DISTRIBUTION AND FEEDING PREFERENCES OF

FREE-LIVING NEMATODES ASSOCIATED WITH

THE KELP, Macrocystis integrifolia (LAMINARIALES)

by

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B.Sc., McGill University, 1977

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biological Sciences

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SIMON FRASER UNIVERSITY

April 1981

Approval

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Degree: Master of Science

Title of Thesis: Distribution and feeding preferences of free-living
                  nematodes associated with the kelp,
                  Macrocystis integrifolia (Laminariales)

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Title of Thesis/Project/Extended Essay

Distribution and feeding preferences of free-living nematodes

associated with the kelp, Macrocystis integrifolia (Laminariales)

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ABSTRACT

Free-living nematodes are a major component of the fauna of marine interstitial environments and are frequently associated with intertidal and subtidal algae. A study was done to categorize the nematodes of a kelp, _Macrocystis integrifolia_ Bory, in the Bamfield region of Barkley Sound, British Columbia, Canada. The feeding preferences of the pre-dominant free-living nematode species found on the _M. integrifolia_ blades were evaluated.

Nine species (belonging to six families) of nematodes were found on the blades and three of them comprised 91-99% of the nematode fauna. Two monhysterids (_Monhystera disjuncta_ and _M. refringens_) and a chromadorid _Prochromadorella neapolitana_) occurred in all monthly samples. About 50% of the nematodes on the blades from July to October was _M. refringens_, which was at its peak population level during these months. During the fall, the _M. refringens_ population declined to low levels prior to a progressive increase in population commencing in February. _M. disjuncta_ was relatively abundant throughout the year and, in particular, during the late winter and early spring. _P. neapolitana_ occurred in relatively large numbers in July and subsequently declined to a very low population in the winter and spring.

Nematode distribution on _M. integrifolia_ appeared to be related to blade age and the associated food sources on the blade. Both monhysterids occurred in greatest abundance on the bottom blades of _Macrocystis_ plants and on the middle

blades of plants in deep water. Low numbers of P. neapolitana
occurred throughout the entire depth gradient on both bottom
and middle blades. Few of these three species occurred on the
top blades. Nematode species other than these three con-
tributed little to the abundance and distribution patterns
observed on the Macrocystis blades.

All three predominant nematode species showed specific
responses to available bacterial and diatom food sources in
feeding experiments. P. neapolitana exhibited a significant
preference for diatoms, particularly Cocconeis scutellum
and Gramatophora marina, over the bacteria species under both
simulated summer and winter conditions. M. refringens showed
no preference towards bacteria or diatoms but exhibited some
preference for particular diatom or bacteria species. Under
both environmental simulations M. disjuncta showed a marked
preference for rod-shaped bacteria.

The probability that the seasonal abundance and distri-
bution of these marine nematodes is correlated with the
seasonality of their food sources, bacteria and diatoms,
is suggested.

ACKNOWLEDGEMENTS

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INTRODUCTION

Free-living nematodes are the most abundant component
of the meiofauna in most coastal and oceanic sediments. They
occur from above the highwater mark into the deepest oceanic
trenches. Abundance and distribution studies of nematodes
have been primarily in the intertidal and subtidal inter-
stitial environments (Nicholas, 1975). Observers on sandy
beaches in East Cornwall (U.K.) found that the nematode
population constituted 50% of the total number of meiofauna
inhabitants (Harris, 1972a). In a subsequent study, Harris
(1972b) observed seasonal variations in the relative proportion
of nematodes in the meiofaunal population ranging from 35.8%
to 67.5% of the total number. A study of core samples from
New York City Beach (U.S.A.) indicated that marine nematodes
numerically made up 85% of the total interstitial fauna of
the area (Martinez, 1975). In the subtidal meiofauna of two
New England (U.S.A.) estuaries, nematodes were the dominant
group, averaging 83% of the total numbers and 64% of the total
biomass (Tietjen, 1969). Further observations by Tietjen (1969)
indicated that the nematode population had marked seasonal
changes in species composition and this was possibly
associated with feeding behaviour. Epigrowth feeders
reached maximum population density in the spring and summer
(a time of high microflora production), whereas the deposit
feeding and omnivorous species had maximum population
densities in the fall and winter when detritus was most

abundant.

