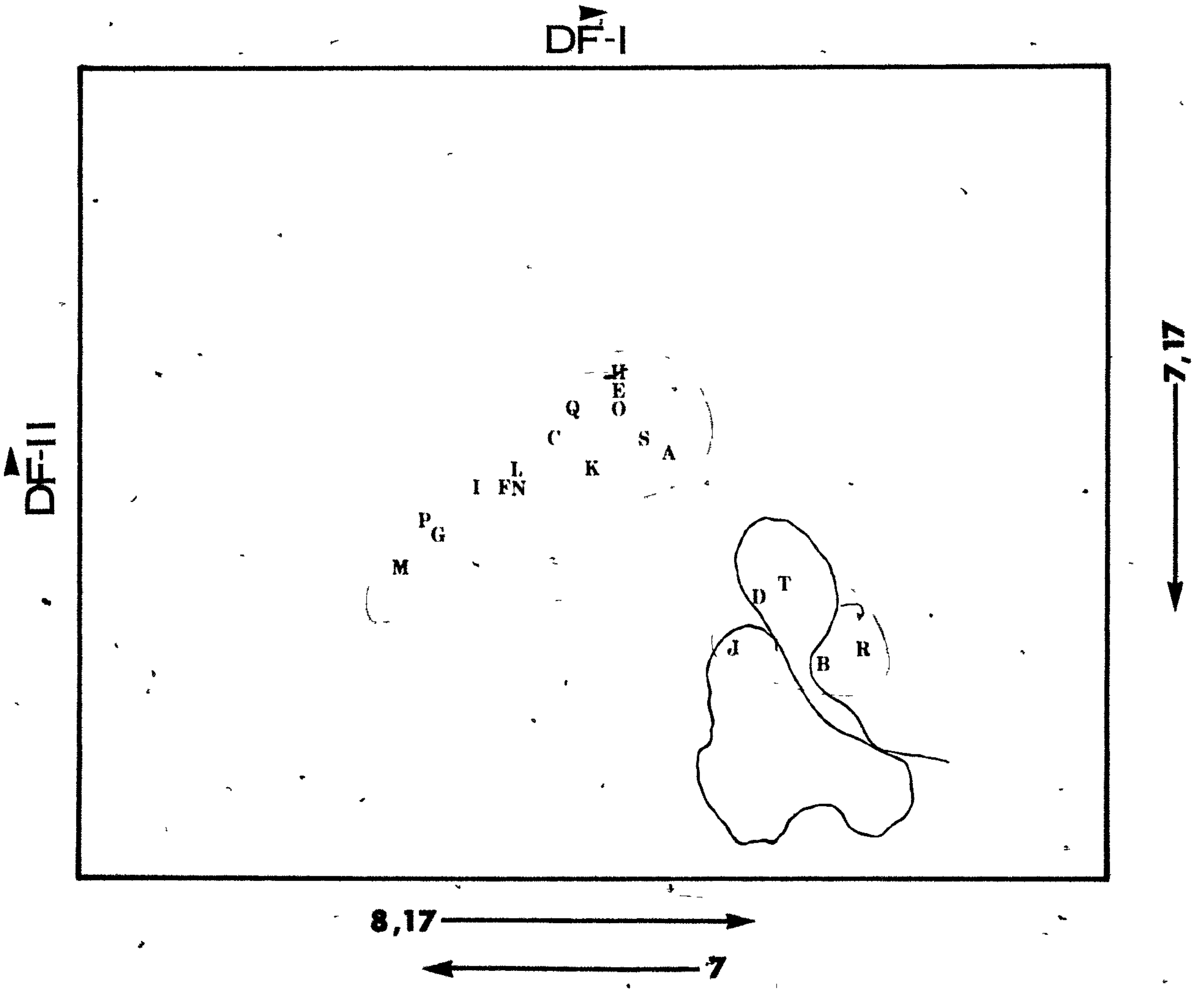


Figure 21. Discriminant function analysis of 19 harpacticoid species in September 1975 at all stations with all physical factors considered. Abbreviations are as in Table of Abbreviations. Lines around centroids are visual aids indicating directions of covariance.

SEPTEMBER

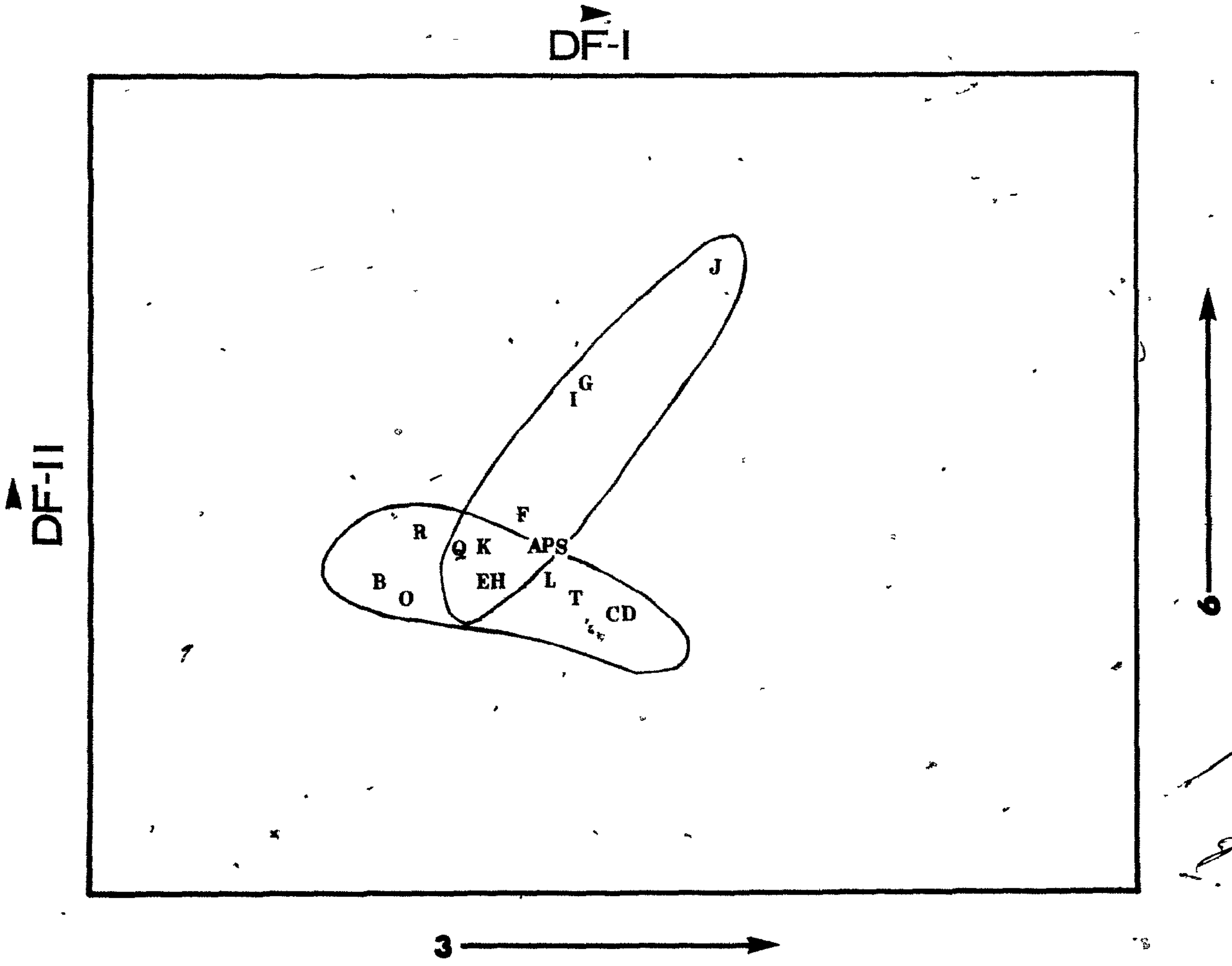


Figure 22. Discriminant function analysis of 10 harpacticoid species in November 1975 at all stations with all physical factors considered. Abbreviations are as in Table of Abbreviations. Lines around centroids are visual aids indicating directions of covariance.

NOVEMBER

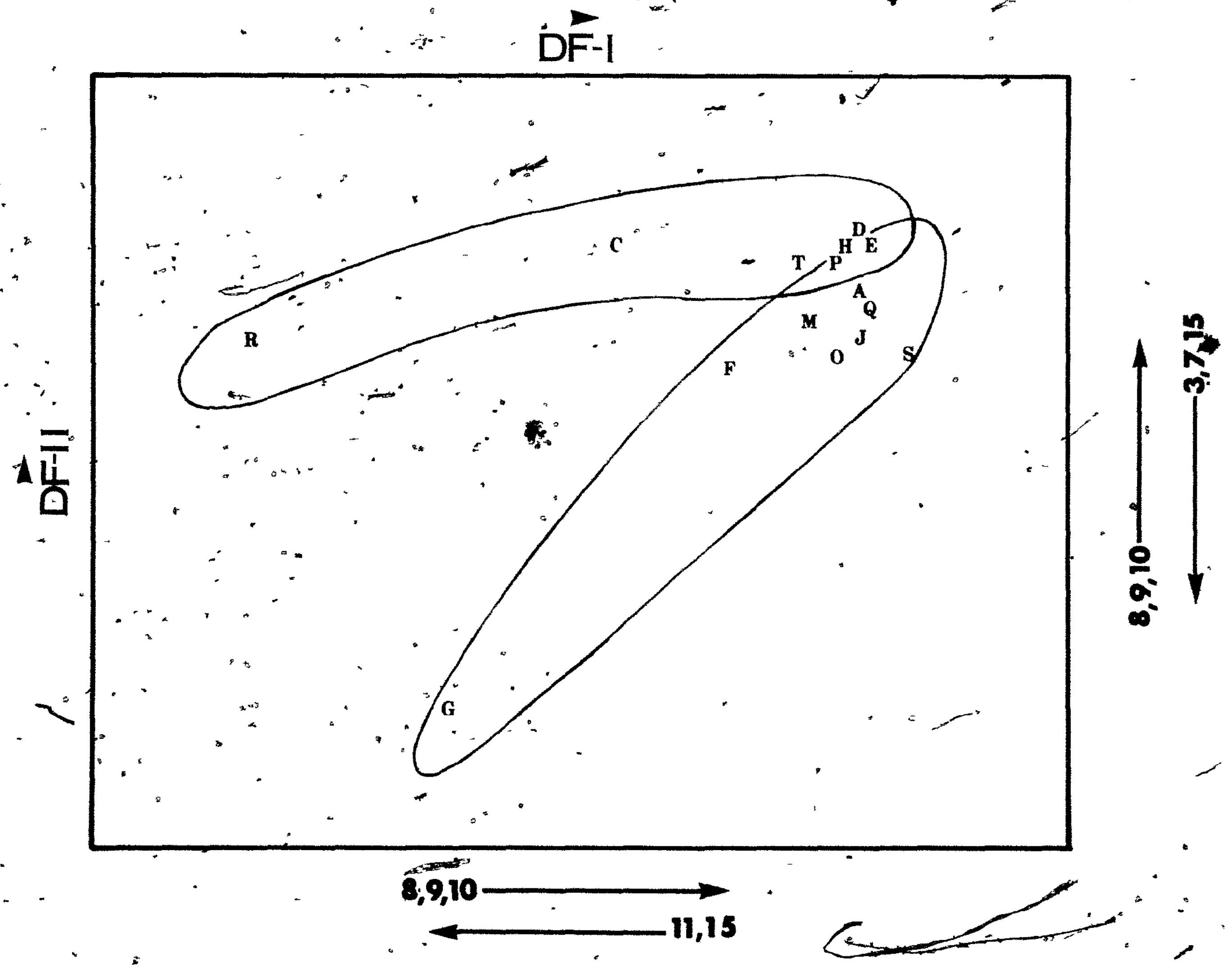
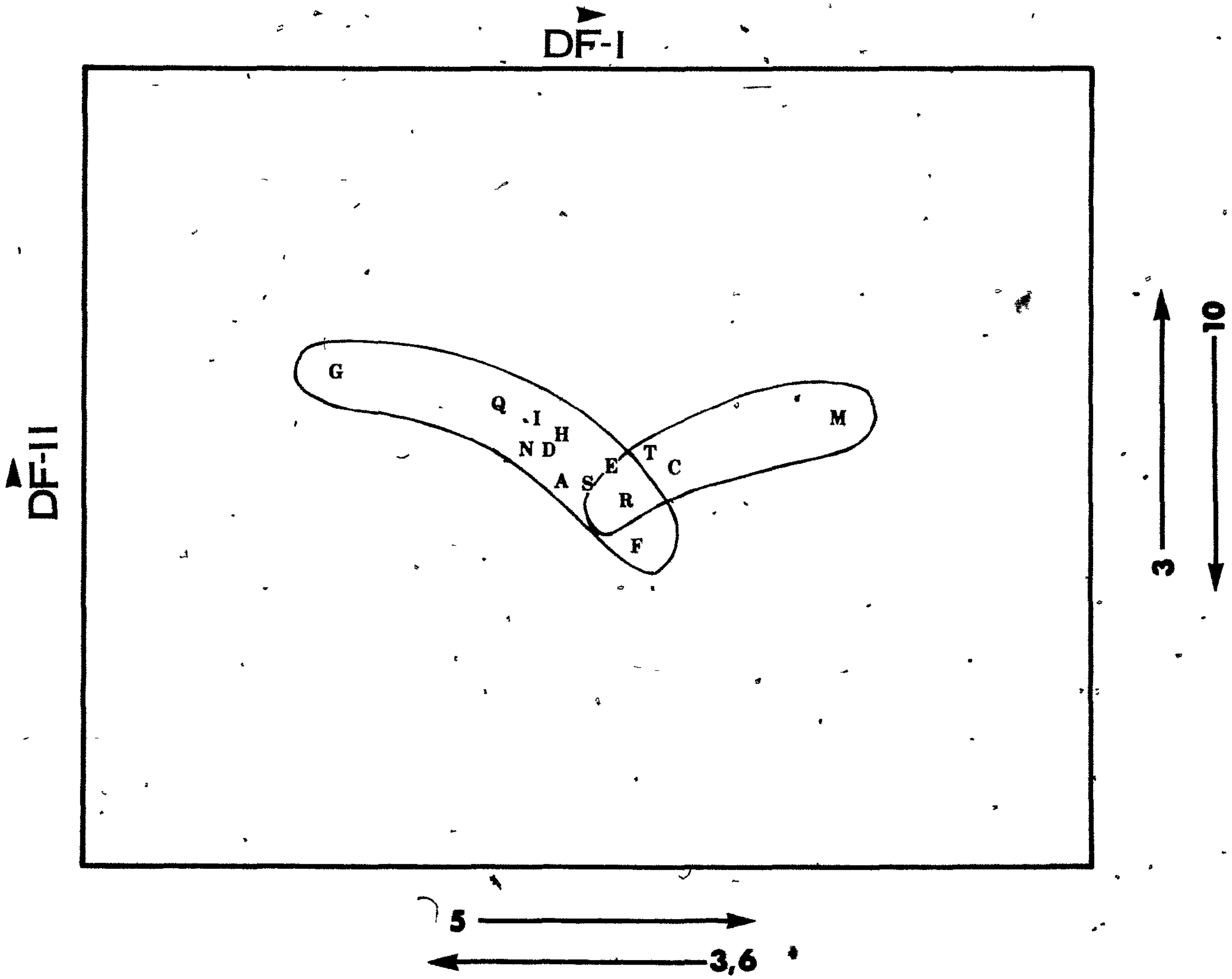


Figure 23. Discriminant function analysis of 19 harpacticoid species ~~in~~ January 1976 at all stations with all physical factors considered. Abbreviations are as in Table of Abbreviations. Lines around centroids are visual aids indicating directions of covariance.

JANUARY



harpacticoids is their feeding and locomotor behaviour. All descriptions below are based on observations of at least 15 gravid females. Males differ anatomically and morphometrically from females and were not considered. The description of Tisbe furcata gives a complete architectural analysis of a typical harpacticoid's mouth.

Family Ectinosomidae

HALECTINOSOMA SP. 1 (Fig. 24 & 25)

Architecture

Description based on adult, gravid female, 234 μm long.

Body - fusiform, brown coloured.

A_1 - 7-segmented. Aesthetasc on segment 4, is 2.5 times longer than last 4 segments combined.

A_2 - with basis. 2-segmented endopod and 3-segmented exopod of which the second segment is shortest. Endopod with medial thorns, surface and 1 barbed seta, terminally with 4 barbed setae and 1 smooth seta. Exopod terminally with 1 barbed and 2 smooth setae.

Md - with 7-dentate cutting edge, coxa-basis with 2 setae. Endopod with 3 setae. Exopod with 2 plumose setae.

Mx_1 - Arthrite with 2 unguiform setae. Basis indistinctly divided with 10 setae.

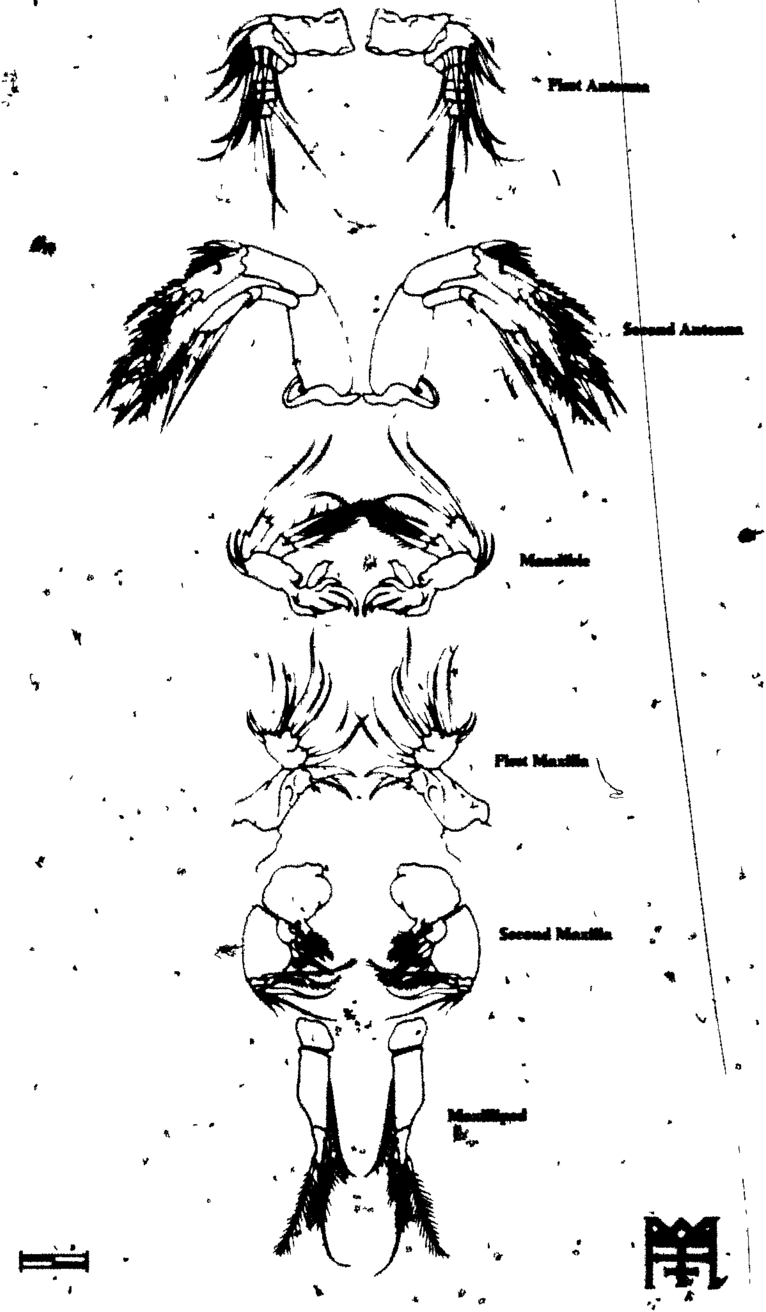
Mx_2 - Syncoxa with 3 endites, middle small with 1 seta, proximal and distal endites with 2 plumose setae each. Basis with 1 spine in mid-apical region. Endopod 2-segmented with 4 naked,

Figure 24. Halectinosoma sp. 1. SEM of oral region. Distance between adjacent white tick marks is 30 μm.

Figure 24. Halectinosoma sp. 1. SEM of oral region, anterior end upward. Magnification: 2500X. A_1 lies beneath curved rostrum. Labrum with horn. Posteriad are A_2, Md, Mx_1 and, below, Mx_2.

Figure 25. Halectinosoma sp. 1. Detail of oral appendages.

Scale: 32 µm.



Halectinosoma sp. 1

and 1 plumose seta.

Mxp - Basis short. Endopod 2-segmented. Proximal segment with 1 plumose seta. Distal segment with 2 plumose and 1 naked seta.

Labrum - reduced to a stout dermal horn.

Legs - well developed as typical for genus.

Caudal Rami - apposable with slender terminal setae.

Kinematics

30 - 40% of H. sp. 1's time was spent in the water column above the bottom. They swam rapidly with strong perpendicular strokes of their thoracic legs. Their path was a spiral directed by abdominal flexions. They dove into sandy sediments burrowing in the top several millimeters. When entering the sediment they opened their caudal rami slowing their pace and directing their movement. When in the sediment, they walked on their knees, as it were, using the setules on the second and third exopod segments to purchase the sediment. Their A_1 was sometimes used in soft sediments.

When approached by a vibrating probe (to simulate the approach of a predator or other source of disturbance) they darted forward. When touched, they contracted their body segments, closed their caudal rami and dropped like a stone through the water. In this position their body was crescent-shaped. Fine setules on the posterior margin of each body segment covered the gap between adjacent somites. Legs were collapsed and pressed against the belly. The animal did not move from this armadillo-like stance for at least 6 seconds after tactile stimulation ended.

When feeding they moved over a small grain of sand and cradled it in their mandibular and maxillary palps. They abraded its surface with alternating sweeps of their A_2. Jerky head movements were probably related to use of the horn on their upper lip as a pick. Food particles, whole small diatoms and organic debris, once removed from the sand, were sucked into the esophagus by rapid peristaltic movements of their syringe-like gut.

<u>PSEUDOBRADYA</u> SP. 3 (Fig. 26 & 27).

<u>Architecture</u>

Description based on adult, gravid female 1.2mm long.

Body - fusiform. Tan to dark gold in colour.

A_1 - 5-segmented. Aesthetasc on segment 3, extends 2 times the length of last 2 segments beyond end of A_1.