The bottom sediments are not the sole marine environment inhabited by free-living nematodes. One habitat that has been insufficiently studied, in spite of nematode abundance, is the microhabitat immediately surrounding marine macroalgae. The most notable contributions to this area have been those of Wieser who did an extensive taxonomic survey of marine nematodes associated with seaweeds in Chile (1953, 1959a) and in Plymouth (U.K.) (1952). In the Plymouth study, eight species of intertidal algae were sampled and he found that nematode species distribution was dependent on the algal species and the silt content of the area. Colman (1940) found nematodes to be widely distributed in all samples of the brown algae Ascophyllum and Laminaria and the red alga, Gigartina. Relative numbers as high as 247.8 individuals for every 10.0 g wet weight of seaweed were recorded. A study of Fucus serratus Linnaeus, in Sweden showed relatively low numbers of associated nematodes and the highest concentration occurred in June (6.05 individuals/g wet weight of algae) (Hagerman, 1966).

More recent studies of nematode-algae associations have considered the abundance and distribution of particular feeding types, and the parameters affecting this ecological pattern. Nematode populations on the brown alga, Sargassum, in the Adriatic Sea, are greatly affected by the thickness of the epigrowth on the algae (Ott, 1967). Epigrowth feeders are predominant on the thalli of these plants.

Studies on the nematode fauna associated with turtle grass
beds, Thalassia testudinum Konig, in Florida, with Laminaria
hyperborea Gunn, holdfasts off Britain, and Sargassum
species off Japan have shown similar results (Hopper
and Meyers, 1967a, 1967b; Moore, 1971; Mukai, 1971).
Nematode distribution and abundance on Macrocystis pyrifera
(Linaeus) C. Ag., in California was shown to be closely
related to blade age and position (Wing and Clendenning,
1971). The degree of shelter and the accumulation of detri-
tus afforded by seaweeds permits particular patterns of
nematode abundance and feeding strategies (Moore, 1971;
Wieser, 1952b).

Investigations of trophic relationships in the marine
environment have shown that meiofauna food webs encompass
a wide variety of complexities and interactions. Each
major taxonomic group has been split into distinct and
different feeding types, with each species feeding on as
varied a diet as can be found in their environment. Recent
comprehensive studies have shown a great diversity of feeding
within these taxa. Marine nematodes are without exception
to these generalized observations.

A large number of marine ecology studies include
reference to marine nematodes which are notoriously difficult
to identify. This resulted in the classification of nema-
tode species based on their respective feeding habits.
Although it is incomplete, it provides a basis for analysis
of their food preferences. The four categories, as

postulated by Wieser (1952a), are based on a correlation of stomal morphology with observations on feeding habits. Wieser's four groups are:

1A. <u>Selective deposit feeders</u>: with or without very reduced stomal cavity. Food, which must be soft and in suspension, is ingested by oesophageal suction. Large and hard particles are not ingested.

1B. <u>Unselective deposit feeders</u>: stoma with unarmored cup-shaped or cylindrical cavity. Oesophageal suction supplemented by the movements of the lips and stoma in ingesting food. Food, in suspension, includes relatively large hard objects, such as diatoms, as well as finer material.

2A. <u>Epigrowth feeders</u>: stoma with teeth, rods or plates. Food may be scraped from surfaces for ingestion, or cells may be pierced and the contents sucked out.

2B. <u>Predators and omnivores</u>: stoma with powerful armature of teeth and plates. Prey may be swallowed whole, or small animals or algal cells may be pierced and the contents sucked out (Nicholas, 1975).

A study on the nematode fauna associated with kelp holdfasts showed 52% of the species belonging to the omnivore category, 24% epigrowth feeders, 18% selective deposit feeders and 6% unselective deposit feeders (Moore, 1971).

These results indicated that the most important sources of food were the epibiota growing on the algae and that the sparse occurrence of the deposit feeders reflected the scarcity of suitable deposits within the holdfast habitat.

Detritus is an important factor limiting the distribution and abundance of nematode faunas (Tietjen, 1966). Teal and Wieser (1966), investigating the ecology of nematodes in a Georgia salt March (U.S.A.), observed that areas subject to the highest organic detritus levels constituted the most productive habitats for nematode abundance. From these studies, Tenore et al. (1977) have suggested that it is not the detritus which supplies the energy but rather the associated microbiota particularly bacteria. Bacteria have been suggested as the source of much of the deposit-feeders nourishment (Zobell and Feltham 1937, 1942). These bacteria for the most part, along with blue-green algae, diatoms, yeasts, fungi and microscopic stages of some brown algae are present on the surfaces of detritial and granular surfaces (McIntyre and Munson, 1973; Meadows and Anderson, 1966). Investigation on the distribution of these microscopic populations have suggested that local and geographical differences are likely paralleled by the productivity of the environment and these observed differences may account for the localized distribution of various nematode species.

Observations from an experimental sand ecosystem showed that a marine nematode population varied directly with

the relative bacterial numbers and that the vertical
zonations of the bacteria and nematode were strikingly
similar (Boucher and Chamroux, 1976).

Nematodes have a variety of nutritional associations
with certain species of filamentous fungi (Meyers, 1963).
An Aphelechoides sp. develops and reproduces on viable
mycelia of Dendryphjella arenaria. Studies by Meyers and
Hopper (1966, 1967), with fungal substrates, found a
dominant nematode fauna (Metonchalaimus sp.) colonizing the
fungal mats. Whereas a number of marine nematode investiga-
tions have probed trophic relationships in terms of species
abundance and levels of attraction; a number of studies have
tried to characterize nematode biotic associations by way
of feeding experiments and gut contents. Jennings and
Colman (1970) found large amounts of mud and silt in the
guts of a marine nematode, Pontonema vulgaris Bastian,
suggesting the digestion of bacteria and any other organic
materials present in the substrate. The marine Monhystera
species have been shown to have detritus throughout the gut
and feeding experiments successfully maintained
Monhystera species on the bacteria: Arthrobacter, sp.,
Pseudomonas sp., Vibria sp. and Flavobacterium sp.
(Chitwood and Murphy, 1964). Observations on the marine
nematode, Chromadora macrolaimoides Steiner, a species
equipped with a long stoma armed with three movable teeth
used to scrape food from substrate, indicated it to be very
selective in its ingestion and digestion of algae. Twenty

species of algae, mostly diatom species, were tested, with
the result that only eleven were effectively utilized and
of the eleven, only five could sustain growth to ten
generations (Tietjen and Lee, 1973). A related study by
Tietjen and Lee (1977) comparing feeding habits of two epi-
growth feeders and two non-selective feeders suggested that
not only was selective ingestion a significant factor in
nematode feeding habits, but so also was selective digestion.

The objectives of this study were to characterize the
abundance, seasonality and distribution of the predominant
marine nematode species inhabiting M. integrifolia
beds. Then, using diatoms and bacteria isolated from M.
integrifolia blades, determine food preference and relate
these findings to their seasonality and distribution on
M. integrifolia blades.

DESCRIPTION OF STUDY SITE AND ASSOCIATED KELP

This study of marine nematodes associated with the large brown kelp, Macrocystis integrifolia Bory, was located in Dodger Channel (48 50' 04" N, 125 11' 55" W) in the Barkley Sound region of Vancouver Island, British Columbia, Canada (Fig. 1). The kelp bed extended 16.0 m out from the shoreline and had a depth range from -1.2 to -5.5 m below mean zero tide. The study site's substrate was characterized by sand, rock rubble and small rock outcroppings. In summer, the kelp bed was fairly sheltered from wave action but during the winter was semi-wave exposed due to the direction of the prevailing winds.