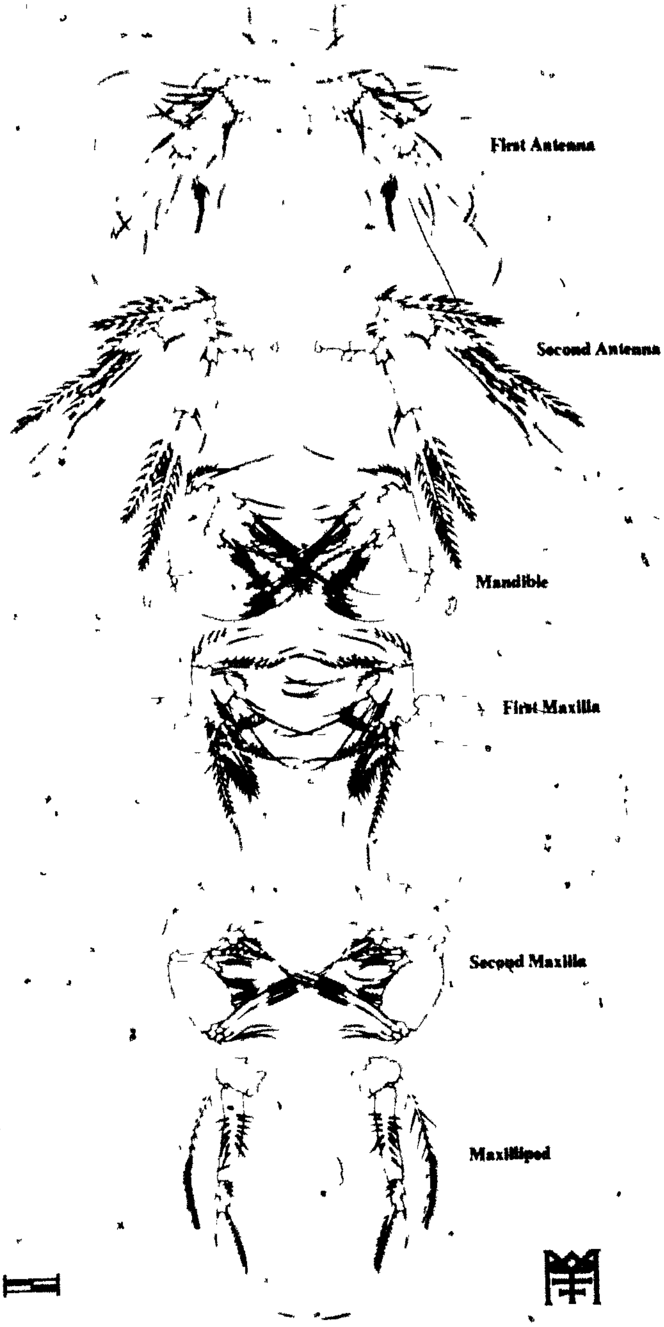
A_2 - with allobasis. Endopod 1-segmented with thorns and 1 barbed setae on medial edge, terminally with 4 barbed and 2 smooth setae. Exopod 3-segmented, first and second segments with 1 smooth ~~seta~~ each, third segment terminally with 2 barbed setae.

Md - precoxa curved with 2 plumose setae at base of 5-dentate pars incisiva and distal edge with serations. Coxa-basis with 1 barb[redacted] smooth seta. Small exopodite with 3 plumose setae. Endopod with 7 setae as figured. A chitinous, wedge-shaped flange extends from the junction of the precoxa and coxa-basis.

Figure 26. Pseudobradya sp. 3. SEM of entire oral region. Magnification: 1900X. Figure 27 gives appendicular details.

Figure 27. Pseudobradya sp. 3. Detail of oral appendages.

Scale: 32 μm.



Pseudobradya sp. 3

Mx_1 – Arthrite of precoxa with 3 unguiform setae: proximal plumose, middle armed with 2 rows of barbs, distal plumose with a large hilt. Remaining portion of appendage indistinctly segmented with 9 smooth and 4 barbed setae as figured.

Mx_2 – Syncoxa with 3 arthrites: proximal with 2 smooth and 1 barbed seta, middle with 1 smooth and 1 barbed seta, distal with 1 plumose, 1 smooth and 1 barbed seta.

Mxp – Basis small with 1 long, plumose seta. E[illegible]opod 2-segmented. First segment with 2 rows of thorns. Second segment with 2 smooth and 1 barbed seta as figured.

Labrum – reduced to a ridge.

Legs – well developed and with spinules on anterior surface of segments.

Kinematics

Pseudobradya sp. 3 spent more than 50% of its time in the water column above the bottom swimming in spiral paths using its abdomen as a rudder. When approached or touched by a vibrating probe, it usually dove into the sediment and burrowed deep into the top centimeter.

It fed on large grains of sand which it cradled in its mouth using the paddles of its Mx_2 and the palps of the Md and Mx_1. It scraped food from the sand with the barbed setae of its A_2 and swallowed suspended particles with strong peristaltic suction.

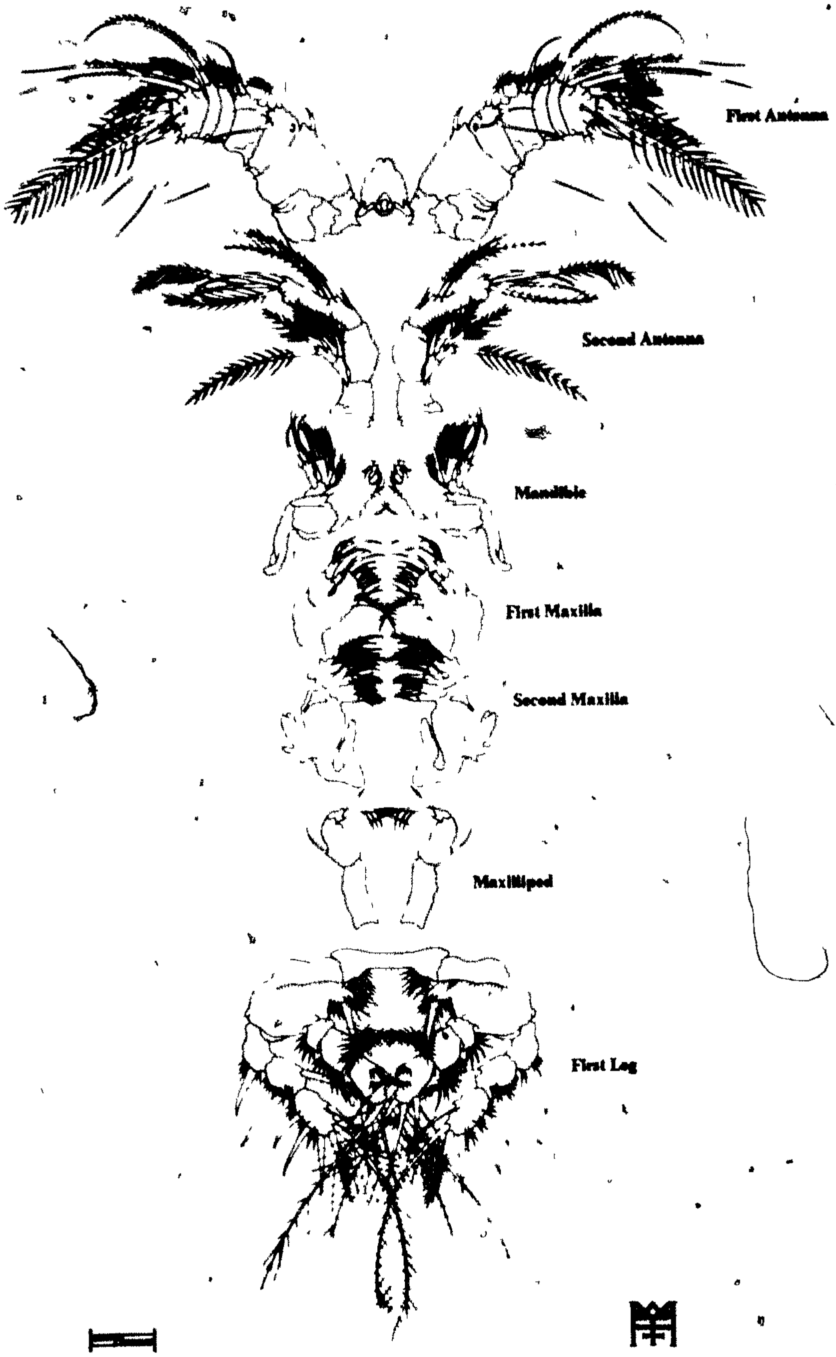
Family Tachidiidae

MICROARTHRIDION LITTORALE (Fig. 28).

Description based on adult gravid female 630 μm long.

Figure 28. *Microarthridion littorale.* Detail of oral appendages.

Scale: 48 µm.



Microarthridion littorale **[Poppe] 1881**

Body - deeply segmented, coloured white and often dirt covered.

A_1 - 6-segmented with numerous thorned, barbed and rake setae oriented ventro-anteriorly. Last segment with aesthetasc.

A_2 - with basis. Endopod 2-segmented, last segment with 3 plumose setae medially and 2 plumose and 3 smooth setae terminally. Exopod 2-segmented. First segment with 1 plumose seta. End segment with 1 plumose seta medially and 2 rake setae terminally.

Md - with 8-dentate pars incisiva and a crowned, bidentate pars molaris. Coxa-basis with 1 seta. Endopod 1-segmented with 6 setae. Exopod 1-segmented with 4 setae. Precoxa with lateral, triangular flange.

Mx_1 - Arthrite with 1 spinulose, 2 bifid and 7 stout, smooth setae. Coxa with 2 naked setae. Basis with 4 satae.

Mx_2 - Syncoxa with 4 arthrites with 8 setae as figured. Basis with 6 setae as figured.

Mxp - basis elongate. Endopod terminally with rake-claw and 1 smooth seta.

Legs - 4 swimming legs very setulose, extending from laterally displaced bases. First segment of endopod reduced. Both rami curve ventro-medially producing a vaulted space circumscribed by intercoxal plate, inner mound of bases and endopods. Outer, exopod girdle, thorn covered with stout setae.

Kinematics

M. littorale swam most of the time, alighting on soft sediments to feed. To eat, it raked detrital rubble from the sediment with the setae of its A_1 and passed it within the arch of its A_2 to the Md - Mx_1 complex where food was sorted from the rubble. Discarded rubble was moved by the Mx_2 within the archway made by the claws of the Mxp and passed to the vaulted space between the swimming legs. The debris was then rapidly and smoothly moved down this passageway by strokes of the endopods and bases and ejected below the abdomen. In this way, the animal, initially with its back toward the sediment surface, dug several millimeters into the bottom.

Family Tisbidae

TISBE FURCATA (Figs. 29 to 47)

Architectural Aspects

The harpacticoid copepod, *Tisbe furcata* was a raptorial feeder --- it grasped for food rather than filter it from the water. Its morphology was adapted to grab, crush and poke food into the animal's mouth. *T. furcata* fed on nematode prey and balls of detritus.

The appendages of the oral region circumscribed a frustal space ventral to the mouth (Fig. 47). This space was bordered: 1) anteriorly by the proximal segments of the A_1 (Figs. 29, 30 and 31), A_2 basis and endopod (Figs. 32, 33 and 34) and the labrum (Figs. 30 and 35), 2) laterally by the lateral and distal

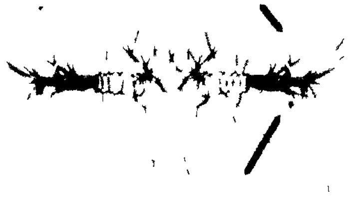
Figures 29, 30 & 31. <u>Tisbe furcata</u>. First antenna. Arrows indicate direction and extent of appendicular movement.

Figure 29. (upper) Posterior view. Scale: 40 µm.

Figure 30. (lower left) Lateral view. Scale: 10 µm.

Figure 31. (lower right) Ventral view. Scale: 20 µm.

First Antenna



Figures 32, 33 & 34. *Tisbe furcata*. Second antenna. Arrows indicate direction and extent of appendicular movement.

Figure 32. (upper) Posterior view. Scale: 40 μm.

Figure 33. (lower left) Lateral view. Scale: 10 μm.

Figure 34. (lower right) Ventral view. Scale: 20 μm.

2nd Antenna

Figure 35. Tisbe furcata. Posterior view of labrum. Scale: 40 µm.


Labium

Figures 36, 37 & 38. *Tisbe furcata*. Mandible. Arrows indicate directions and extent of appendicular movement.

Figure 36. (upper) Posterior view. Scale: 40 μm.

Figure 37. (lower left) Lateral view. Scale: 10 μm.

Figure 38. (lower right) Ventral view. Scale: 20 μm.


Mandible

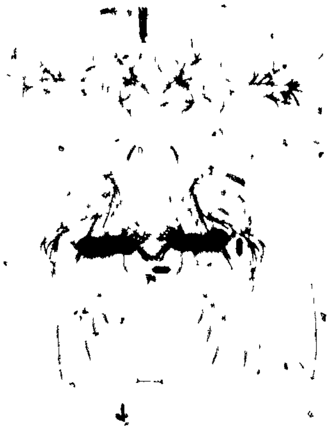
Figures 39, 40 & 41. Tisbe furcata. First maxilla. Arrows indicate direction and extent of appendicular movement.

Figure 39. (upper) Posterior view. Scale: 40 μm.

Figure 40. (lower left) Lateral view. Scale: 10 μm.

Figure 41. (lower right) Ventral view. Scale: 20 μm.


First Maxilla


b.

Figures 42, 43 & 44. Tisbe furcata. Second maxilla. Arrows indicate direction and extent of appendicular movement.

Figure 42. (upper) Posterior view. Scale: 40 µm.

Figure 43. (lower left) Lateral view. Scale: 10 µm.

Figure 44. (lower right) Ventral view. Scale: 20 µm.


te nd Maxilla

Figures 45, 46 & 47. Tisbe furcata. Maxilliped. Arrows indicate direction and extent of appendicular movement.

Figure 45. (upper) Posterior view. Scale: 40 μm.

Figure 46. (lower left) Lateral view. Scale: 10 μm.

Figure 47. (lower right) Ventral view. Scale: 20 μm.

portions of the Mx_1 protopod (Fig. 40), the body of the Mx_2 (Fig. 43) and the lateral margins of the carapace (Figs. 30 and 31); 3) posteriorly by the proximal region of the Mx_2 (Figs. 43 and 44) and Mxp (Figs. 46 and 47) protopods and the labium (Fig. 29) and 4) ventrally by the distal and medial setae of the A_2 endopod (Fig. 34) and the claws of the Mx_2 and Mxp (Figs. 44 and 47). The volume of this frustum of a pyramid was approximately 4.7×10^4 μm^3, a volume similar to that of a sphere 100 μm in diameter or the size of a fine grain of sand. This volume varied with the size of the individual copepod and with the position of the mouth parts. Its volume seemed to control the size of detrital sphere fed upon. (A positive correlation of body size and food size has been found by Fryer (1957a, 1957b) for raptorial cyclopoids).

A_1 - The A_1 seemed to be primarily a sensory and swimming organ. All setae of the A_1 were tapered and smooth (Fig. 29). There were no setae on the posterior surface of the A_1 (Figs. 29, 30 and 31), i.e. no setae projected toward the mouth.

A_2 - The A_2 was used directly in the feeding process. Its endopod arched up to 75 μm below the ventral surface of the head (Fig. 33) and was equipped with long, strong, naked setae which recurved medio-ventrally (Figs. 32, 33 and 34). A spur lay on the median, distal corner of the A_2 endopod (Fig. 32). The A_2 exopod closed the gap beneath the arch of the A_2 endopod (Figs. 32, 33 and 34).

Labrum-Md-Mx_1 - The Labrum (Figs. 30, 31 and 35) projected 33 μm below the ventral surface of the head. In the space immediately below and posterior to the labrum, the Md and Mx_1 were compactly arranged. The cutting or biting edges of the Md apposed directly posterior to an area of reinforced exoskeleton on the inner surface of the labrum. This area had two crescent-shaped buttresses and a system of ridges and groves similar to those on a file or washboard.

The posterior surface of the mandibular protopod (Fig. 36) was grooved to fit the surface setae of the Mx_1 (Fig. 39). The flat surface of the distal blade of the Mx_1 protopod was turned laterally and was couched in the hollow of the Md palps (Figs. 38 and 41). The proximal portion of the Mx_1 protopod was medially concave, creating a cradle for objects entering the mandibular area.

Mx_2 - The Mx_2 was equipped with a large prehensile claw which curved in all three dimensions (Figs. 42, 43 and 44). This claw was fitted with a stout, spinulose seta at its base. This seta seemed to act as a pressure sensitive stop or hilt (see kinematics, below). There was a fine, lash-like seta projecting from an endite on the Mx_2 protopod. This seta projected anterio-laterally from the resting Mx_2 and may have served a sensory function.

Mxp - The Mxp, with its prehensile claw, sat on a basal segment which projected from the midline of the head. The volume swept clear by this claw lay behind and ventral to that circumscribed by the claw of the Mx_2.

Kinematic Aspects

Tisbe funata is a fast swimmer spending much time moving from epibenthic to epiphytic habitats. Its leg movements involved no lateral displacements. Poda were simply moved forward and backward at approximately 40-50 times per second. Feeding was observed to take place only on a substrate surface. When a food particle was first encountered, it was either: 1) impaled or grabbed and pushed to the mouth directly by the Mx_2 or 2) was embraced by the body and setae of the A_2 and secondarily manipulated to the mouth by the Mx_2. In either case the A_2 was important in holding particles within the oral frustum. When a food item was first encountered, there was no activity in the Md or Mx_1. Mxp seemed most useful in guarding the posterior and ventral most margins of the oral frustum against escape of 'reluctant' food and in twirling balls of detritus. The Mxp also helped the Mx_2 by pressing food to the dorsal surface of the mouth. At no time was the claw of the Mxp fully apposed to the body of the appendage. Throughout the feeding process the Mx_2 seemed most dextrous and useful. Its body could pivot on its basal segment circumscribing an arc which extended from the base of the Mx_1 to the lateral edge of the basal stalk of the Mxp. At the same time the claw of the

Mx_2 could be swung anteriorly and ventrally to the medial edge of the Md palps. When used to grasp or impale an object, the body of the Mx_2 was swung to its posterior-most position. The claw was then closed in a strong dorso-posterior thrust. The extent of this lunge seemed limited by the presence of the seta at the base of the Mx_2 claw. After the claw was closed, the body of the Mx_2 was pivoted forward ramming the food item into the heretofore quiescent Mx_1 and Md.

Once a food particle was oriented with its long axis parallel to the main axis of the copepod's body, the Md and Mx_1 were triggered into action. The sensory physiology of this event is unknown. However an analysis of the structure of the oral region suggests that the two spinulose setae on the medio-posterior margin of the Mx_1 arthrite (Figs. 39 and 41) and/or the spinulose seta on the medio-dorsal face of the Md cutting edge (Fig. 36) are the most likely candidates for sensory organs in this area.

The Md and Mx_1 always act in concert. The Mx_1 moved rapidly and repeatedly through an elliptical path, the major axis of which was transverse to the major axis of the copepod's body. The effect of this movement was to direct and, perhaps, propel food directly into the biting edges of the Md.

The movement of the Md was very difficult to define. Most of its movement was in the transverse direction. In addition to transverse biting, the cutting edges appeared to roll across each other just as they were fully apposed. From a study of the anatomy of the Md and labrum, four masticatory events seem likely.

1) The slight roll may crush and squeeze food items between the cutting edges and pars molaris of the Md.

2) The transverse apposition of the biting edges may shear large food items into smaller ones. This shearing action may be either facilitated by the rolling motion or may, in fact, cause the apparent roll.

3) The transverse biting may abrade anteriorly directed food particles against the ridges on the posterior face of the labrum thus crushing them further.

4) If the partes molaris of the Md's are fully apposed during transverse movements of the Md, food items dorsal to the cutting edge of the Md could be squeezed dorsally to the oesophagus. Food particles once crushed were swallowed by powerful foregut peristalsis. These waves of contraction moved posteriorly throughout the ingestion process.

Tisbe furcata seemed able to reject a prospective food item at three times in the ingestion process: 1) when approaching stationary detritus or plant particles, the copepod could reject the item after it had apprehended the particle with its A_1, 2) after the particle had made contact with the Mx_1 and Md and 3) after mastication. The last two rejection events may have an identical sensory basis. Rejection after mastication was facilitated by reverse peristaltic contractions of the foregut, rapid transverse movement of the Md and Mx_1 and very delicate manipulation of the tip of the Mx_2 claw at the ventral border of the labrum to remove the unwanted particle from between the blades of the Md. The ecological significance of this last type of rejection is unknown. The peristaltic contractions which attended this event seemed violent and nearly arhythmic. This activity seemed very strenuous and may be an exceptional occurrence.

Family Thalestridae

DACTYLOPODIA SP. 1 (vulgaris) (Fig. 48)

Architecture

Description based on adult, gravid female 750 μm long.

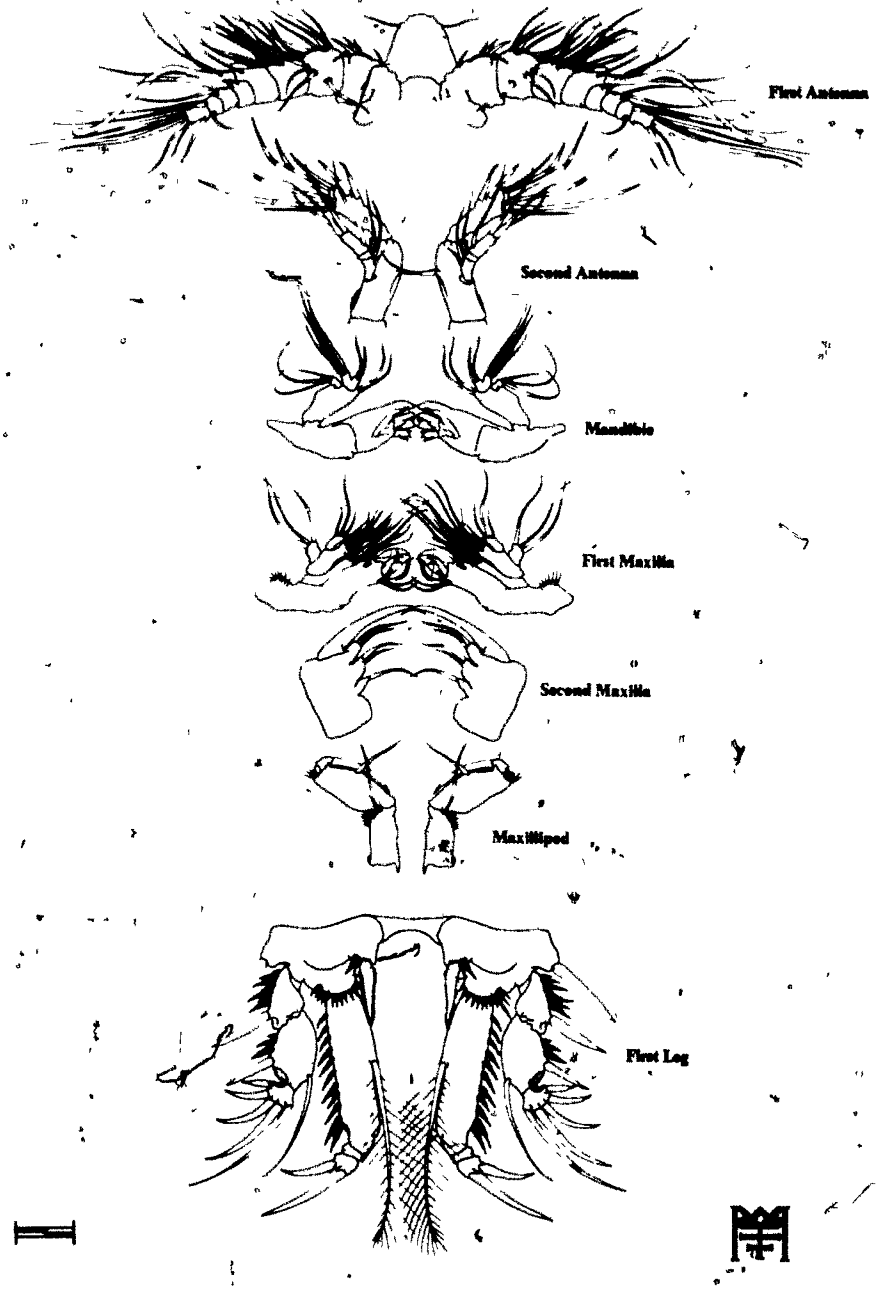
Body - rotund, red coloured.