Macrocystis integrifolia, (Fig. 2), is the largest member of the Phaeophyceae found on the British Columbia coast (Scagel, 1971). It is characterized by having a large flattened rhizome-like holdfast from which arise many dichotomously branched haptera which are used to secure the plant to the substrate. From this holdfast extend erect stipes ranging up to 0.5 cm in diameter and 10.0 m in height. Large blades arise at intervals along the stipe. The blades may range from 15.0 cm to 1.5 m in length and 5.0 cm to 25.0 cm in width. The blades are flattened, deeply furrowed, denticulate along the edges and have at their point of attachment a pneumatocyst. The main intercalary meristem is located near the top of a stipe, with a secondary meristematic region located at the distal end of the

Fig. 1:   Location of Dodger Channel study site in the
           Barkley Sound region of Vancouver Island, B.C.

49°N

VANCOUVER

S

Vancouver Island

48°N

125°15'W

123°W

S — Bamfield Study Site

125° 15' W

10'

5'

124

Flemming I.

Deer Group

Trevor Channel

Dixon I.

Diana I.

Aguilar Pt.

Folger I.

50'

Bamfield Inlet

PACIFIC
OCEAN

VANCOUVER
ISLAND

48° 47'
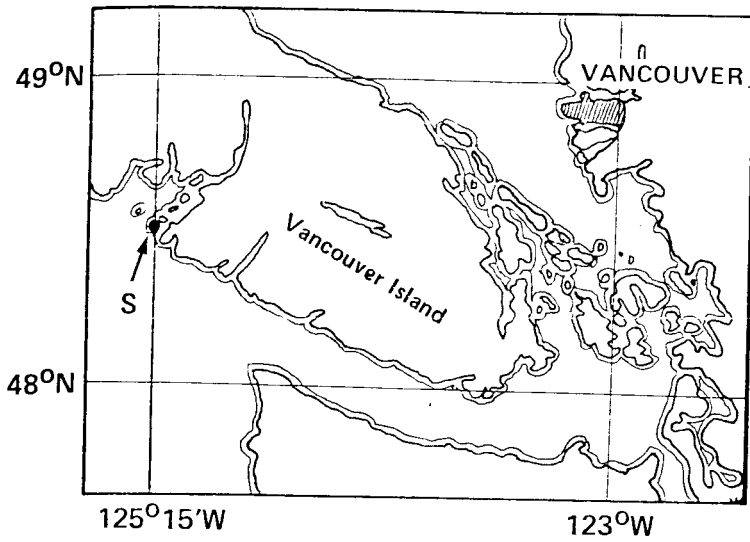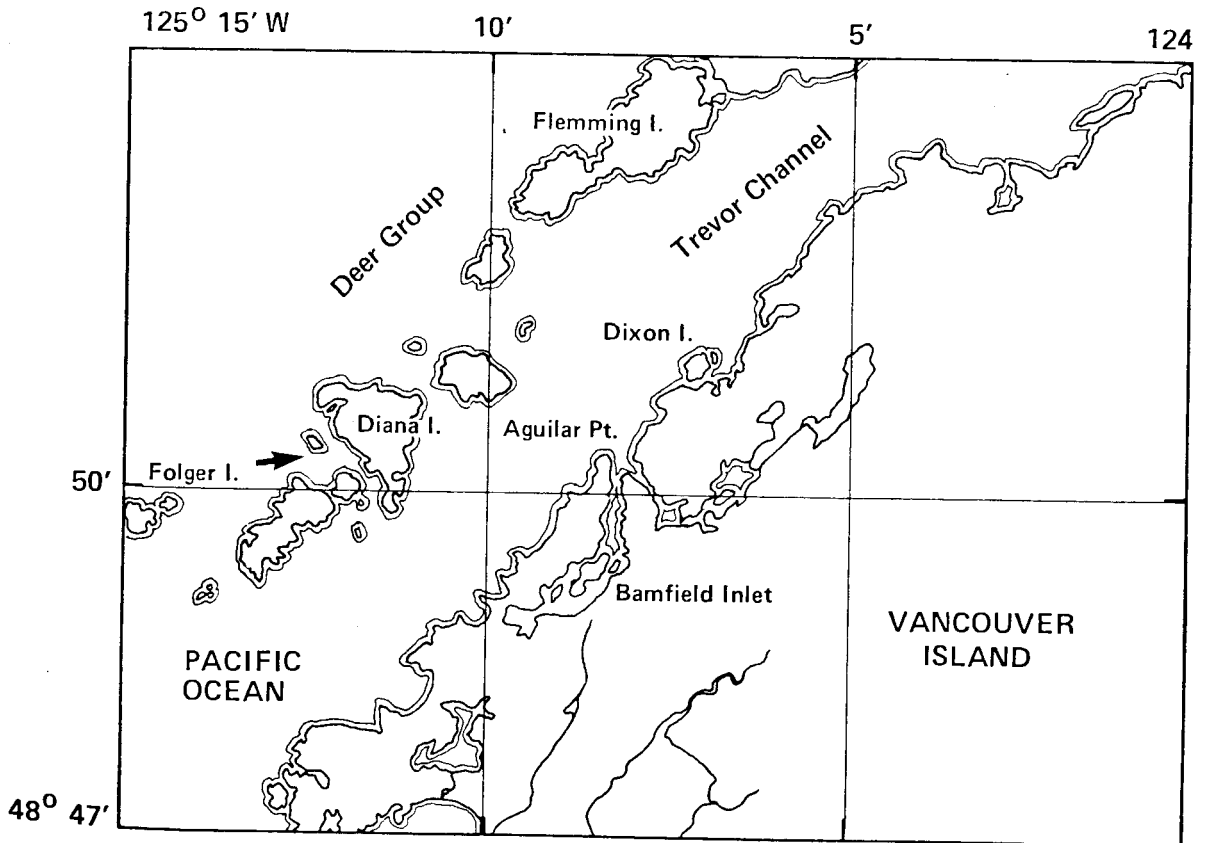
Fig. 2:   Semi-diagrammatic sketch of Macrocystis sp.
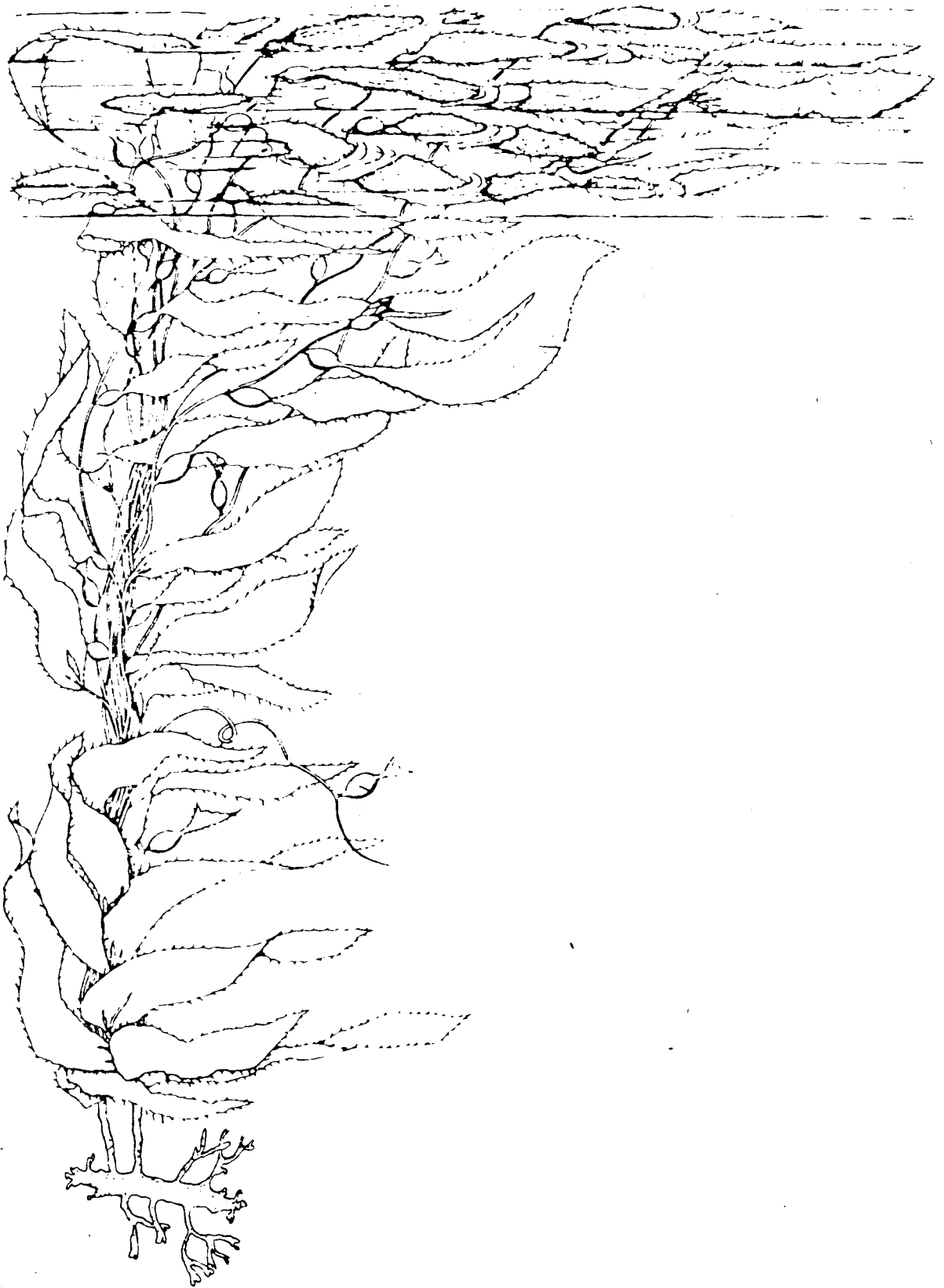
pneumatocyst.