A_1 - 8-segmented. Aesthetasc on segment 4 extends twice the length of the 4 terminal segments beyond end of A_1. Many smooth setae anteriorly directed.

A_2 - allobasis with 1 smooth, medial seta. Endopod 1-segmented with 2 medial spines, terminally with 1 bifid, 3 recurved and 1 plane seta. Endopod 3-segmented. First segment with 2 setae, middle with 1 seta and end with 1 medial and 3 terminal setae.

Figure 48. Dactylopodia sp. 1. Detail of oral appendages.

Scale: 32 μm.



Dactylopodia sp. 1

Md - Precoxa with 4 dentate pars incisiva and bidentate lacinia mobilis which is crowned with a very thick dermal layer. Basis with 2 setae, endopod with 6 setae, exopod with 3 setae as figured.

Mx_1 - Arthrite with 4 unguiform setae and 6 smooth setae and barbs. Coxa with 4 setae. Basis with 4 setae. Endopod 1-segmented with 4 setae. Exopod 1-segmented with 3 setae.

Mx_2 - Syncoxa with 3 arthrites, each with setae as figured. Basis produced into 1 robust claw.

Mxp - Basis with 1 seta. Endopod 2-segmented, prehensile. First segment with 1 seta, second segment terminally with 1 claw.

P_1 - endopod robust and prehensile. Exopod robust with large outer spines and hyaline area at joint of second and third exopod segments.

Kinematics

This species inhabited algae, especially flat surfaces. It swam strongly but not swiftly. It ate by sweeping diatoms and organic debris from the surface of the algae into its mouth with its A_2 aided by the palps of the Mx_1. The terminal setae of the A_2 were often held and cleaned of attached debris by the claw of the Mxp. Food was crushed with rapid movement of the large, flat-toothed Md.

Family Diosaccidae

STENHELIA DIVERGENS (Figs. 49 & 50).

Architecture.

Description based on adult gravid female 522 μm long.

Body - rotund anteriorly, white coloured.

A_1 - 8-segmented. Aesthetasc on segment 4, extending only once the length of last 4 segments beyond end of A_1. Numerous smooth setae anteriorly directed.

A_2 - Allobasis with 1 seta. Endopod 1-segmented, medially with thorns and 1 seta, terminally with 3 smooth, 2 recurved and 1 barbed seta. Exopod 3-segmented, first and middle segments with 1 seta each. Third segment with 1 medial and 3 terminal setae.

Md - Precoxa proximally with 2 setae. 7-dentate pars incisiva, bidentate lacinia mobilis with small dermal crown. Basis medially with 4 small setae, terminally with 3 large setae. Endopod 1-segmented with 3 setae, the inner most one prolonged forming a lateral border to oral region. Exopod 1-segmented with 6 setae as figured.

Mx_1 - Arthrite terminally with 4 unguiform setae and with 2 surface setae. Coxa with 3 setae. Basis recurved posterio-ventrally with 7 setae. Endopod 1-segmented with 4 setae. Exopod 1-segmented with 2 setae.

Mx_2 - Syncoxa with 4 arthrites with setae as figured. Basis with 1 strong and 1 small terminal seta. Endopod with 2 smooth setae.

Figure 49. Stenhelia divergens. SEM of oral region. Manification: 2100X. Note diatoms under setae of Mx_1. Labrum (upper center) with frill. Diatoms cradled below setae of Mx_1. See Figure 50 for appendicular details.

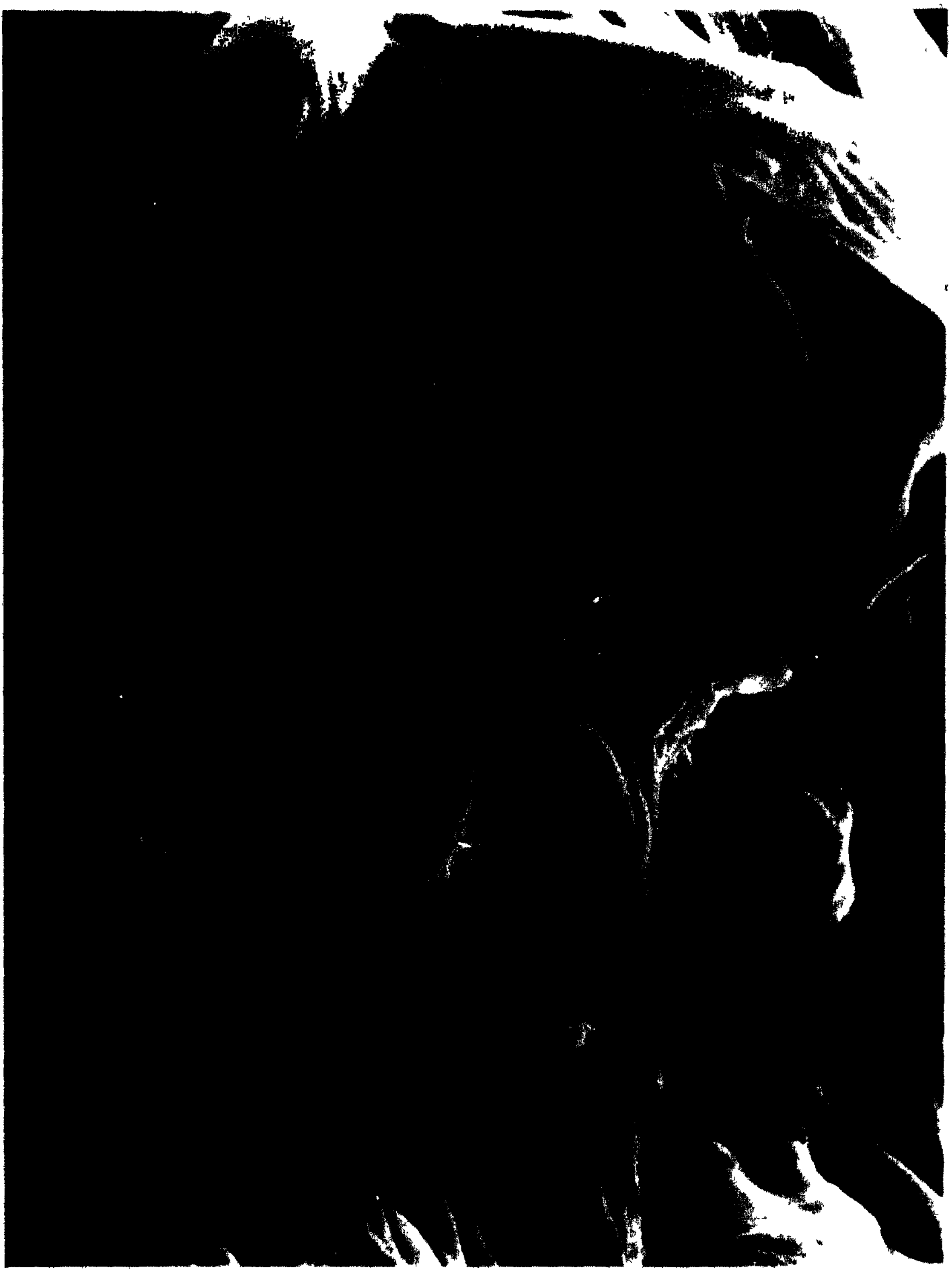
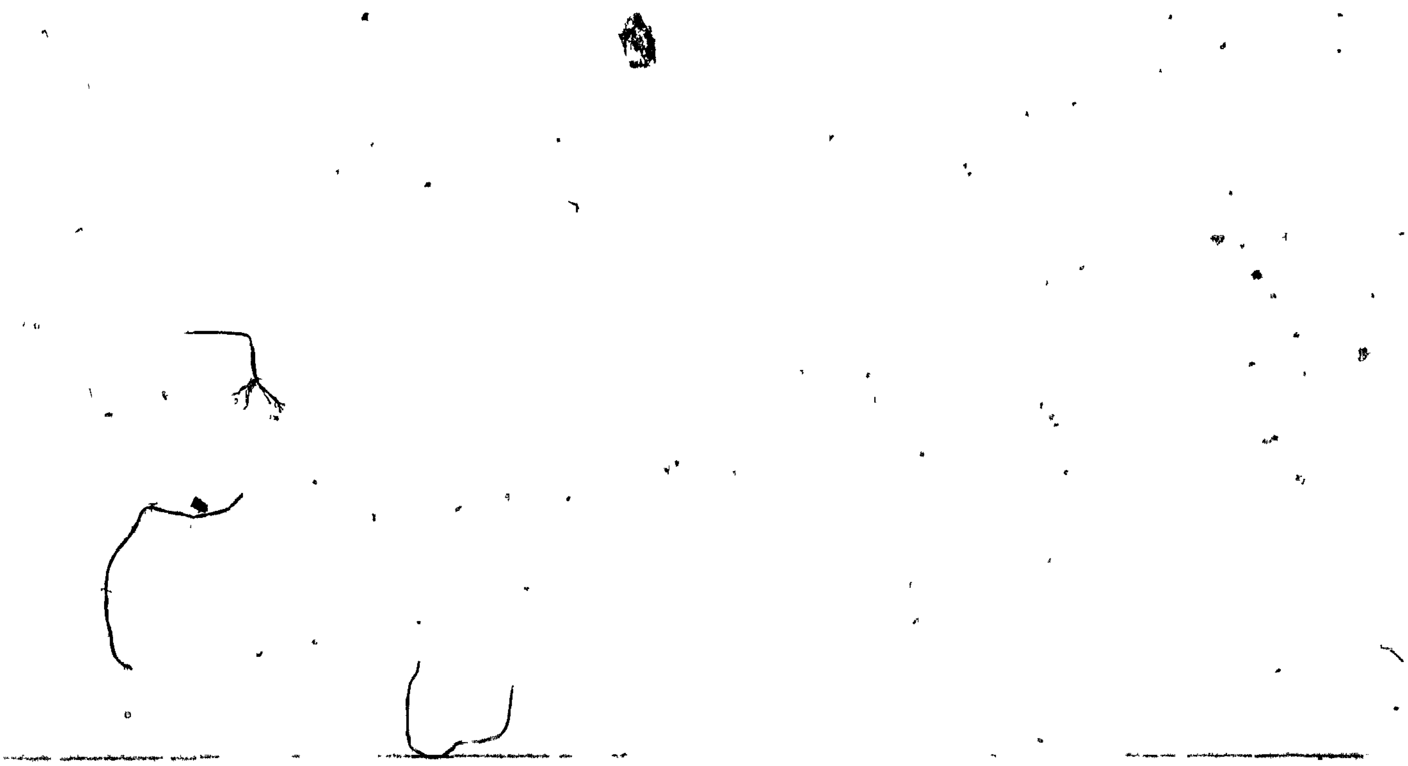
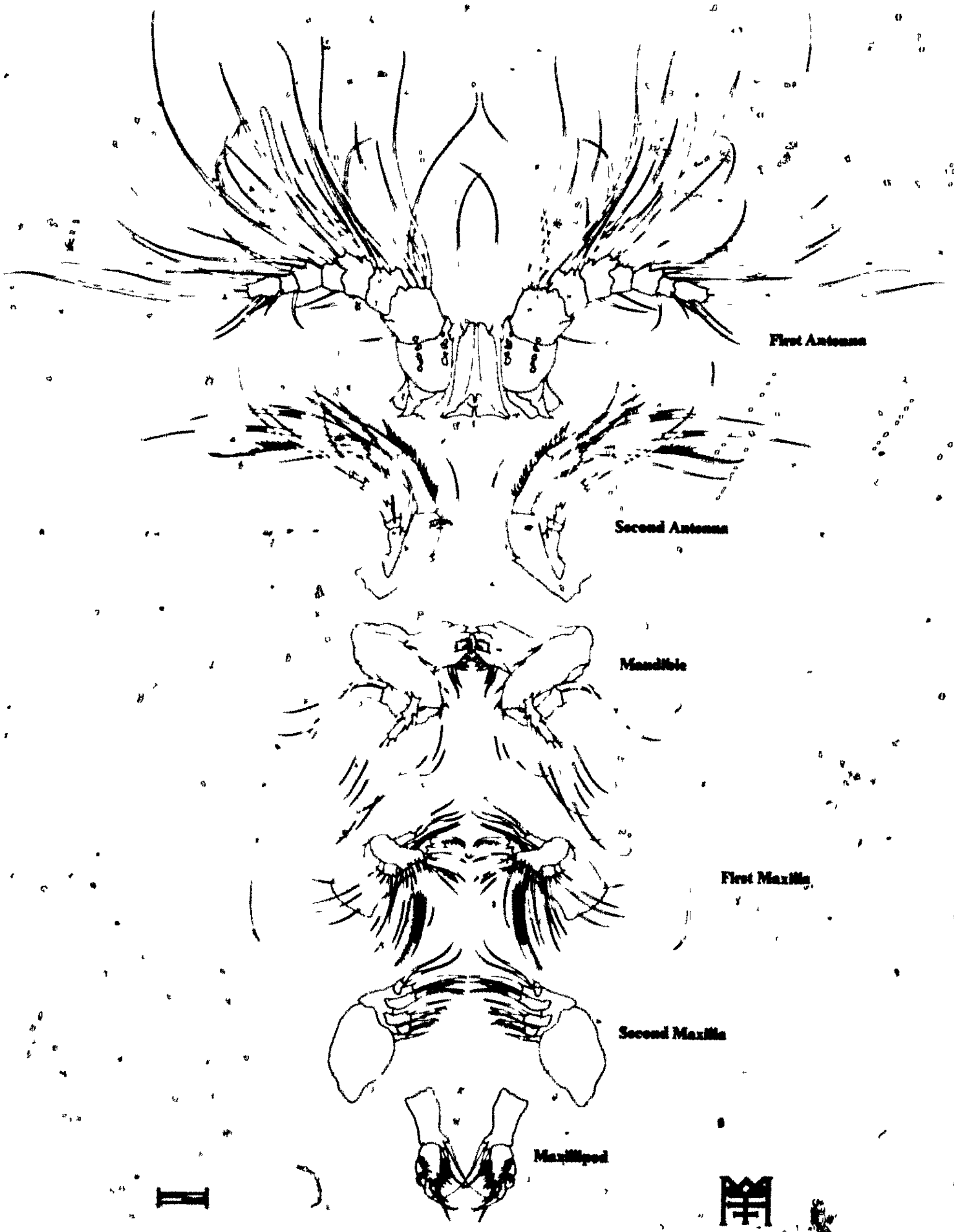


Figure 50. Stenhelia divergens. Detail of oral appendages. Scale: 32 µm.





Stenhelia divergens **Nicholls 1939**

Mxp - Basis with 2 setae. Endopod 2-segmented. First segment thorn covered with 1 large seta. Last segment terminally with 1 short claw and 1 seta.

Labrum - curved posteriad with thick fringe of micro-hairs at its ventral-most tip giving it the appearance of a barber's brush.

Kinematics

S. divergens burrowed deeply into the sediment and ate free-living, pennate diatoms. It swept the diatoms up and pushed them toward the mouth with the Mxp. The palps of the Mx_1 covered the ventral surface of the mouth pressing the diatoms to the mouth. Below this fan of setae, the Mx_2, Mx_1 arthrite and Md crushed and sheared open the diatom frustules. The contents of the diatoms were moved and sucked toward the mouth below the hairy frill on the labrum (Fig. 49). This species was never seen eating foods other than diatoms. However, another, undescribed species from St. Margarets Bay, N.S., which inhabits fine muds, was seen eating surface material from balls of detritus. This second species has an oral morphology which is quite different from that of S. divergens. SEM examination of S. normani polluta Monard, S. palustra (Brady) and S. longicaudata Boeck from the Mediterranean Sea, Bermuda and Eastern North America showed that all these species have oral morphologies similar to those of S. divergens and, from evidence of diatoms fixed in their mouth parts, appear to eat diatoms in the same way as S. divergens.

AMPHIASCUS MINUTUS (Fig. 51 & 52).

Architecture

Description based on adult, gravid female, 540 µm long.

Body - white coloured.

A_1 - 8-segmented. Aesthetasc on segment 4, extends far beyond end of A_1. 1 medial, plumose seta. All other setae smooth.

A_2 - Allobasis with 1 medial seta. Endopod 1-segmented with thorns and barbs medially and 6 terminal setae. Exopod 3-segmented with 5 setae as figured.

Md - Cutting edge with 1 proximal, seta, 10-dentate pars incisiva and 3-dentate lacinia mobilis. Basis with 4 setae one of which extends across the anterior face of the labrum. Endopod 1-segmented with 7 setae. Exopod 2-segmented with 3 setae as figured.

Mx_1 - Arthrite terminally with 4 unguiform setae and 4 slender setae, surface with 2 setae. Coxa with 2 setae. Basis with 3 setae. Endopod with 5 setae. Exopod with 2 setae.

Mx_2 - Syncoxa with 3 arthrites each with 1 spinulose, unguiform seta and 1 fine seta. Basis produced into a claw. Endopod with 4 setae.

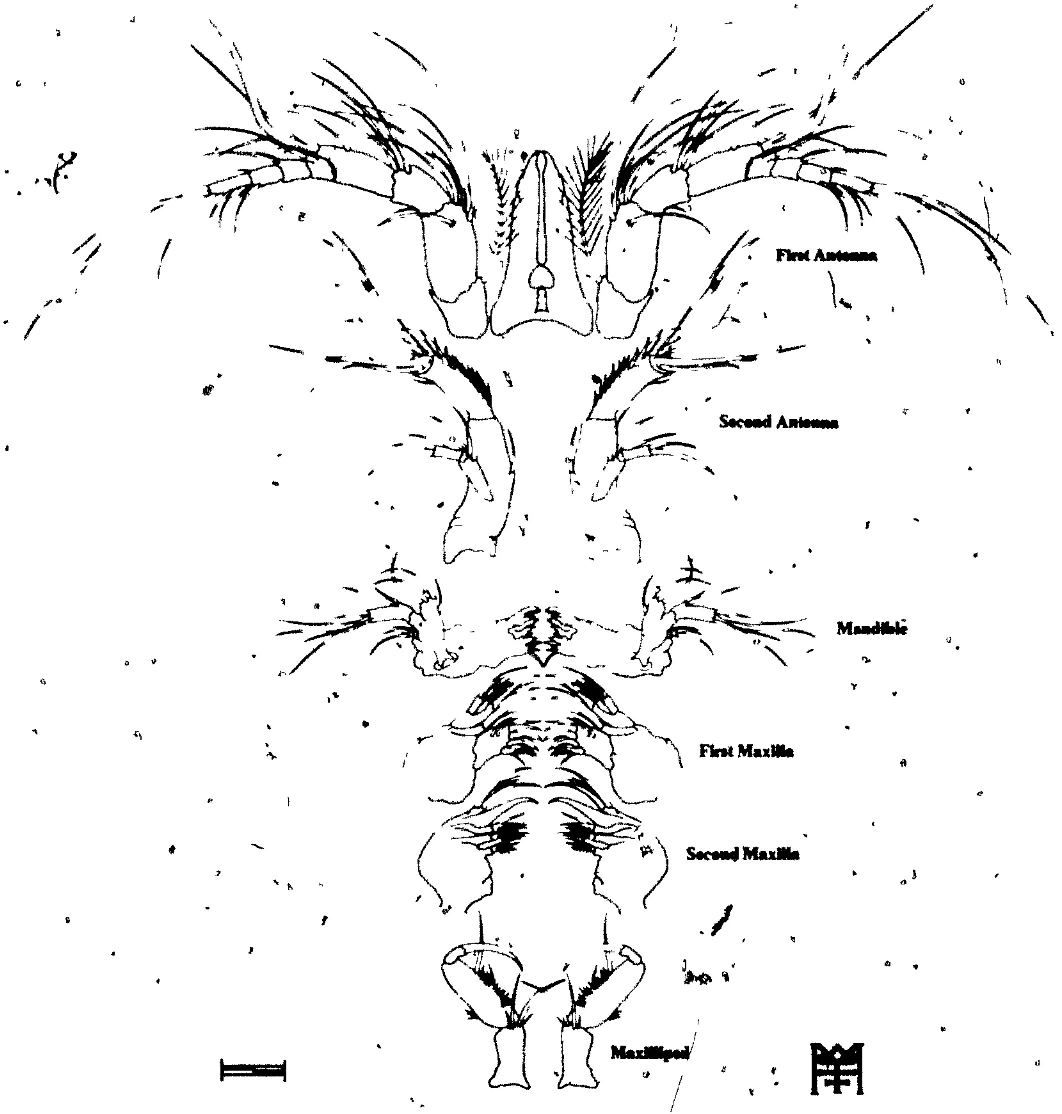
Mxp - Basis with 4 setae. Endopod 2-segmented. First segment with 2 setae and 1 row of spines. Last segment with terminal claw.

Labrum - flat, plate-like.

Legs - well developed.

Figure 51. *Amphiascus minutus.* SEM of entire oral region. Distance between adjacent white tick marks is 30 μm. Md, Mx_1 and Mx_2 are clustered below ventral tip of plate-like labrum (centre).

Figure 52. <u>Amphiascus</u> <u>minutus</u>. Detail of oral appendages. Scale: 32 µm.



Amphiascus minutus **[Claus] 1863**

Kinematics

A. minutus burrowed through the surface, flocculent layer (0.5 cm deep) with frequent excursions into deeper sediments. It fed on balls of detritus when observed in the lab. It held the ball in its mouth with its A_2 and Mxp. It spun the ball about, slowly fondling it with its Mx_2. It cleaned particles from the ball using its Mx_1 and Md.

AMPHIASCOIDES DEBILIS (Fig. 53 & 54).

Architecture

Description based on adult, gravid female 378 µm long.

Body - white coloured.

A_1 - 8-segmented. Aesthetasc on segment 4 extends only 0.5 times length of last 4 segments beyond end of A_1. All setae short and smooth.

A_2 - With allobasis as figured. Endopod 1-segmented, with 8 setae as figured. Exopod 3-segmented with 4 setae as figured.

Md - Cutting edge with proximal seta, 4-dentate pars incisiva and bidentate lacinia (?). Palp indistinctly divided. Basis with 3 setae. Endopod with 8 setae. Exopod with 5 setae.

Mx_1 - Arthrite with 2 surface setae and terminally with 8 setae as figured. Coxa with claw and 1 seta. Basis with 5 setae. Endopod with 4 setae. Exopod with 1 seta.

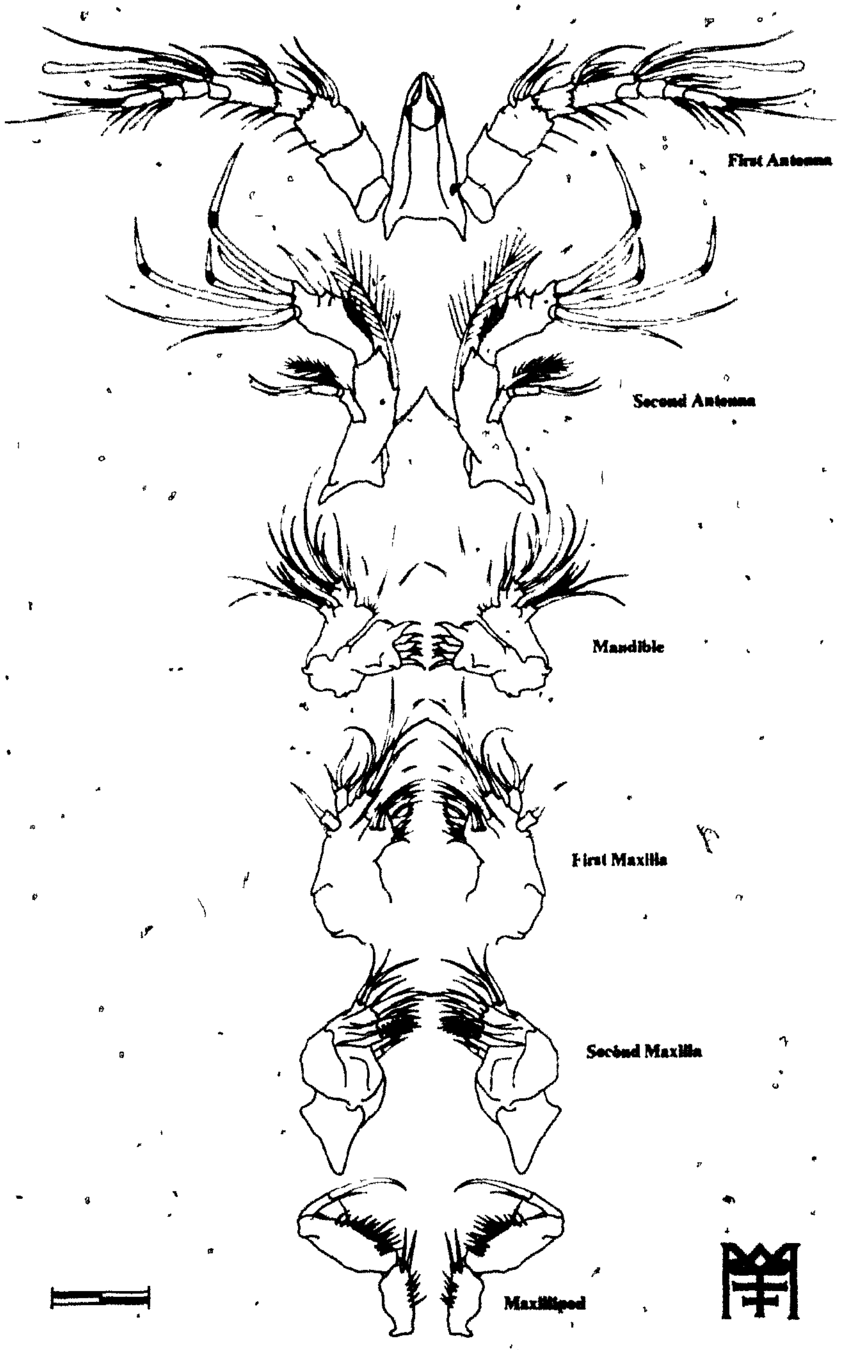
Mx_2 - Syncoxa with 3 arthrites as figured with basis and Endopod.

Mxp - Basis with thorns and 2 setae. Endopod 2-segmented. Last segment with terminal claw and seta.

Labrum - flat and plate-like.

Figure 53. Amphiascoides debilis. SEM of oral region. Distance between adjacent white tick marks is 30 µm.

Figure 54. Amphiascoides debilis. Detail of oral appendages. Scale: 32 μm.



Amphiascoides debilis [Giesbrecht] 1881

Kinematics

This animal burrowed into the flocculent layer of the sediment, often penetrating to the compact layer. It fed on balls of detritus cleaning food bits from the surface. These balls were held in the mouth by the A_2 and Mxp. The palps of the Mx_1 and Md were used to balance the particle in the oral region.

Family Ameiridae

AMEIRIA PARVULA (Figs. 55 & 56)

Architecture

Description based on adult, gravid female 376 µm long.

Body - thin, opaque white in colour.

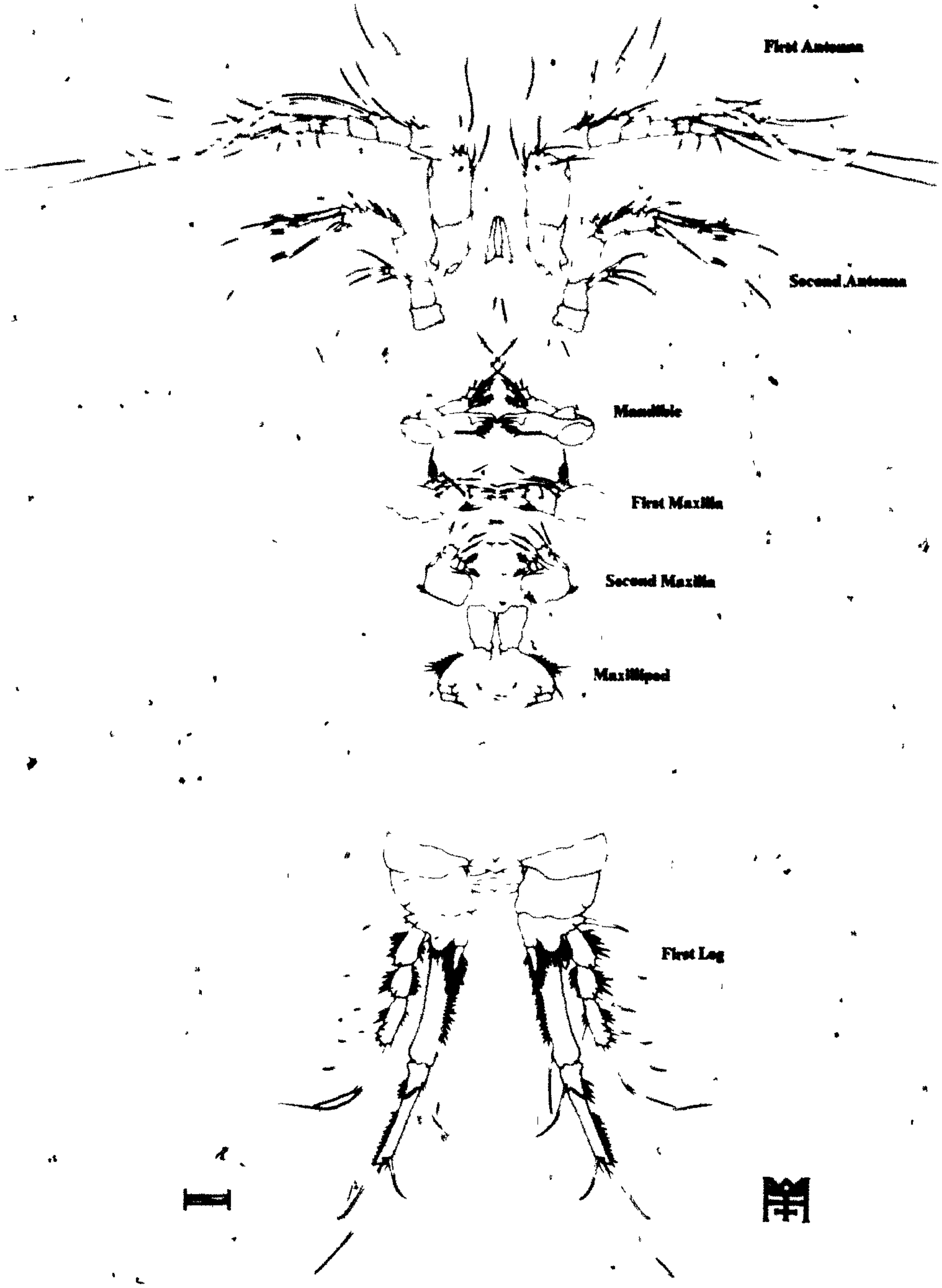
A_1 - 8-segmented. Aesthetasc on segment 4 extends 2 times the length of the last 4 segments beyond end of A_1, robust and surrounded by setae which seemed to guide the course of its extension.

A_2 - Small (vis á vis A_1) with basis. Endopod 2-segmented, last segment with medial thorns and 2 large setae, terminally with 4 recurved and 2 smooth setae and 1 thorn. Exopod 2-segmented, first segment with 2 setae, second segment much smaller than first with 2 setae.

Md - Cutting edge proximally with 1 nude seta, 6-dentate pars incisiva, tridentate lacinia. Basis with 1 plumose and 1 spatulate seta which extends to the anterior surface of the labrum. Endopod with 4 setae.

Figure 55. *Ameiria parvula*. SEM of oral region. Distance between adjacent white tick marks is 30 μm. Note: three parasitic (?) ciliate protozoans lie on intercoxal plate between Mxp and P_1.

Figure 56. *Ameira parvula*. Detail of oral appendages. Scale: 32 µm.



Ameiria parvula [Claus] 1866

Mx_1 - Arthrite with 2 surface setae, terminally with 1 trifid seta, 2 unguiform setae and 2 fine setae. Coxa with 1 terminal claw. Basis with 4 setae.

Mx_2 - 1 arthrite with 2 stout plumose setae. Coxa with 1 quadrafid and 1 smooth seta. Basis with 1 claw and 1 smooth seta. Endopod with 2 setae.

Mxp - Basis long. Endopod 2 segmented, first segment with 1 smooth seta, last segment terminally with 1 claw and 1 seta.

Labrum - with two rows of spines on posterior surface. Plate-like.

P_1 - Prehensile endopod armed with thorns.

Large inter-coxal plate separates Mxp from P_1. This region was often colonized by ciliate parisites (Fig. 55).

Md, Mx_1, Mx_2 and Mxp form a small compact mound below the plate-like labrum. Because the A_2 is morphometrically reduced, this complex is well exposed to the surface of the animal's substrate. These appendages were organized to produce a single point of activity at the ventral tip of the labrum.

<u>Kinematics</u>

Ameiria parvula and A. longipes were often found in coarse sediments along the road at the edge of the estuary. They located food items by constantly sweeping the surface of their substrate with their long A_1. Once food was located, the animal moved its mouth over the area. With rapid picking, their Mx_2 and Mx_1 removed particles from the surface which were then ingested. Their

P_1 and Mxp seemed to be used only to steady the animal on the substrate. These species appeared to be very selective epistrate feeders. The trifid and quadrafid setae of the Mx_1 and Mx_2 may act as tiny files in this mode of feeding.

Family Cletodidae

<u>ENHYDROSOMA</u> <u>LONGIFURCATUM</u> (Fig. 57).

Description based on adult, gravid female 468 µm long.

Body - Worm-like, somites distinctly divided by membranous regions. Golden-brown in colour, often dirt covered. Body sometimes covered in spots of red and black mineral deposits.

A_1 - 5 (6?) -segmented. Aesthetasc on segment 3. With 4 barbed setae on segment 5 and 3, directed anterio-ventrally.

A_2 - Allobasis with 1 seta. Endopod 1-segmented medially with 1 seta and several spines. Terminally with 1 large, barbed seta, 4 smooth setae and a spine. Exopod 1-segmented with 2 plumose setae.

Md - Cutting edge with 1 proximal seta and 5-dentate incisiva. Basis with 1 rake and 2 smooth setae.

Mx_1 - Arthrite with 3 unguiform setae. Coxa with 4 smooth and 1 plumose seta.

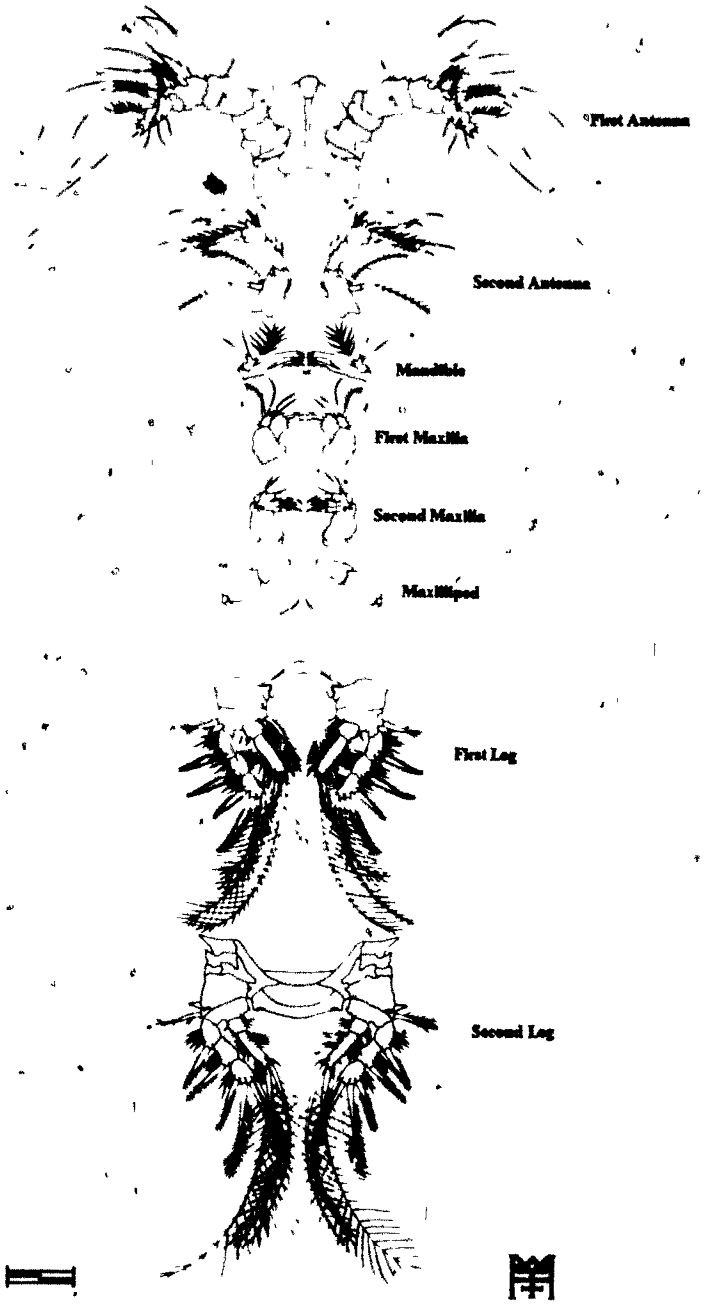
Mx_2 - 2 arthrites with setae as figured. Basis with 1 claw and 1 seta. Endopod reduced to 2 setae.

Mxp - naked, 2-segmented endopod with a simple, terminal claw.

Legs - All 4 "swimming" legs very setulose.

Figure 57. Enhydrosoma longifurcatum. Detail of oral appendages.

Scale: 32 μm.



Enhydrosoma longifurcatum Sars 1909

Endopod reduced to 2 segments, distally with 2 sensory (?) spines on inner edge and 2 plumose setae. Both rami curve ventro-medially producing a vaulted space circumsribed by the intercoxal plate, inner mound of the basis and endopod. Outer exopod girdle thorn covered with stout setae. Coxa of P_1 connected to intercoxal plate by a laterally extended ball and socket joint. Lateral flexion possible. The P_2 coxae composed of unfused dermal plates multiply-connected to intercoxal plate. Some lateral flexion observed. P_3 to P_4 (unfigured) with fused coxae and intercoxal plates. Little lateral flexion possible.

Kinematics

E. longifurcatum burrowed deeply into the sediment, often penetrating reduced, compact layers. It swam downward without rest until its back was covered with some object, sediment, fine piece of wire, etc., Once covered it slowed its movement and would stop all motion for several minutes at a time.

It burrowed by raking fine sediments from its path with the barbed setae of its A_1, passing the rubble within the arch of the A_2 and over the oral appendages. The rubble was carried within the arch of the Mxp to the vaulted space between its legs. Then with rapid beats of the endopods and bases, the rubble was carried down the legs and ejected beneath the abdomen. When feeding, food was sorted from the rubble as it passed over the Mx_2, Mx_1 and Md.

LEIMA VAGA (Figs. 58, 59 & 60)

Architecture

Description based on adult, gravid female 720 µm long.

Body - White coloured, sometimes covered with mineral and organic detritus.

A_1 - 6-segmented. Aesthetasc arising from bifid seta on segment 4. Numerous plumose, barbed and rake setae.

A_2 - Allobasis medially with 1 plumose and 1 smooth seta. Endopod 1-segmented, medially with 2 setae and thorns, terminally with 1 plumose, 1 rake and 4 smooth setae. Exopod 1-segmented with 1 rake and 3 plumose setae.

Md - Cutting edge with 7-dentate incisiva and 4-dentate lacinia. Palp indistinctly divided with 1 very large spinulose seta which extends over labrum and with 5 other setae as figured.

Mx_1 - Arthrite with 10 terminal and 2 surface setae. Coxa with 2 setae. Basis indistinctly divided. Terminally with 2 barbed setae and with 6 other setae as figured.

Mx_2 - 2 arthrites with 3 setae each as figured. Basis with 6 setae as figured.

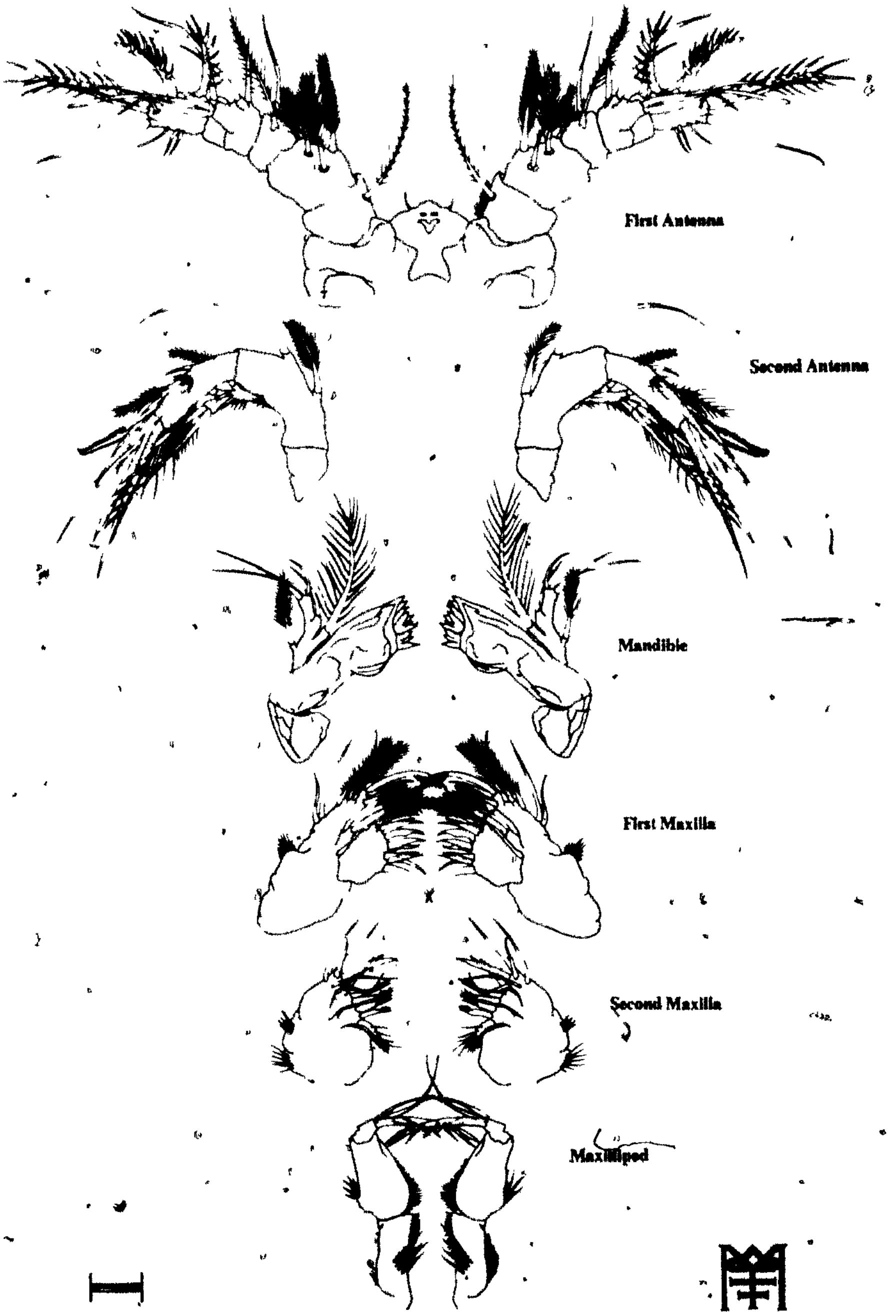
Mxp - Basis extended above mouth with numerous hairs and setae. Endopod 2-segmented. First segment with numerous hairs and spines. Last segment terminally with 2 setae and one rake-like claw.

Labrum - with setule frill at tip and reinforced chitinous ridges on posterior surface.

Figure 58. Leima vaga. Ventral view of entire head. Scale: 32 μm.