The holdfast of M. integrifolia is perennial and new
stipe and blades are produced throughout the year with
production rates and distribution varying seasonally (Druehl,
1978; Lobban, 1978). With respect to blade age, three stages
are recognized; growing tissue, mature tissue and senescent
tissue (Lobban, 1978).

MATERIALS AND METHODS

I. Field Survey

a) Sampling Procedure

To ascertain the distribution of free-living marine
nematodes on M. integrifolia, a single, weighted transect line
was randomly established in a kelp bed in Dodger Channel.
The line was secured approximately 2 m inshore from the edge
of the kelp bed and extended through the kelp, perpendicular
to the shore line and secured 33 m out from the inshore
point by cement blocks. Prior to its placement in the kelp
bed, the line was marked with coded surveyor's tape at 2 m
intervals. Blades of M. integrifolia were collected monthly
for one year from July 1978 to July 1979 and subsequently bi-
monthly until November 1979, using SCUBA equipment. No data
was collected for December 1978, August and October 1979. The
closest plant within 1.0 m radius of each marker on the tran-
sect line was selected for sampling. At each sampling,
three blades were removed; one from a height of 1 m from the
plant holdfast, one at 1 m from the distal end of the plant
and the third at a point between the first two sampled blades.
Specific care was taken to sample only vegetative blades and
not sporophylls. Twelve plants at 2 m intervals were sampled
on each sampling date.