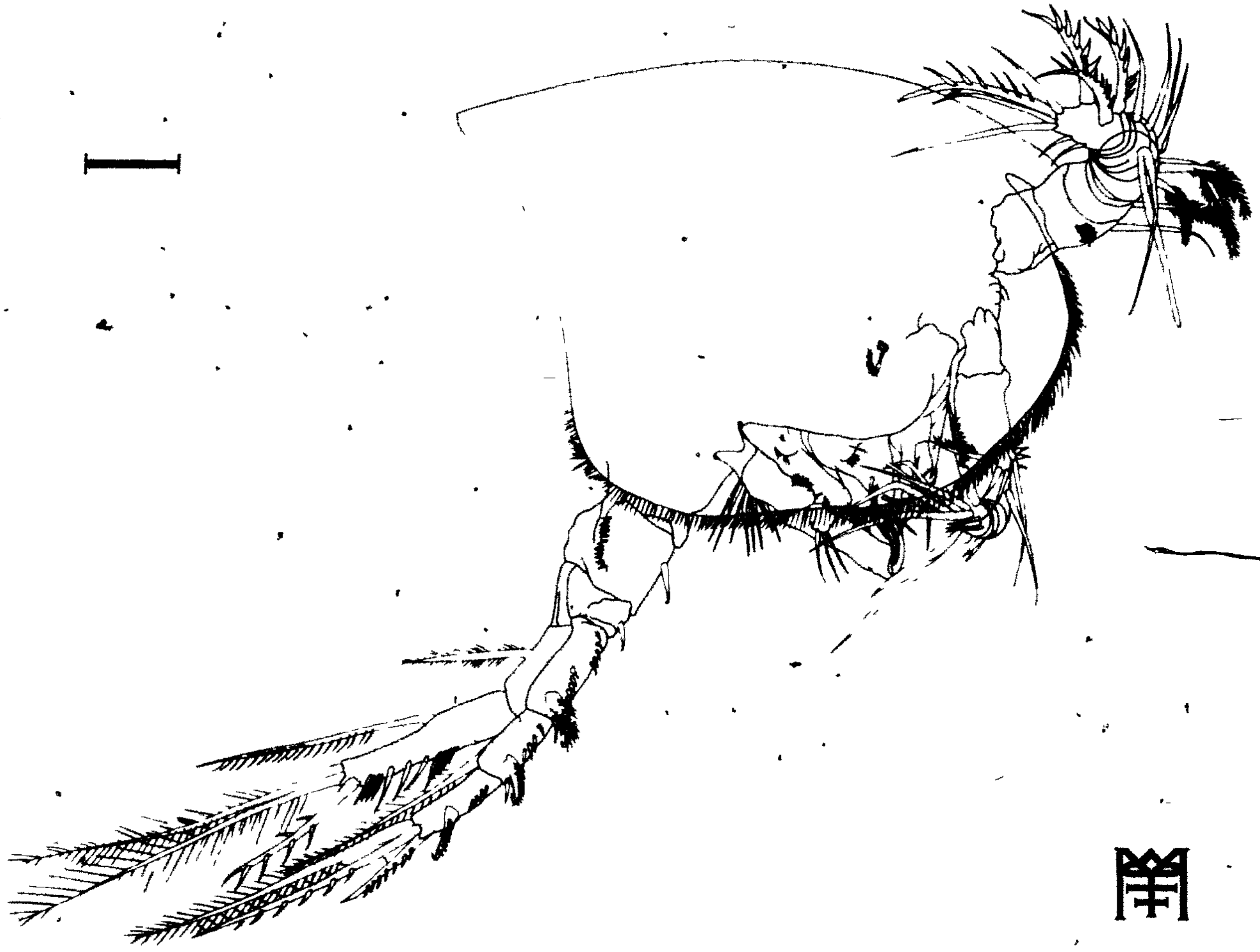
Leima vaga **Willey 1923**

Figure 59. Leima vaga. Detail of oral appendages. Scale: 32 µm.



Leima vaga **Willey 1923**

Figure 60. *Leima vaga*. Lateral view of entire head. Scale: 32 µm.



Leima vaga **Willey 1923**

Oral rim of caripace with setule frill.

Legs - Swimming legs well developed and setulose. Bases lay at angle to midline so that legs create a groove down the thorax-abdomen when closed. Bases, exopods and endopods capable of substantial lateral flexion in P_4 and progressively less in anterior legs except P_1.

Kinematics

L. vaga lived in the water column and alighted on the bottom only to feed. It was probably the fastest moving harpacticoid on the marsh. When swimming the legs were brought forward in a folded state, closely hugging the contours of the belly. As the bases became erect the legs began to fall from under the body. Once fully perpendicular (terminal segments and setae lagged behind a bit) the legs were fanned out laterally with the P_4 outermost then, in order, P_3, P_2 and P_1 grading inward. As the legs reached their full lateral extent, they were thrust ventrally and backward. Once fully back, they collapsed against the midline of the belly and the stroke began again. In leaps to escape the approach of a vibrating probe, the A_1 was used with the legs and the P_1 was extended outward overlapping and even exceeding the lateral reach of the P_4 .

To feed, the animals alighted upside down, on the sediment and picked up balls of detritus with their A_1. These balls were picked up by the barbed setae of the last 3 A_1 segments and passed to the A_2 which moved in a diagonal path from the outermost edge of the A_1 to the sides of the labrum. The ball was guided in its posteriad movement by the spinulose setae of the Md. Once in the region of the Md and Mx_1, the ball of detritus was rapidly twirled beneath the arching setae and claws of the A_2 and Mxp by rapid movements of the Mx_2. Once the surface of the ball had been cleaned, it was tossed down the groove formed by the swimming legs and kicked upward and away.

Family Laophontidae

HETEROLAOPHONTE CAPILLATA (Figs. 61 & 62).

Architecture

Description based on adult, gravid female 720 µm long.

A_1 – 6-segmented. Aesthetasc on segment 4. Numerous smooth setae.

A_2 – Allobasis with medial thorns. Endopod 1-segmented with medial spines and 2 setae, terminally with 4 large and 2 small setae. Exopod 1-segmented with 3 setae.

Md – Cutting edge with proximal seta. 4-dentate incisiva and 6-dentate lacinia. Palp with 4 setae.

Mx_1 – Arthrite with 6 large setae. Coxa with 2 setae. Basis with 1 claw and 3 setae. Endopod with 2 setae.

Mx_2 – 2 endites with 1 large setulose claw and 1 seta each. Basis with 1 very large setulose claw and 2 surface setae.

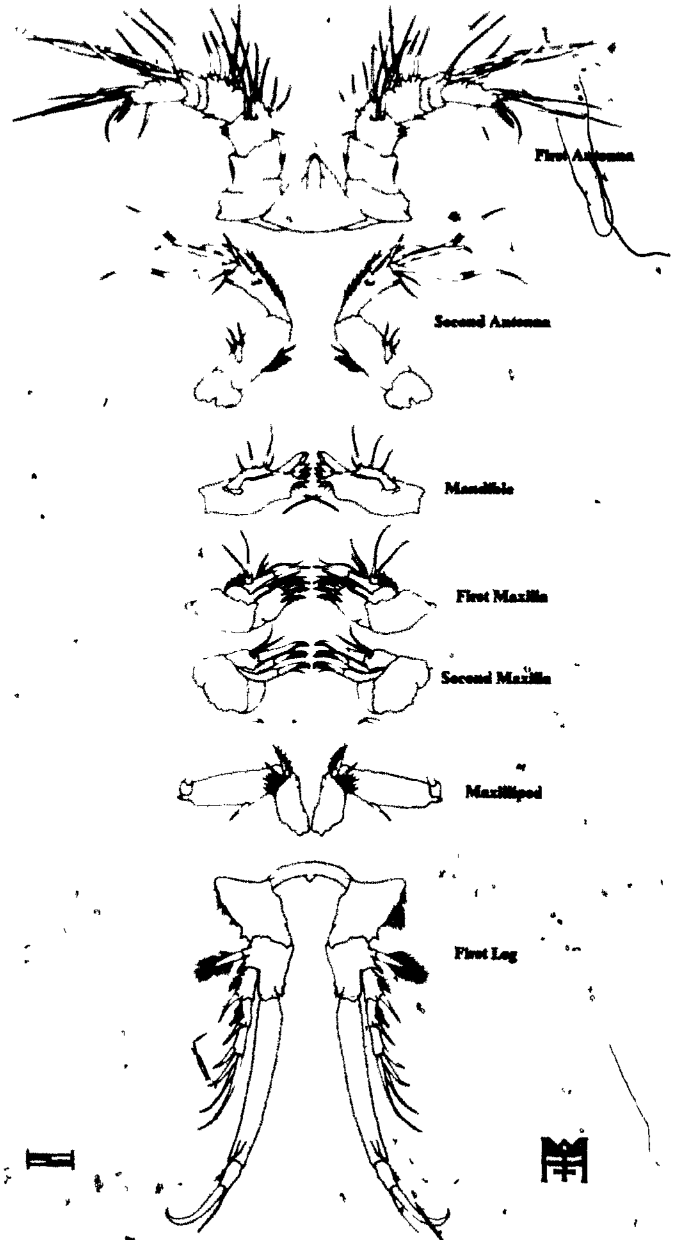
Mxp – Basis with barbed seta and spines. Endopod 2-segmented. First segment with lateral seta. Second segment with terminal claw.

P_1 – Endopod with terminal claw and small seta, prehensile. Coxa ventrally prolonged. Exopod recessed on outer edge of basis.

Figure 61. Heterolaophonte capillata. SEM of oral region, forward-looking, oblique view. Magnification: 2000X. See Figure 62 for details of appendage structure.

Figure 62. <u>Heterolaophonte</u> <u>capillata</u>. Detail of oral appendages.

Scale: 32 μm.



Heterolaophonte capillata [Wilson] 1932

Kinematics

H. capillata fed on edges of detritus and on cylinders of bluegreen algae and worm tubes. Though found in sand, its microhabitat-demand for a linear edge or cylinder was profound. Without a linear object to clutch, specimens would move about without resting. Legs were thrust in spasm-like movements and the body undulated like a worm. Once such an object was provided, the animal grasped it within its P_1 and Mxp and slowed its movements often to a complete halt. Once on a linear substrate the animal could feed.

To feed on a cylinder, the copepod maneuvered its body to place the cylinder perpendicular to the long axis of the body between the P_1 endopod and oral appendages. The P_1 was hooked around the cylinder by tilting the coxa of the leg backward, the basis and endopod forward and the exopod backward, thus taking the exopod away from movements of the Mxp. Then, using its other walking legs, the animal swung its body around and around the cylinder eating slowly along a path which spiraled around the cylinder.

When feeding on rectilinear edges, the P_1 and Mxp were used as grappling hooks to steady the beast as it either walked along the edge or moved the edge down the long axis of its body.

In both cases, food was picked from the surface using the Mx_2 and Mx_1 claws and crushed with the Md.

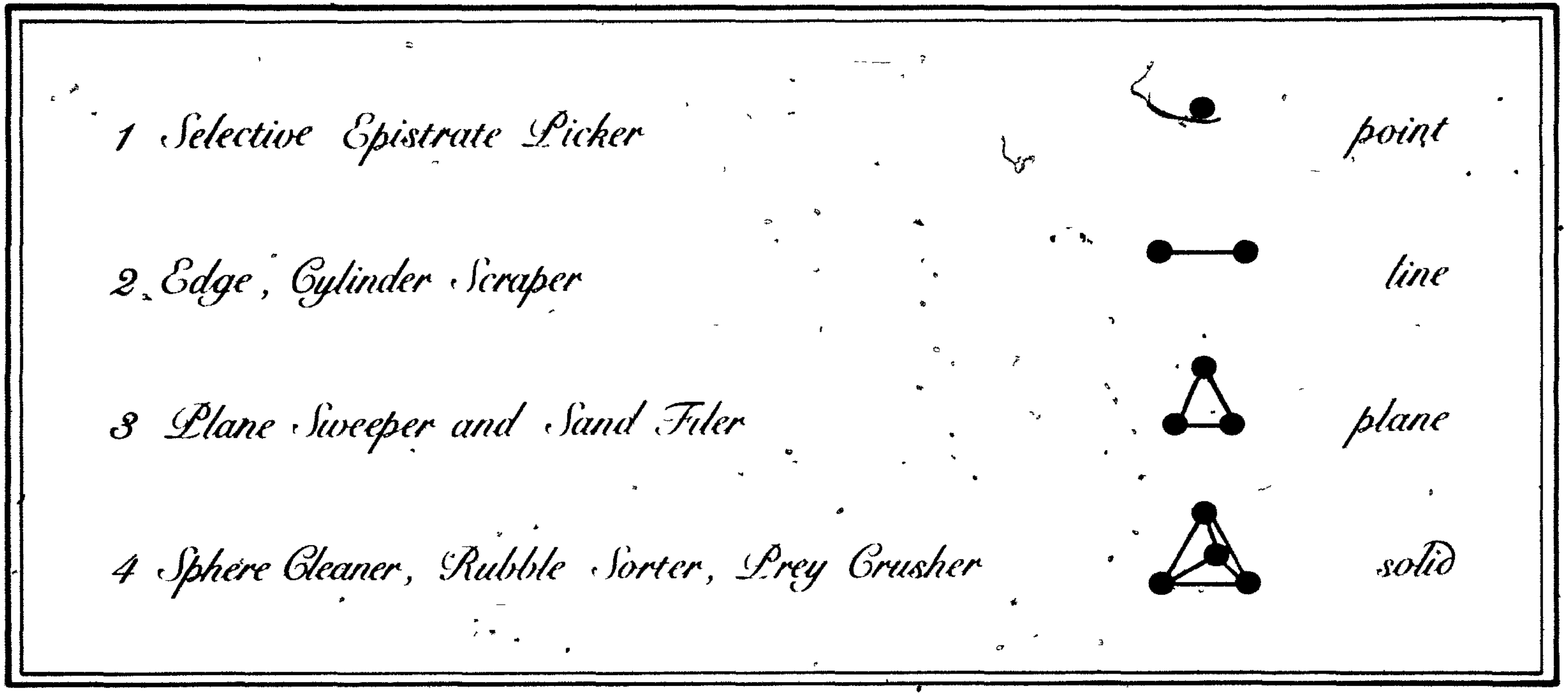
H. capillata and H. discophora were capable of delicate asymmetric manipulation of their oral appendages. In other species, Tisbe furcata for example, movements of the two A_2 or Mxp were coordinated bilaterally across the mouth. In Heterolaophonte these same appendages were often coordinated diagonally across the mouth. This may manifest a higher level of nervous integration in the laophontids.

H. capillata and H. discophora have the same feeding habits and microhabitat preferences except that H. discophora preferred muddier substrates. SEM observation of H. sigmoides from Bermuda indicated that this species eats in the same way as the others. This Bermudian species was collected on mats of bluegreen algae and worm tubes.

Summary of harpacticoid feeding types

These feeding data can be used to define 4 feeding groups (Table 3). 1) Point feeders. Selective epistrate pickers, like Ameiria parvula and A. longipes have a broad labral plate and small oral appendages compactly arranged about its ventral tip. The long A_1 has a disproportionately long aesthetasc (Chemoreceptor). The A_2 are allometrically reduced. The animal carefully locates a food site on large mineral and organic surfaces and feeds only from that spot. The world of these copepods appears to be a series of trophically meaningful points surrounded by undesirable, unselected "noise".

Table 3. The four feeding types of harpacticoids.


1 Selective Epistrate Picker
point
2 Edge, Cylinder Scraper
line
3 Plane Sweeper and Sand Filer
plane
4 Sphere Cleaner, Rubble Sorter, Prey Crusher
solid

2) Line feeders, like Heterolaophonte capillata and H. discophora, remove food from the edge of rectilinear solids and cylinders using the tiny hooks and claws of their oral appendages while clutching the substrate with the grappling hook on the endopod of their P_1. They can asymmetrically move their oral appendages. Their world is a line, a rectilinear edge or a cylinder. On it they live and from it they obtain their food. For them points, planes and tiny solids seem completely unperceived, unsought and unused.

3) Plane sweepers and sand filers. This is a heterogeneous group. Of the first type, Nitocra typica and Dactylopodia sp. are the best examples. These sweep food into their mouths from large planar surfaces of organic debris using their A_2. Sand filers, like Halectinosoma sp. 1, Pseudobradya spp., and probably Heteropsyllus nunni, scrape their food from pits and faults on grains of sand. For all beasts in this second class, food is a fine grained resource spread richly over the surface of the small particles on which they feed. In larger sand sizes, food becomes a coarse grained resource, as pointed out above, and point feeders become common. In short, for plane feeding copepods, the world is 2-dimensional; points, lines and solids are little appreciated.

4) Finally, there are those copepods that eat only from

particles perceived to be solids. Of these there are three kinds. (a) prey crushers, like Tisbe furcata, are large, have A_1's lacking barbed setae, have prehensile Mx_2 and Mxp and proximal sensory setae on the arthrite of the Mx_1, Md cutting edge and Mx_2 basis. (b) Sphere cleaners for example, Amphiascus minutus, Amphiascoides debilis, again, T. furcata, Mesochra spp. and Leima vaga, twirl spheres, organic floccules of various sizes in their mouths cleaning food from the surface. These organisms can either have barbed setae on their A_1 (L. vaga) or lack them. The A_2 is well developed. The setae of the Md palps often cross the anterior surface of the labrum, probably serving to locate and guide the particle entering the oral region from the A_1 and A_2. The Md cutting edge usually has a well developed lacina mobilis, especially in specimens that encounter diatoms (see also S. divergens below). (c) Rubble sorters, like Microarthridion littorale and Enhydrosoma longifurcatum sort food from rubble, which is smoothly moved over their mouths through the action of the oral appendages. They are characterized by barbed setae on their A_1 and a vaulted space running down between their legs. Diatom feeders like Stenhelia divergens must be considered a kind of rubble sorter but specially adapted to feeding on free-living diatoms. The description of this species, above, will designate this feeding type.

This classification scheme can be judged on four criteria:

parsimony, homogeneity, specificity and continuity. (These criteria are similar but not identical to ones advocated by Kant in his *Critique of Pure Reason* and *Critique of Judgement*.) (a) Parsimony requires that the fewest possible classes be used. Class distinctions should have few theoretical assumptions while being as theoretically heuristic as possible. The above taxonomic system fulfills this demand *in extremum.* It defines both the habitat and trophic relations of harpacticoids in one simple, four part scheme. (b) homogeneity demands that members of a class have morphological, behavioural or other characters in common thus allowing generic designation. This requirement has been satisfied only for the fauna of West Lawrencetown. Since the behaviour of organisms can change without morphological manifestation (see competition in *Tisbe* below), the homogeneity of each of the above classes *must* be checked each time a new community is surveyed. For this reason, no key to the feeding groups of harpacticoids is proposed. (c) Specificity demands that each class be capable of natural division into subspecific categories. This serves as a check on over generalization. This has been done for three of the four groups (it is difficult to imagine how the point feeders could be subdivided). (d) Continuity demands that a gradual transition from class to class be possible. This last aspect is the forte of the taxonomic system proposed above. It must first be recognized that continuity does not demand a hierachical ordering of classes. In the present case, for example, point feeders probably did not arise from line feeders but rather arose from plane sweepers. Line feeders probably arose from solid feeders whose food particles became so large that only rectilinear edges (corners) could easily be fed upon.

In short, the taxonomic system proposed above is parsimonious, homogeneous, specific and provides a functional basis for understanding copepod evolution. In the future it can be used to propose hypotheses concerning systematic relationships among harpacticoids and between the Harpacticoida and the other copepod orders.

Harpacticoid Habitat and Temporal Distributions, II.

Returning to Fig. 17, a final point can now be made. Although discriminated by physical variables, the two assemblages appear determined by past or present *biological* interactions vidence the fact that most similar feeding types do not overlap in habitat or time. For example, the two epibenthic sphere cleaners (*Tisbe* and *Leima*) are in different assemblages. So are the rubble sorters *Microarthridion* and *Enhydrosoma*. *Ameiria longipes* and *A. parvula* appear to share the same habitat but *A. longipes* is present in spring and summer and *A. parvula* occurs in the fall. Similarly, the congeners, *A. minutus* and *A. propinquus* are separated by time. Of the three congeners of

Mesochra, most M. pygmaea occur in the fall. Of the others, M. sp. 1 is small and generally lives deeper in the sediment than does M. lilljeborgi. Of the co-occurring species of Pseudobradya, P. sp. 1 occurs abundantly during March and May, P. sp. 2. during November and January and P. sp. 3 occurs abundantly in July and September when the others reach their numerical minimum. The other, smaller, sand filer, Halectinosoma sp. 1 reaches its numerical maximum in winter when the largest species of Pseudobradya (sp. 2) is most abundant.

These data imply that biological interaction is important in understanding patterns of harpacticoid habitat and temporal distribution. The large number of adaptations related to habitat isolation and trophic specialization, described above, imply that there were strong competitive pressures in the past. The present segregation of feeding types into two habitat and temporal ensembles manifest this history. The influence of physical variables on harpacticoids seems reduced to the secondary role of providing sand for sand filers, etc.

There is one contemporary example of ecological overlap that will be used to substantiate the importance of biological interactions (competition) on meiobenthic community structure: Amphiascus minutus and its systematic relative, Amphiascoides debilis.

Competition

Competition is a process occasioned by ecological overlap. It can involve exploitation of a limiting resource or interference with access to a limiting resource (Park, 1962; Miller, 1967). Its end result is a change in the probability of the competing species' persistence (fitness). It is this change in fitness which mediates habitat selection and resource allocation.

The result of competition is not unique to its process (Lane, 1971). Changes in physical variables, and biological interactions such as predation, mutualism, symbiosis and parasitism can also affect fitness. Indeed, it is this whole set of interactions that condition patterns of ecological distribution and occasion changes in morphology, physiology, behaviour, demographics, etc. However for any particular species ensemble, competition (pairwise or diffuse) may be a primary influence on their ecology.

The process of competition can be defined with regard to 1) the subjects of the interaction (intra- and interspecific) 2) the kind of interaction (direct interference or indirect exploitation) and 3) with regard to the object of the interaction (e.g. Andrewatha and Browning, 1961; MacArthur, 1972b) Wiegert, in press). In so far as objects seem to empirically determine the kinds of interactions appropriate to them, a reduction of class 2 terms above to kinds in class 3 is possible

(Bohrer, personal communication). This notion has been only marginally discussed by others (Nicholson, 1957; Andrewatha and Browning, 1961; Case and Gilpin, 1974; Gill, 1974; Wiegert, in press).

Resources have two properties; they can be renewable/non-renewable and consumable/non-consumable. Thus there can be four kinds of resources (Table 4).

Type I. Food is a renewable and consumable resource. When it limits the growth of populations, exploitative competition can occur. Exploitation has been described as regulating such diverse populations as blowflies (Nicholson, 1957) and protozoa in laboratory cultures (Gause, 1934). This mechanism was described by Nicholson (1957) as a "scramble" in which factors other than the activity of the competitors determine the rate of resource supply.

Type IV. Space is a non-renewable, non-consumable resource. Direct, interference competition can occur when space limits populations' growth. This limiting resource can be, for example, the surface of intertidal rocks (Connell, 1961), predator-free space (Huffaker and Laing, 1972) or space free of chemical (allelopathic) agents (Gill, 1972).

Type II. Some habitats grow but are not consumed by organisms living on them. For example, cryptic communities and decapod crustaceans living on corals (Jackson and Buss, 1975, Abele, 1976; Abele and Patton, 1976) appear to compete within

Table 4. The four types of ecological resources.

Table 4

	consumable	non-consumable
renewable	I	II
non-renewable	III	IV

habitat through interference mechanisms. Exploitation may occur with competition for new habitats. This aspect has not been studied.

Type III. The rock and wood habitats occupied and eaten by boring bivalves (pholads and teredinids) can be, with respect to the animals life time, a non-renewable but consumable resource. Competition within and between habitats has not been extensively studied in this important group of animals (Turner and Johnson, 1971; Turner, 1973). It appears to involve exploitation within and interference between habitats. Brooding of larvae may have evolved as a mechanism of exploitation. Planktonic larvae and rapid occupation of new wood surfaces may enhance interference ability. Another example, cited by Andrewatha and Browning (1961), is the natural history of blowflies inhabiting animal carcases in Australia (Waterhouse, 1947).

In this report two cases of competition (Type I and IV above) are documented. The cognitive status of the data adduced should be understood.

Field observation of direct interactions are necessary and often sufficient substantiation of Type IV competition. However, Type I competition, by its very nature (indirect interaction), requires experimental verification -- which is beyond the scope of this study. Nevertheless, voluminous evidence will be advanced from field data to defend the Type I hypothesis. Such circumstantial evidence, though, _per se_, unconvincing, satisfies the purpose of the present study.

Type I Competition

Hypothesis: Amphiascus minutus and Amphiascoides debilis can live in the same place at the same time and eat food attached to detrital particles in the same way. When their body size (and thus oral size and food size) distributions overlap, they compete. This hypothesis assumes 1) the body size of the copepods is related to the size of food particle eaten as is true of raptorial cyclopoids (Fryer 1957a, 1957b) and 2) food limits the growth of the two populations.

If this hypothesis is correct, then the species' numerical and habitat distributions may be negatively correlated during periods of body size overlap.

Evidence: Fig. 63 indicates the body size distribution of the two species as a function of seasonal temperatures. (Note: nauplii are not included in any of these analyses). Fig. 64 gives the relationship between body size and the area of the base of the oral frustum for both species.

During March, 1975 the body size distributions of the two species overlapped. The abundances of the two species were negatively correlated (Pearson coefficient = -.2034). The habitat of A. minutus was reduced to three mud stations at one end of the estuary (Fig. 65).

During the summer months of July and September 1975, the

Figure 63. Mean body sizes (with 95% confidence intervals) of Amphiascus minutus and Amphiascoides debilis as a function of seasonal temperatures.

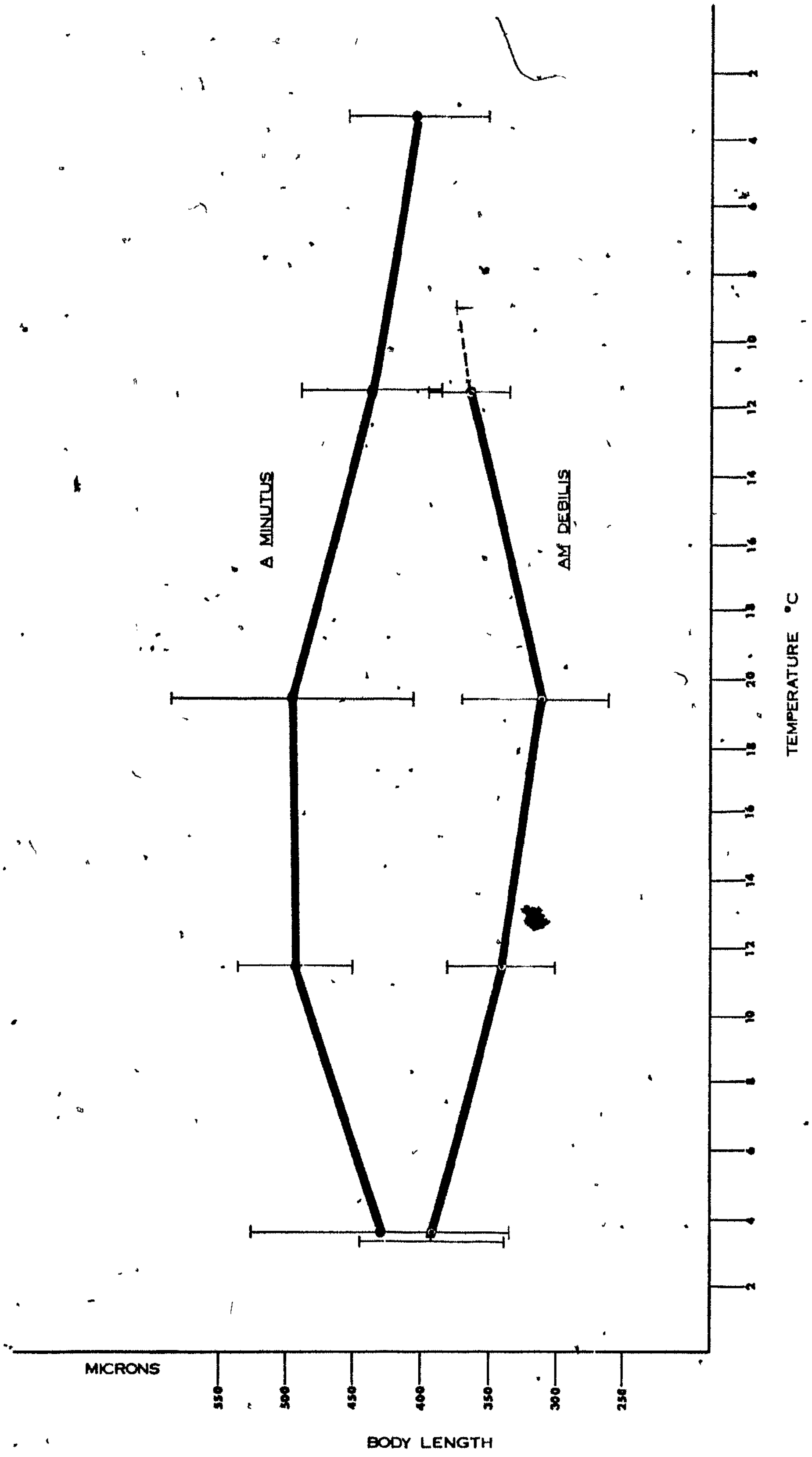

A MINUTUS
AM DEBILIS
TEMPERATURE °C
2
4
6
8
10
12
14
16
18
20
18
16
14
12
10
8
6
4
2
MICRONS
550
500
450
400
350
300
250
BODY LENGTH

Figure 64. Morphometric development of the basal area of the oral frustum of <u>Amphiascus minutus</u> and <u>Amphiascoides debilis</u> as a function of body size. Nauplii and first and second copepodites are omitted.

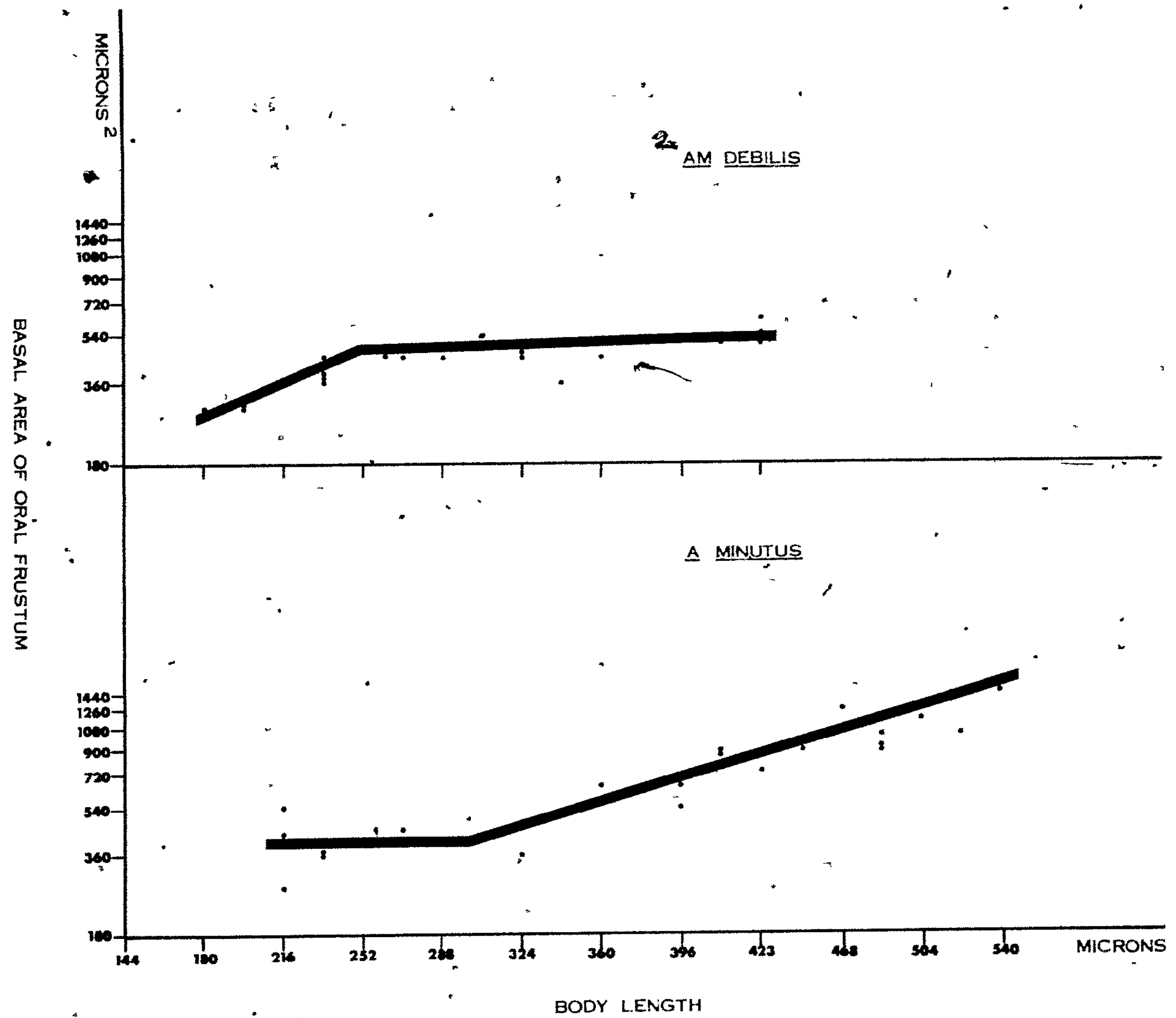

MICRONS ^{2}
AM DEBILIS
1440
1260
1080
900
720
540
360
180
A MINUTUS
1440
1260
1080
900
720
540
360
180
144
180
216
252
288
324
360
396
423
468
504
540
MICRONS
BASAL AREA OF ORAL FRUSTUM
BODY LENGTH

Figure 65. Estuarine habitats of <u>Amphiascus</u> <u>minutus</u> and <u>Amphiascoides</u> <u>debilis</u> in March 1975.

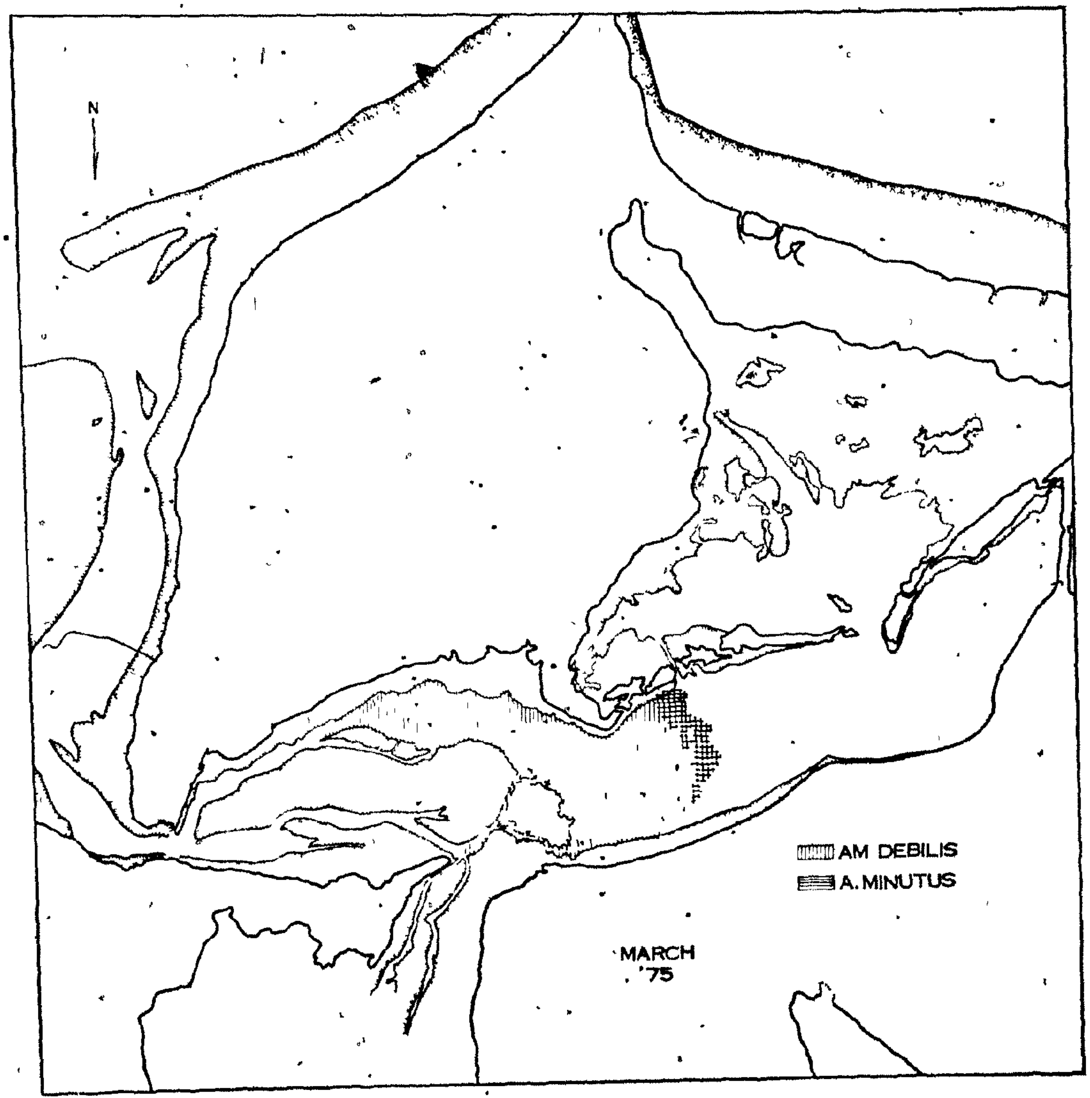

N
AM DEBILIS
A. MINUTUS
MARCH
'75

Figure 66. Estuarine habitats of *Amphiascus minutus* and *Amphiascoides debilis* in July 1975.

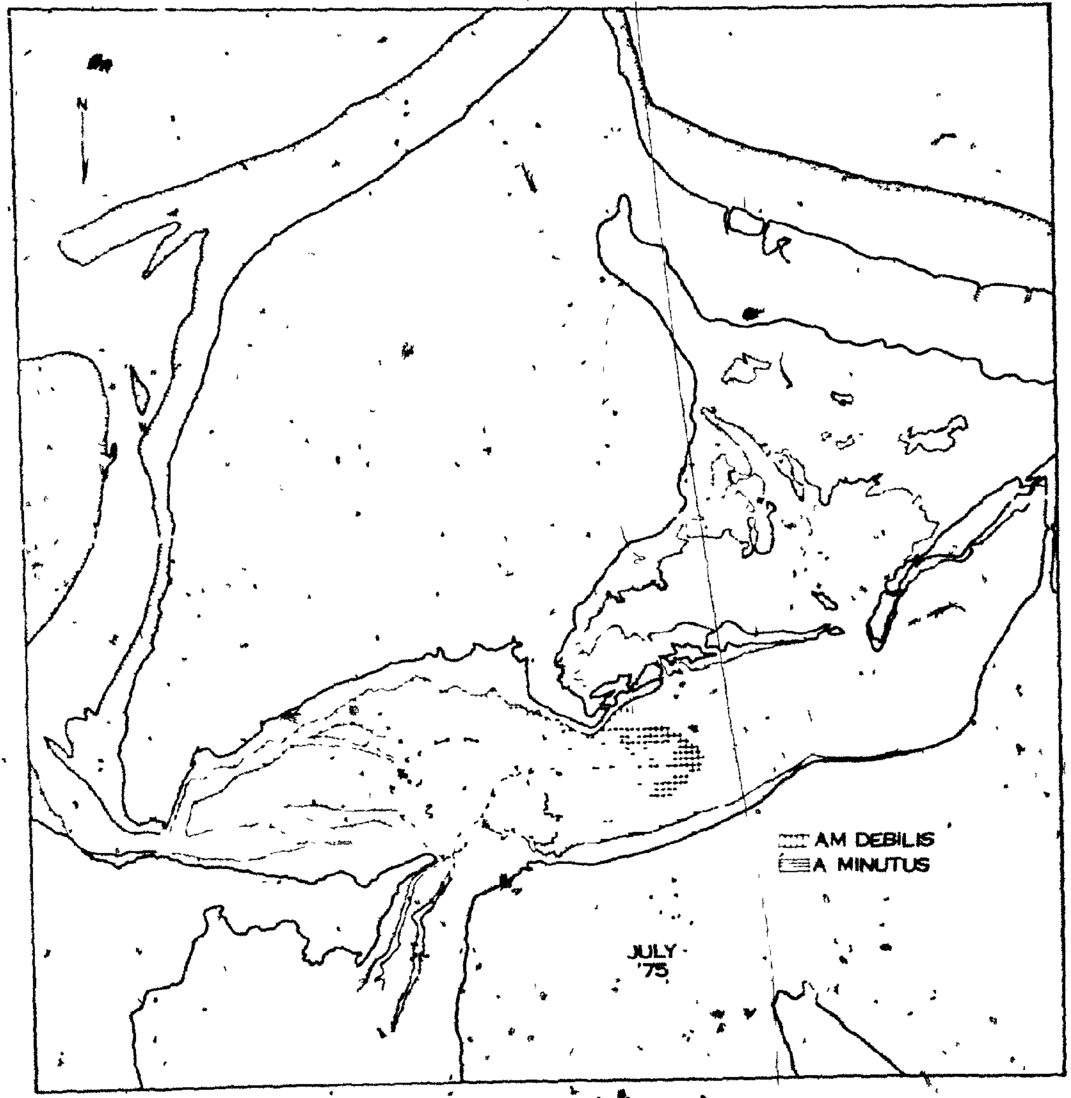

N
▤ AM DEBILIS
▤ A MINUTUS
JULY
'75

Figure 67. Estuarine habitats of <u>Amphiascus</u> <u>minutus</u> and <u>Amphiascoides</u> <u>debilis</u> in January 1976.

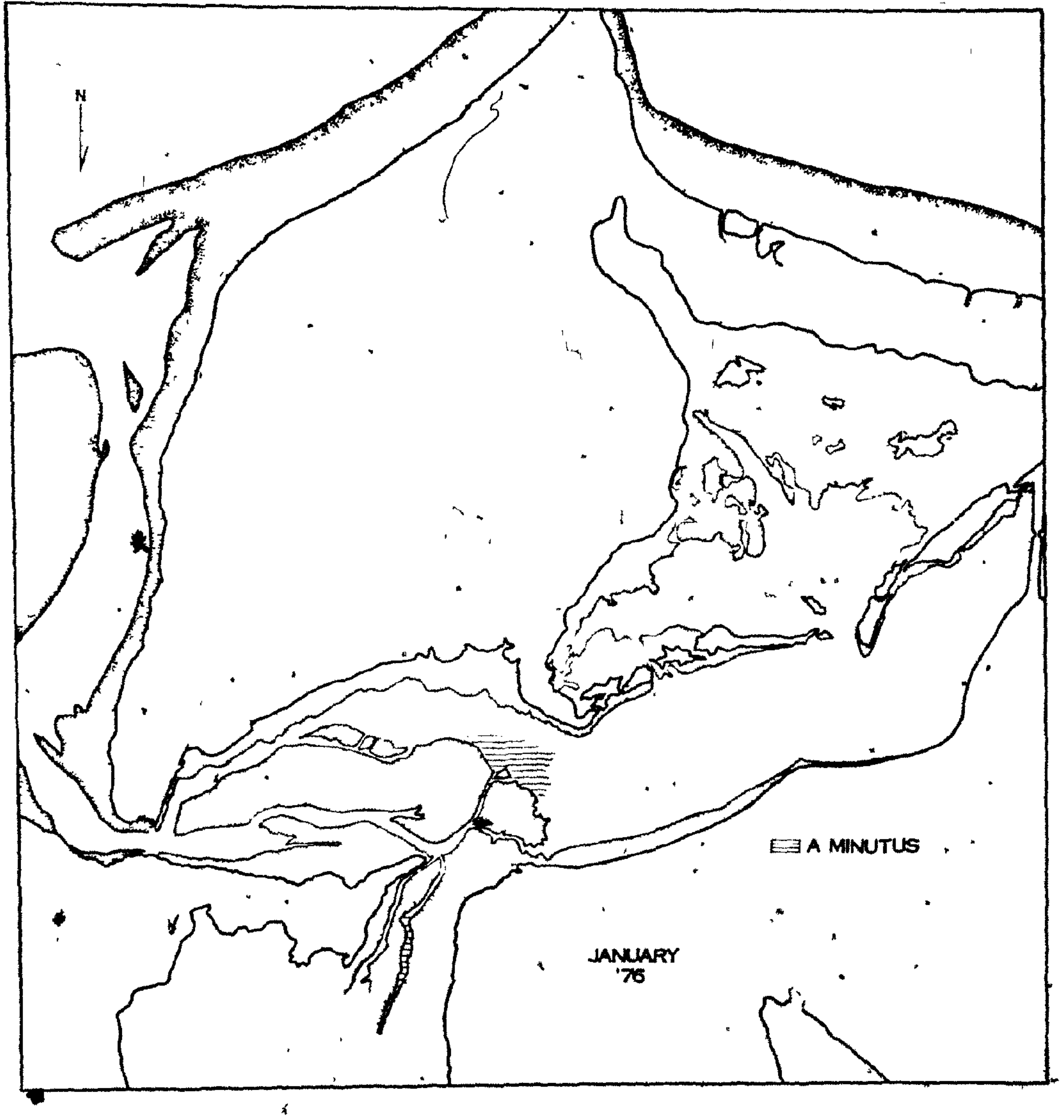

N
▤ A MINUTUS
JANUARY
'76

Figure 68. Seasonal abundances of juveniles, males, females and gravid females of 11 harpacticoid species expressed as a cumulative percent in each month of the yearly total.

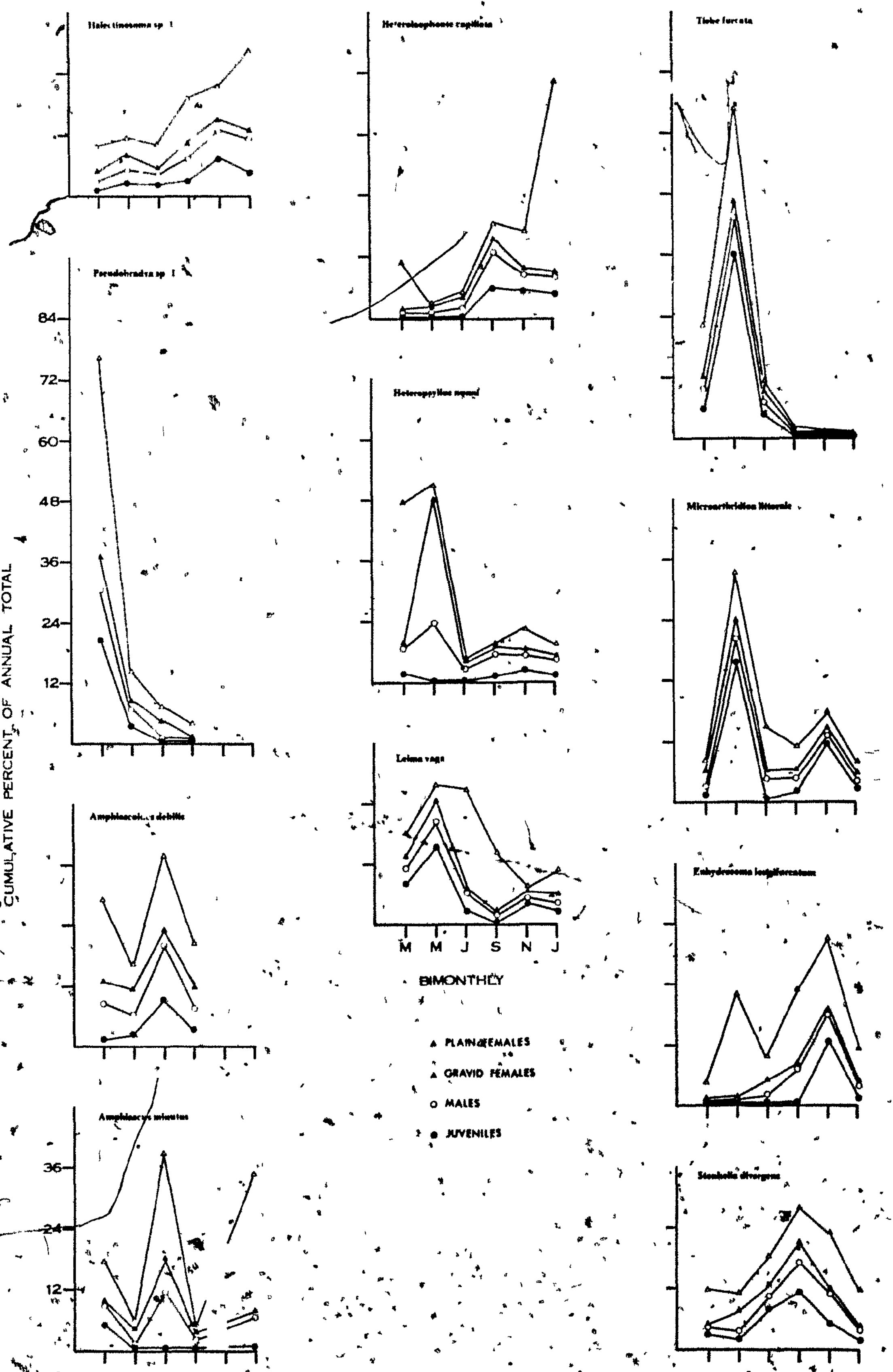
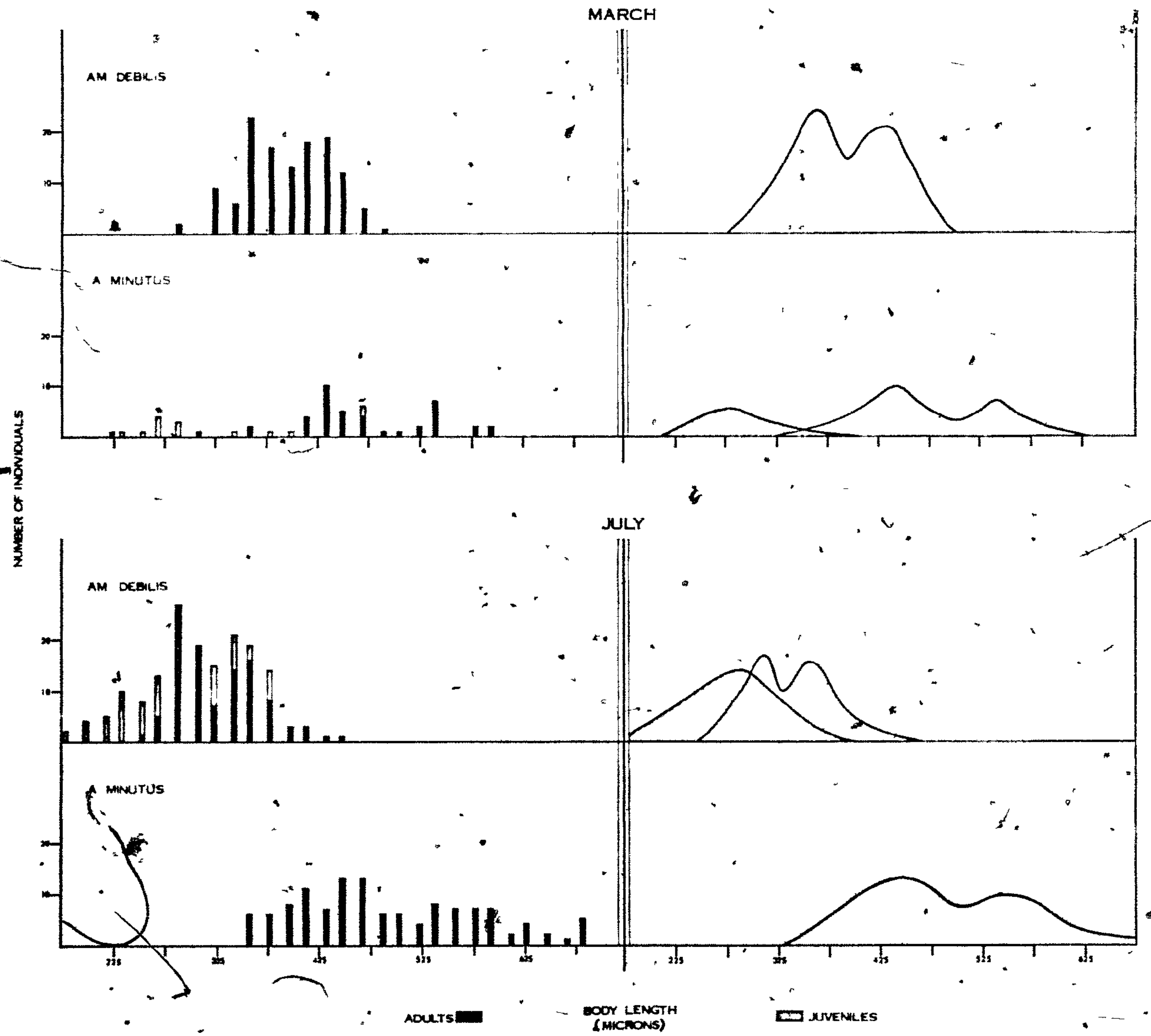

Halectinosoma sp. 1
Heterolaophonte rapillosa
Tisbe furcata
Pseudobradya sp. 1
84
72
60
48
36
24
12
CUMULATIVE PERCENT OF ANNUAL TOTAL
Heteropsyllus nunni
Microarthridion littorale
Leimia vaga
M
M
J
S
N
J
BIMONTHLY
Amphiascoides debilis
Enhydrosoma longifurcatum
PLAIN FEMALES
GRAVID FEMALES
MALES
JUVENILES
Amphiascus minutus
36
24
12
Stenhelia divergens

Figure 69. Frequency distribution of adult and juvenile (excluding nauplii) body sizes of *Amphiascus minutus* and *Amphiascoides debilis* during March and July 1975.


MARCH
AM DEBILIS
A MINUTUS
JULY
AM DEBILIS
A MINUTUS
NUMBER OF INDIVIDUALS
20
10
225
325
425
525
625
ADULTS ■
BODY LENGTH (MICRONS)
▭ JUVENILES

mean body size of *A. minutus* increased and that of *Am. debilis* decreased (Fig. 63) The 95% confidence intervals of their body size distributions did not overlap. Their numbers became positively correlated (+.4085) and their habitats almost completely covaried (Fig. 66). At this time both species reached their yearly density maximum (Fig. 68).

As temperature declined in the fall an[illegible]inter, the body size distribution of the two species reconverged and *Am. debilis* was lost from the estuary. *A. minutus* inhabited all sediment types sampled (the total area sampled however was reduced by ice cover). This interaction seems to have affected the reproductive pattern and allometric development of both species.

In March 1975 the body size distribution of *A. minutus* was bimodal due to the presence of a relatively large number of small copepodites (Fig. 69) (secondary bimodality of adult distribution is due to differences in the sizes of males and females). Thus the body size distribution of *A. minutus* circumscribed that of *Am. debilis.* *A. minutus* may have been able to exploit both larger and smaller food sources than could *Am. debilis*.

In the summer of 1975 (Fig. 69) the body size distribution of the two species no longer overlapped very much. *Am. debilis* adults were smaller than during the previous winter and copepodites were abundant, thus shifting the size distribution downward even farther. The body size of adult A. minutus were unchanged, but no copepodites were observed.

The allometric development of the oral frustum (Fig. 64) deserves further comment. The size of the oral frustum of A. minutus remained nearly constant during copepodite stages and rose rapidly with adult growth. Am. debilis did just the opposite, growing most rapidly as a juvenile and remaining almost constant in its adult life. The asymptote of Am. debilis' oral growth corresponded almost exactly to the inflexion region on the growth curve of A. minutus. Thus the allometry of oral growth in A. minutus circumscribed the region of greatest exposure to competition by adult Am. debilis. This may be either a result of present competition or a developmental adaptation to avoid it.

Consequences:

1) In the summer of 1975 when the two populations appeared not to compete, the oral size ratio (larger to smaller) separating the species was 2.5. In the previous March when their numerical distributions were very negatively correlated this ratio was 1.6.

In the following winter, as the species' oral size ratios again passed through the 1.6-1.4 competitive threshold, Am. debilis was lost.

In the study of species interaction many authors have shown that congeneric species are more similar when allopatric than when sympatric. Thus these morphometric changes with sympatry are called character displacement and are taken as evidence of present or historical competition. (e.g. Brown & Wilson, 1956). The ratio of size displacement usually found is 1.6-1.4 (Hutchinson, 1959).

Grant (1972) critized the inference of competition showing that latitudinal changes in morphometric characters can not substantiate a hypothesis of contemporary competition unless anomalies in the size gradient occur in the regions of geographic overlap. In the present study, the morphometric threshold of competition was observed to be a ratio of 1.6-1.4. In the present study, the gradient of morphometric change was not latitudinal but temporal. It can not be claimed that the morphometric changes observed were caused by competition. Rather, it is claimed that the winter body size convergence occasioned competition. Grant's critique of latitudinal gradients notwithstanding, the morphometric threshold of 1.6-14. seems to be a real empirical touchstone for competition theory.

2) In the winter of 1975 when the abundance <u>A. minutus</u> fell precipitously, its body size distribution became strongly bimodal. There were many copepodites occupying oral and body size ranges below that of <u>Am. debilis</u> and adults of <u>A. minutus</u> with bodies and mouths much larger than those of <u>Am. debilis</u>.

In the region of body sizes between juvenile and adult A. minutus there were few representatives. It seems reasonable to conclude that for A. minutus in the winter of 1975, there was a selective advantage to staying young, i.e. morphometric growth would mean passing through a body size range leading inevitably to competition. Although there were many gravid A. minutus females present all year round, the retention of large numbers of juveniles in the population only occurred when the two species were present and competing, i.e. the winter of 1975 (Fig.68).

If this tendency toward bimodality, due to the selective advantage of staying young, persisted, neotenous events might be favourably selected. The Family Diosaccidae, of which these species are part, exhibits many instances of assumed neoteny (e.g. Marcotte 1974). Competitive interaction of the type outlined here may be one mechanism leading to selection of such events.

Type IV Competition

During April, 1976 the number of _Tisbe_ sp. in a small marsh at Cranberry Cove, N. S. rose above 1,500 individuals - 10 cm $^{-2}$. Upon observation, two behavioural morphs in the population became evident. Since the reproductive status of these morphs is unknown, they are designated by colours (Green and White), not species names. _Tisbe_ Green (Table 5) spent 94% ± 3% of its time gently walking on the surface of the detrital sediments. _Tisbe_ White spent fully 1/3 of its time swimming in the water column. It alighted on the bottom only long enough to feed. Both "colours" fed on organic spheres, approximately 125 μm in diameter. Their oral morphologies were identical except for a 1.25 difference in the length of their respective Mxp claws (Fig. 70). However, their feeding behaviour did differ. _Tisbe_ Green, the ground-dweller, carfully located food items on the bottom and then twirled its food slowly in its mouth often stopping to chew at one spot on the surface for up to 3 minutes at a time. _Tisbe_ White, the swimmer, dashed onto the bottom, rapidly chose a food item, spun it about in its mouth and quickly flitted back into the water. It never stayed on the bottom long enough to feed on more than 3 items without swimming away.

These differences in feeding and locomotor behaviour may have been a result of competition for space. _Tisbe_ White is

Table 5. <u>Tisbe</u> White and <u>Tisbe</u> Green. Comparison of their behavioural morphologies.

Table 5

	Tisbe White	*Tisbe* Green
% of time on sediment	66%	94%
Sediment relations	Dives and burrows into first mm of sediment; disrupts sediment texture.	Moves gently though swiftly on sediment surface; seldom disrupts sediment texture.
Tactile response	Immediate response to touch or approach of other copepods especially *T.* green.	Immediate response to touch by some other copepods and large nematodes; usually unaffected by *T.* white.
Feeding behaviour	Grabs detrital balls in rapid succession and spins them in mouth gleaning particles from surface indiscriminately.	Grabs detrital balls at leisurely pace and feeds only at selected sites on the particle.

Figure 70. *Tisbe* Green and *Tisbe* White. Detail of Maxilliped.

Scale: 24 µm.

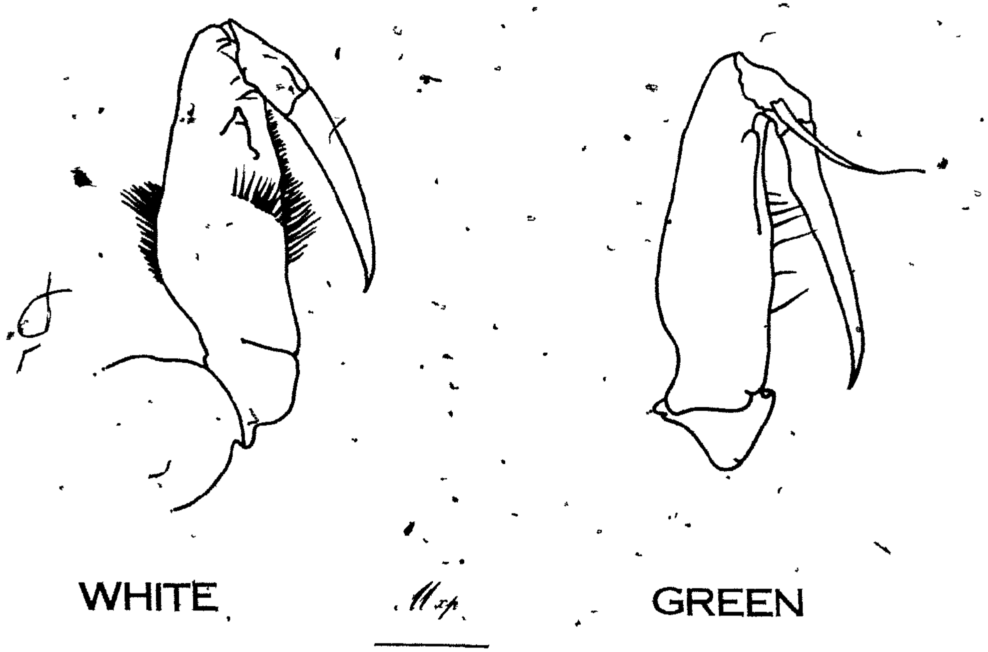
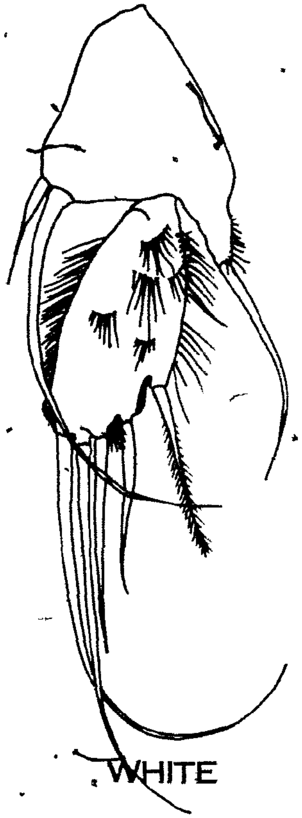

WHITE
11μ
GREEN

Figure 71. *Tisbe* Green and *Tisbe* White. Detail of P_5. Scale: 24 µm.



P_5

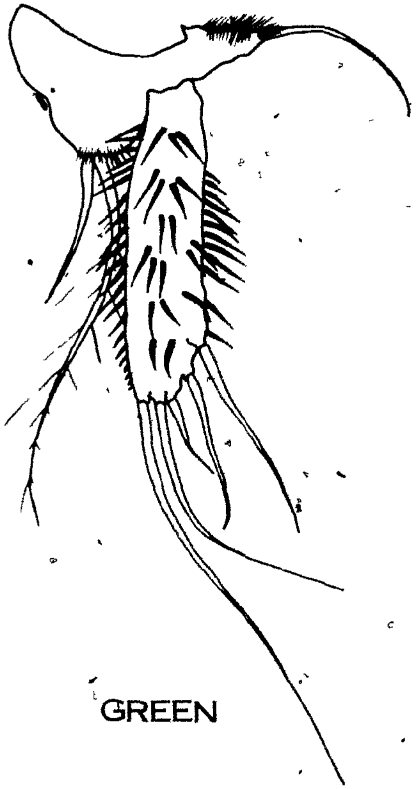


Figure 72. Tisbe Green and Tisbe White. Detail of Genital Field. Scale: 24 µm.


WHITE
GREEN

very sensitive to the approach or touch of other copepods especially Tisbe Green. When stimulated, it swims upward, away from the sediment. Tisbe Green, on the other hand, is relatively insensitive to tactile stimuli from other copepods. It can even be frequently walked on without a locomotor response. Thus, competition for (copepod free) space led to habitat displacement. There was no morphological evidence of trophic competition. The changes in feeding behaviour seemed commensurate with the changes in habitat.

This habitat isolation seems to be reflected in the reproductive morphologies of the two colours (Figs. 71, 72). There appears to be a coherent pattern of genital differentiation. Sexual isolation may be either incipient or complete. Thus it appears that competition for space by a direct interference mechanism (differential response to tactile stimuli) has resulted in partial habitat isolation and incipient or complete sexual isolation.

Consequences

1) If this is an intraspecific interaction, it is difficult to imagine the proximate benefit accruing Tisbe White by fleeing into the water column when approached by T. Green since by swimming it uses more energy and is more likely to be preyed upon. An ultimate advantage might be enhanced dispersion of T.

White's offspring. The social intolerance of T. White may in fact be limited to only periods of time when a female is gravid (this was not examined). Similar behavioural patterns have been reviewed by Chitty (1967) who suggested they could regulate population numbers in terrestrial mammals. The genetic mechanism by which this regulation might be achieved is unclear.

2) There have been numerous studies of the genetic make-up of species in the genus *Tisbe*. Many sibling species have been demonstrated to co-occur. The ecological consequences of this co-occurrence have not been studied. The present report provides a basis for understanding the kinds of ecological adaptations co-occurring species (colours) of this genus may exhibit.

SUMMARY

It has long been recognized that the structure of meiobenthic communities is highly correlated with variables in their physical environment. Sediment grain size, temperature, salinity and oxygen concentrations have all been shown to be important factors in discriminating faunal assemblages (Smidt, 1944, 1951; Kanwisher, 1955; Noodt, 1956; Capstick, 1959; Wieser, 1959; Delamare-Deboutville, 1960; Swedmark, 1964; Gray, 1965, 1966, 1967; Jansson, 1966, 1968; Coull, 1968). The correlation and description of meiobenthic communities according to physical variables has consumed much effort (e.g. Remane, 1933; Noodt, 1956; Ivester and Coull, 1977 and the present report). Still, little is known of the biological meaning of these correlations --- how the variables are experienced and how the organisms change in response to their perceptions. Further the biological factors affecting meiobenthic community structure have been little studied. Predation is known to occur (Smidt, 1951; Muus, 1967) but knowledge of its effect on population and community structures is limited to the work of Heip and Smol (1975) in which a single predator-prey model was evaluated. Competition has not been documented in nature, although Fava (1971), working with culture populations of Tisbe spp., has shown that local extinctions can occur in one generation.

This study has approached the meiobenthic communities of West Lawrencetown in two ways: perceptual and interactive.

1) Perception: Studies which correlate meiofauna with

physical variables assume that because a physical variable is measurable, i. e. available to human perception, it can affect meiofauna. Correlation coefficients somehow measure this effect. Lack of perfect correlation is due to (a) an unmeasured variable, (b) dependent variables (c) biological vagaries, e.g. response lags and reproductive stochasticity. The assumption is false.

Harpacticoids perceive their environment organically with their legs and body size as much as with their senses of taste and touch. Their organic and sensory perception mediates their environmental experience and determines which factors will influence their diversification. In short, copepods not only adapt to their environment, they define it. For harpacticoids, organic perception has made substrate shape an environmental imperative and chemo - and proprioreceptors have made detection of resource grain possible. These two modes of perception condition the ecological distribution of the animals. Patterns of correlation with derived and covarying physical factors may be trivial.

There are many implications of these results. For example: a) Meiofauna live at a scale entirely different from our own. Correlation of preserved faunas with variables measured at human scales with methods developed for other purposes (e.g. sieve analyses of sediment particle sizes) is insufficient for understanding meiofauna and the environmental factors which contribute to their ecological distribution and long-term persistence. b) Individual metabolism will be strongly affected by the presence of preferred substrates. Heterolaophonte capillata and Enhydrosoma longifurcatum, for example, will be energetically more active without their preferred sediment present than with it. c) Laboratory culture of harpacticoids has been successful for only a few species (Battaglia, 1970; Coull and Dudley, in press). This lack of success may be related to the absence of microhabitats, food particle shapes and food distributional patterns appropriate to the species to be cultured.

2) Interaction: Competition appears to be a primary force leading to the diversification and ecological distribution of some harpacticoids. Populations in the same feeding group did not co-occur in habitat or time without showing some demographic, behavioural or morphometric change. This understanding of the biological condition of meiobenthic community structure has been a major benefit of the present report.

Predation was not examined. However from the studies of Willey, 1923; Muus, 1967; Kazinski, Feller and Clayton, 1973; Heip and Smol, 1975; Coull and Dudley, in press, two effects of predation on the meiobenthos are clear. (a) Epibenthic species (e.g. Tisbe, Leima, Microarthridion, and perhaps some ectinosomids) are more susceptible to predation than are inbenthic species. (b) Populations respond to predation with demographic changes: endogenous - delayed naupliar development when juveniles are less susceptible to predation either because of small size or inbenthos habitat, and exogenous - differential mortality of older individuals either because of large size or epibenthic habitat. (A similar demographic result of predation has been reported for intertidal macrofauna by Paine, 1976).

This strong demographic effect of predation can substantially modify the outcome of competition between populations which rely on demographic adjustments to structure their interactions, e. g. A. minutus and Am. debilis.

Epibenthic life differs "interactively" from inbenthos life precisely insofar as the effects of competition and predation are compounded on the surface and not below. Predation can modify competition; it need not eliminate it (sensu Paine, 1969). For example, MacArthur (1972a) has mathematically demonstrated how predation can modify the outcome of competition by changing r and K thus altering the stability of the interaction and its equilibrium point. From the essay of Huffaker and Laing (1972) it is clear that if two competing species are preyed upon, they can even come to compete for predator-free space. The compound effects of competition and predation have not been studied for either macrofauna or meiofauna. Harpacticoids seem well suited for this purpose.

With this understanding of the perceptual and interactive foundation of harpacticoid life in the meiobenthos, a new examination of copepod systematics can begin. Hypotheses concerning the mechanisms leading to the origin and maintenance of harpacticoid species diversity can be framed. For example, the genus Tisbe is morphologically conservative. There are many sets of sibling species (Volkmann,1972a, 1972b, 1973). Bilateral symmetry is the rule, assymmetries are exceptional. Adult population structures are relatively invariant. However, behaviour is plastic. In the case history described above, differences in behaviour resulted in partial habitat isolation and divergence in genital morphology was apparent. In the diosaccid genera, Amphiascus and Amphiascoides, behaviour seemed stereo-typed and invariant. Here morphology was plastic. Morphometric variation was the rule and bilateral assymmetries were common especially in the walking legs of Amphiascoides debilis. At the population level substantial changes occurred in the sex ratios and age class composition of the population during the study period.

In the family Tisbidae, morphological conservatism is reflected in the low number of morphologically defined genera. Behavioural plasticity is reflected in the large number of co-occurring congeners, many of them sibling ensembles. In the Diosaccidae, morphological liberality has led to many morphologically defined genera some of which are related through neoteny. Behavioural conservatism has, in general limited speciation to morphometric mechanisms promoting neoteny.

It seems clear from this that behaviour and morphology are not part of a hierarchical response system available to all copepods alike. Rather, history (probably the selection of an epibenthic existence by Tisbidae and an inbenthos life for most diosaccids) acts to direct speciation mechanisms by limiting the response potential of some whole lines of copepod diversification. Familial patterns are the product of this history and its limitations.

EPILOGUE

There is a Grain of Sand in Lambeth that
Satan cannot find
Nor can his Watch Fiends find it: tis translucent
and has many Angles
But he who finds it will find Oothoon's
palace, for within
Opening into Beulah every angle is a
lovely heaven.

Wm. Blake (Jerusalem)

Spatial metaphors such as "station", "place" and "niche" are usually the corner stone for ecological studies which describe animal or plant distributions. These spatial concepts were used by naturalists in the 18th Century to describe causes of plant occurrences and extinctions (see Lyell, 1832). With evolutionary theory, ecological "place" became the basis for a model of adaption (Darwin, 1859; see also Hardin, 1961). Thus interest was shifted from extinction to origin (speciation). With Grinnell (1917), Gause (1934) and Hutchinson (1957), "niche" became the model of competition, the kernel of Malthusian selection.

This tendency to rely on spatial metaphors as repositories of causality is not unique to biology. Indeed, it has been a hallmark of science after Kant (e.g. Williams, 1965). The present report has tried to minimize reliance on the metaphors of niche for four reasons.

1) The reduction of animal-environment and animal-animal interactions to an axial (causal) representation violates *lex parsimoniae* when, on an evolutionary time scale, random mutations endlessly expand the number and kind of spatial dimensions required to "explain" an interaction.

2) Following from (1), it seems impossible to use spatial representations to predict the trajectory of an evolving system through "environment space" when even the number, leave alone the kinds, of dimensions are *a priori* unknowable. With this model one at best can know only the rules according to which one organic state follows from some previous state(s). One cannot predict either the direction or the intensity of the transition. There are no laws stating the patterns according to which these events can occur (but see below).

3) More fundamentally, niche theory invites the fallacy misplaced concreteness when it encourages a notion of "place" as subject and organism (population) as adjective. This can lead to two mistakes. (a) The "environment" (usually defined by the conscious observer) takes on object status. Empty niches can exist and organisms adapt to fit niches, like round pegs to square

holes. Thus the meaning of niche escapes definition by the phenotype and takes on an empirical reality of its own.
(b) The organism is reduced to modifying the shape of niches by interactions along environmental dimensions. Its role in defining the kinds and numbers of these dimensions can be lost. Indeed, it is precisely insofar as organisms create meaning from environmental perceptions that environment is intelligible at all (Patten, in press).

4) Niche, naively defined by habitat, time and food, as outlined in the introduction, can be an impediment to understanding the marine meiobenthos. As described above (results), the habitat and food source of meiobenthic niches for harpacticoids are the elusive "sides" of an ecological Möbius strip, a cycle on which behaviour, physiology, anatomy and developmental patterns intermingle in a non-hierarchical manner. The time niche of the meiobenthos is the order of changes in community structure, e.g. adjustments to competition and predation.

Instead of space metaphors and operational reductions, the origin and maintenance of diversity in the meiobenthos may be best understood by seeking the patterns by which these interacting systems change. One touchstone must be the empirical reality of competitive (morphometric) thresholds and character displacement. Does the recurring ratio of 1.4 -1.6

(Hutchinson, 1959; MacArthur, 1972a) manifest the pattern by which selection pressures are propagated through a community? Are rates of evolution influenced not only by the force of natural selection (Fisher's theorem) but also by its pattern of propagation?

A second starting point might be to ask not why there are so many kinds of animals but why there are so few. At stake is the relationship between the shape (patterns of functional relationships) and the size (number of functional terms) of communities. Do communities, like the horse skulls studied by D'Arcy Thompson (1971), undergo qualitative transformation in their relational network when quantitatively expanding or contracting (i.e. when the fitness of a functional group changes or when new functional groups are added): Are there discontinuities in these transformations (i.e. are there real, discrete communities)? Do demands set by the qualitative structure of communities limit their quantitative expansion? Finally, is there any real, meaningful distinction to be made between the qualitative and quantitative structure of communities, i.e. is the second derivative on environment space isomorphic with the network shape of the communities? This is similar to asking whether terms can be reduced to logical relations in an abstract formulation of ecological theory. In short are the dance and the dancer one?

This present thesis grew out of normal, paradigmatic questions about meiofauna, their environment and their relationships. It ends asking whether or not we even have a language in which to frame them. It seems clear to this author that we may not. A new understanding of the terms and logical relations appropriate to theories explaining the origin and maintenance of organic diversity is necessary. Perhaps this language, like the one Galileo sought in the "Book of Nature" is written in geometric symbols. Perhaps this language, like the heaven Blake sought, lies in grains of sand ---- at the bottom of the sea.

References

Abele, L. G. (1976). Comparative species richness in fluctuating and constant environments: coral-associated decapod crustaceans. Science 192: 461-463.

Abele, L. G. & W. K. Patton (1976). The size of coral heads and the community biology of associated decapod crustaceans. J. Biogeogr. 3: 35-47.

Andrewartha, H. G. & T. O. Browning (1961). An analysis of the idea of "resources" in animal ecology. J. Theoret. Biol. 1: 83-97.

Battaglia, B. (1970). Cultivation of marine copepods for genetic and evolutionary research. Helgolander wiss. Meeresunters 20: 385-392.

Brown, R. (1814). General remarks, geographical and systematical on the Botany of Terra Australis. In M. Flinders, Voyage to Terra Australis. London.

Brown, W. L., Jr. & E. O. Wilson (1956). Character displacement. Syst. Zool. 5: 49-64.

Candolle, A. L. P. P. de (1855). Geographie botanique raisonnée. Masson, Paris.

Capstick, C. K. (1959). The distribution of free-living nematodes in relation to salinity in the middle and upper reaches of the river Blyth estuary. J. Anim. Ecol. 28: 189-210.

Case, T. J. and M. E. Gilpin (1974). Interference competition and niche theory. Proc. Nat. Acad. Sci. U.S.A. 71(8): 3073-3077.

Chitty, D. (1967). The natural selection of self-regulatory behaviour in animal populations. Proc. Ecol. Soc. Australia 2: 51-78.

Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacles Chthamalus stellatus Ecol. 42: 710-723.

Coull, B. C. (1968). Shallow water meiobenthos of the Bermuda Platform. Ph. D. Thesis, Lehigh Univ., Bethlehem, Pa. 189 pp.

Coull, B. C. (1973). Estuarine meiofauna: a review: trophic relationships and microbial interactions. In, Estuarine Microbial Ecology, L. H. Stevenson & R. R. Colwell, Eds. Univ. S. Carolina Press, Columbia, 499-512.

Coull, B. C. & B. W. Dudley (1976). Delayed naupliar development of meiobenthic copepods. Biol. Bull. 150: 38-46.

Dale, N. G. (1974). Bacteria in intertidal sediments: factors related to their distribution. Limnol. Oceanogr. 19(3): 509-518.

Darwin, C. (1859). On the Origin of Species.... J. Murray, London. 490p.

Delamare-Deboutteville, C. (1960). Biologie des eaux souterraines littorales et continentales. P. Hermann, Paris. 740 pp.

Elmgren, R. (1976). Baltic benthos communities and the role of the meiofauna. Contrib. Askö Labor. Univ. Stockholm. 31pp.

Fava, G. (1972). Études sur la compétition interspécifique dans le genre Tisbe (Copepoda, Harpacticoida). In, Fifth European Marine Biology Symposium. Piccin Editore, Padova: 139-152.

Fenchel, T. (1969). The ecology of marine microbenthos IV. Structure and function of the benthic ecosystem.... Ophelia 6: 1-182

Fraser, J. H. (1936). The occurrence, ecology and life history of Tigriopus fulvus (Fischer). J. mar. biol. Assoc. U. K. 20: 523-536.

Fryer, G. (1957a). The feeding mechanism of some freshwater cyclopoid copepods. Proc. Zool. Soc. London 129:1-27.

Fryer, G. (1957b). The food of some freshwater cyclopoid copepods and its ecological significance. J. animal Ecol. 26: 261-286.

Gause, G. F. (1934). The Struggle for Existence. Williams & Wilkins, Baltimore.

Gerlach, S. A. (1971). On the importance of marine meiofauna for benthos communities. Oecologia (Berl.) 6: 176-190.

Gilat, E. (1967). On the feeding of a benthonic copepod, Tigriopus brevicornis. O. F. Müller. Bull. Sea. Fish. Res. Stn. Isreal 45: 79-95.

Gill, D. E. (1974). Intrinsic rate of increase, saturation density and competitive ability II. The evolution of competitive ability. Am. Nat. 108 (959): 103-116.

Grant, P. R. (1972). Convergent and divergent character displacement. Biol. J. Linn. Soc. 4: 39-68.

Gray, J. S. (1965). The behaviour of Protodrilus symbioticus Giard in temperature gradients. J. Anim. Ecol. 34: 455-461.

Gray, J. S. (1966). Factors controlling the localization of populations of Protodrilus symbioticus Giard. J. Anim. Ecol. 35: 435-442.

Gray, J. S. (1967). Substrate selection by the archiannelid Protodrilus rubropharyngeus. Helogländer wiss. Meeresunters. 15: 253-269.

Gray, J. S. (1974). Animal-sediment relations. Oceanogr. Mar. Biol. Ann. Rev. 12: 223-261.

Grinnell, J. (1917). The niche-relationships of the California thrasher. Auk 34: 427-433.

Guille, A. & J. Soyer (1969). Contribution à l'étude comparee des biomasses du macrobenthos et du meiobenthos de substrat meuble au large de Banyuls-sur-Mer II. In, Third European Symp. Mar. Biol.

Hardin, G. (1960). The competitive exclusion principle. Science, N. Y. 131: 1292-1297

Hauspie, R. & Ph. Polk (1973). Swimming behaviour patterns in certain benthic harpacticoids (Copepoda). Crustaceana 25 (1): 95-103.

Heip, C. & N. Smol (1975). On the importance of Protohydra leukarti as a predator of meiobenthic populations. In, 10th European Symposium on Marine Biology. Ostend, Belgium, 2: 285-296.

Hjulström, F. (1939). Transportation of detritus by moving water. *In*, *Recent Marine Sediments,* P. D. Trask, Ed. *Am. Assoc. Petrol. Geol.*, *Tulsa*: 5-31.

Huffaker, C. J. & J. E. Laing (1972). "Competitive displacement" without a shortage of resources? *Res. Popul. Ecol.* *14*: 1-17.

Hulings, N. C. & J. S. Gray (1971). A manual for the study of meiofauna, *Smith. Contr. Zool.* *78*. 87pp.

Humboldt, A. von (1807). Essai sur la geographie des plantes *In*, Humbolt, A. von and Bonpland, A., *Voyage, part 5: Physique generale et geologie*. F. Shoell, Paris.

Humboldt, A. von (1847). *Cosmos*. 3rd Ed. Longman, Brown, Green & Longman, London.

Humboldt, A. von (1850). *Views of Nature*... Transl. E. C. Otte & H. G. Bohn. Bohn, London.

Hutchinson, G. E. (1957). Concluding remarks. *In*, *Cold Spring Harbour Sym. Quant. Biol.* *22*: 415-427.

Hutchinson, G. E. (1959). Homage to Santa Rosalia or Why are there so many kinds of animals? *Am. Nat.* *93*: 145-159.

Ivesler, M. S. and B. C. Coull (In Press). Niche fractionation studies of two sympatric species of Enhydrosoma (Copepoda, Harpacticoida).

Jackson, J. B. J. and L. Buss (1975). Allelopathy and spatial competition among coral reef invertebrates. *Proc. Nat. Acad. Sc. U.S.A.* *72*: 5160-5163

Jansson, B. -O. (1966). Microdistribution of factors and fauna in marine sandy beaches. *In, Veroffenllichungen Inst. Meeres. Bremerhaven II.*, S. Gerlach and Holink Eds.

Jansson, B. -O. (1968). Quantitative and experimental studies of the interstitial fauna in four Swedish sandy beaches. *Ophelia* *5*: 1-71.

Kaczynski, V. W., R. J. Feller & J. Clayton (1973). Trophic analysis of juvenile pink and chum salmon (*Oncorhynchus gorbuscha* and *O.* *keta*) in Puget Sound. *J. Fish. Res. Bd. Can.* *30*: 1003-1008

Kanwisher, J. W. (1955). Freezing in intertidal animals. *Biol. Bull. mar. biol. Lab., Woods Hole,* *109*: 56-63.

Lane, P. A. (1971). A comparative study of the structure of zooplankton communities. Ph. D. Thesis. State University of New York at Albany. 216p.

Lang, K. (1946). A contribution to the question of the mouth parts of the Copepoda. *Ark. für Zool.* *38*(5): 1-24.

Lang, K. (1948a). Copepoda Notodelphyoida from the Swedish west-coast with an outline on the systematics of the copepods. *Ark. För Zool.* *40* (14): 1-36.

Lang, K. (1948b). *Monographie der Harpacticiden.* Hakan Ohlssons Bokt., Stocklholm. 1682p.

Lang, K. (1965). Copepoda Harpacticoidea from the California Pacific Coast. Almquist & Wiksell, Stockholm. 560p.

MacArthur, R. H. (1972a). Strong or weak interactions. In, Growth by Intussusecption, E. S. Deevey, Ed. Trans. Conn. Acad. Arts Sci. 44: 177-188.

MacArthur, R. H. (1972b). Geographical Ecology. Harper & Row, New York, 269pp.

Marcotte, B. M. (1974). Two new harpacticoid copepods from the North Adriatic with a revision of the genus Paramphiascella. Zool. J. Linn. Soc. 55 (1): 65-82.

Marcotte, B. M. (1977). An introduction to the architecture and kinematics of harpacticoid (Copepoda) feeding: Tisbe furcata (Baird, 1837). Mikrofauna Meeresboden 61: 177-190

Mare, M. F. (1942). A study of a marine benthic community with special reference to the microorganisms. J. mar. biol. Assoc. U. K. 25: 517-554.

McIntyre, A. D. (1964). Meiobenthos of sublittoral muds. J. mar. biol. Assoc. U. K. 44: 665-674.

McIntyre, A. D. (1969). Ecology of marine meiobenthos. Biol. Rev. 44: 245-290.

McIntyre, A. D. (1971). Control factors on meiofauna populations. Thalassia. Jugoslavia 7 (1): 209-215.

Miller, R. S. (1967). Pattern and process in competition. In, J. B. Cragg, Ed. Advances in ecological research Vol. 4. Academic Press, New York: 1-74.

Muus, B. (1966). A quantitative three year survey on the meiofauna of known macrofauna communities in the Oresund. Verdl. des Instituts Meeresforscch. 2: 289-292.

Muus, B. J. (1967). The fauna of Danish estuaries and lagoons. *Medd. Danm. Fisk.-og Havunders, 5*: 1-316.

Nicholson, A. J. (1957). The self-adjustment of populations to change. *In, Cold Spring Harbour Symp. Quant. Biol. 22*: 153-173.

Noodt, W. (1952). Marine Harpacticiden (Cop.) aus dem eulitoralen Sandstrand der Insel Sylt. Math. -naturwiss. *Kl. Akad. Wiss. Lit., Mainz, 3*: 105-142.

Noodt, W. (1956). Verzeichnis der im Eulitoral der schleswig-holsteinischen Küsten angetroffenen Copepoda Harpacticoida. *Schr. naturwiss. Ver. Schlesw. -Holst. 28* (1): 42-64.

Noodt, W. (1957). Zur Ökologie der Harpacticoidea des Eulitorals der deutschen Meereskuste und der nagrenzenden Brackewasser. *Z. Morph. U. Ökol. Tiere. 46*: 149-242.

Paine, R. T. (1969). The *Pisaster-Tegula* interaction: Prey patches, predator food preference and intertidal community structure. *Ecology, 50*: 950-961.

Paine, R. T. (1976). Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology, 57*: 858-873.

Park, T. (1962). Beetles, competition and populations. *Science 138*: 1369-1375.

Patten, B. C. (In Press). Systems Approach to the concept of environment. *Contrib. Syst. Ecol.*, Univ. of Georgia.

Perkins, E. J. (1958). The food relationships of the microbenthos, with particular reference to that found at Whitstable. Kent. Ann. Mag. nat. Hist. 1: 64-77.

Pianka, E. R. (1974). The structure of lizard communities. Ann. Rev. Ecol. Syst. 4: 53-74.

Pielou, E. C. (1972). Niche width and niche overlap: A method for measuring them. Ecology, 53 (4): 687-692.

Remane, A. (1933). Verteilung und Organisation der benthonischen Mikrofauna der Kieler Bucht. Wiss. Meeresunters. (Abt. Kiel) 21: 161-221.

Sellner, B. (1973). The effects of diet on the metabolism, morphology and ecology of benthic estuarine harpacticoid copepods. M. S. Thesis. University of South Carolina, Columbia, 60p.

Shelford, V. E. (1911). Physiological animal geography. J. Morphology. 22: 551-618.

Smidt, E. L. B. (1944). The effects of ice winters on marine littoral fauna. Folia geogr. dan. 2:1-36.

Smidt, E. L. B. (1951). Animal production in the Danish Waddensea. Medd. Danm. Fisk.-og Haunders 11: 1-151.

Swedmark, B. (1964). The interstitial fauna of marine sand. Biol. Rev. 39: 1-42.

Thiel, H. (1972a). Die Bedeutung der Meiofauna in Küstenfernen benthischen Lebensgemeinschaften verschiedener geographischer Regionen. Verh. dt. Zool. Ges. Helgoland. 65: 37-42.

Theil, H. (1972b). Meiofauna und Struktur der benthischen Lebensgemeinschaft des Iberischen Tiefseebeckens. "Metor" forsch.-Ergebn. D. 12: 36-51.

Thompson, D. W. (1971). On Growth and Form (reprint) University Press, Cambridge. 345p.

Thorson, G. (1966). Some factors influencing the recruitment and establishment of marine benthic communities. Netherl. J. Sea Res. 3: 267-293.

Turner, R. D. (1973). Wood-boring bivalves, opportunistic species in the deep sea. Science, 180: 1377-1379.

Turner, R. D. & A. C. Johnson (1971). Biology of marine wood-boring molluscs. In, Marine Borers, Fungi and Fouling Organisms of Wood, Jones, E.B.G. & S. K. Eltringham, Eds. Paris: 259-301.

Volkmann, B. (1972a). Species of Tisbe (Copepoda, Harpacticoida) from Beaufort, North Carolina. Arch. Oceanogr. limnol. 17 (3): 223-258.

Volkmann, B. (1972b). Tisbe Battagliai n. sp., a sibling species of Tisbe holothuriae Humes (Copepoda, Harpacicoida). Archo. Oceanogr. limnol. 17 (3): 259-273.

Volkmann, B. (1973). Étude de quatre espèces jumelles du groupe Tisbe reticulata Bocquet (Copepoda, Harpacticoida). Arch. Zool. exp. gen. 114(3): 317-348.

Wiegert, R. G. (In Press). Population models: experimental tools for analysis of ecosystems. <u>In</u>, <u>Proceedings of Colloquium on Analysis of Ecosystems.</u> D. J. Horn, R. Mitchell and G. R. Stairs, Eds. Ohio State University Press, Columbus.

Wieser, W. (1959). The effect of grain size on the distribution fo small invertebrates inhabiting the beaches of Puget Sound. <u>Limnol. Oceanogr. 4:</u> 181-194.

Willey, A. (1923). Notes on the distribution of free-living copepoda in Canadian waters, II. <u>Contrib. Canad. Biol. (N.S.)</u> <u>1</u> (16): 529-539.

Williams, L. P. (1965). <u>Michael</u> <u>Faraday</u>. Basic Books, New York. 531p.

APPENDIX A

The following instruments were used in some of the environmental analyses.

Dissolved O_2 concentration

Yellow Springs Instruments dissolved O_2 meter, model 54

Conductivity/Salinity

Yellow Springs Instruments conductivity/salinity meter, model 33

pH/ Eh

Metrohm portable pH meter and micro probes, models E488, EA153 and EA259

Low Temperature Asher

International Plasma Corporation