The blades were removed by carefully slipping a 38.5 x
13.0 x 7.5 cm plastic bag over the sample blade which was
then detached from the stipe and the bag was immediately
closed and secured with a twist tie. Care was taken to

disturb the blade as little as possible. Each sampling bag was coded and registered on an underwater slate. The coded bags were numbered as to date, transect line marker and depth. This procedure was repeated at each of the other eleven sample points and then the samples were taken to the surface and transported in buckets of seawater to the Bamfield Marine Station laboratory. Time for transport never exceeded 45 minutes.

b)   Treatment of Samples

On arrival at the Bamfield Marine Station, the contents of each bag were fixed with 250 ml of a solution of 10% formalin in filtered seawater and left at room temperature for 24-36 h. Each sample was processed as follows: the bag was agitated so as to thoroughly mix the debris and detritus in the solution and on the blade surface. The suspension was carefully poured through a 44μ brass sieve. The material remaining in the sieve was then washed into a 100 x 15 mm Petri dish. The blade was then carefully removed from the bag and placed into a small bath of 10% formalin in filtered seawater. The plastic bag was washed out with filtered seawater and the suspension filtered as described above. The blade was agitated for approximately one minute and then whilst being suspended by the pneumato-cyst, washed down twice with a 10% formalin solution from a plastic squeeze bottle. The bath solution was filtered twice through a 44μ sieve and the collected residue placed in a 100 x 15 mm Petri dish. Every third blade was examined

under the dissecting microscope (120x) to evaluate the efficiency of this processing procedure for removing nematodes. The cleaned blade was photographed to scale and discarded. These photographs were used subsequently to determine the total surface area of the blade (both sides) using a compensating polar planimeter.

The Petri dish samples were examined under a dissecting microscope and all nematodes were transferred by hand to 1.5 cm diam. watchglasses where they were processed as outlined by Sharma (1978). The nematodes were individually mounted in glycerine on permanent slides for identification and sexing and for enumeration with respect to blade sample.

c)   Statistical Treatment

The collected data were analyzed using a two-level and three-level analysis of variance using programs developed by Davies (1971).

d)   Environmental Parameters

Measurements of temperature and salinity for each of the sampling months were obtained from data collected by Dr. L. Druehl of Simon Fraser University and the Bamfield Marine Station.

e)   Taxonomic Notes

All nematodes found in the samples were identified at least to genus and the most abundant individuals were classified to species with the help of the major taxonomic keys and checklists of Chitwood (1960), Gerlach and Rieman

(1973) and Wieser (1953, 1959b). Those species identified to species had their identity confirmed by Mr. Bruce Hopper, Agriculture Canada, Ottawa.

II.   Feeding Preference Experiments

a)   Culture of Nematodes

Living nematodes, collected at random from the middle and bottom samples of M. integrifolia blades from January to July 1980, were extracted by the sieving process described above and then transferred to 105 cm^2 Corning Tissue Culture Flasks, containing 400 ml of filtered seawater and several small pieces of blade of M. integrifolia. The flasks were incubated at 7 C with a 12/12 hour day (250µW/cm^2)/night cycle. Within 24 h, the culture flasks were transported in an ice chest from Bamfield to the Simon Fraser University laboratory, where they were incubated at 10 C with a 16/8 hour day (250µW/cm^2)/night cycle.

The nematodes were maintained in such an agnotobiotic culture in which every day for the first week 300 ml of the culture seawater was replaced by an equal amount of autoclaved, filtered seawater. Thereafter, this procedure was performed only once per week. The larger competitive and/or predatory invertebrates were removed from the cultures.

The three most abundant nematode species were isolated by hand from these cultures and placed into separate culture flasks containing only detritus and pieces of M. integrifolia in autoclaved filtered seawater. Once each week, 5 ml of monoxenic diatom and bacterial cultures isolated from M. integrifolia blade samples were added to the flasks to supplement the nematodes diet. When the next generation of nematode larvae appeared, additional nematode cultures were initiated,

using the techniques described above. Hence, a large population of each of the three species was maintained in culture and available for the food preference experiments. Observations on the life cycles of these nematode species were made during the development of these cultures.

One half of these nematode cultures were maintained under simulated winter conditions at 5 C with an 8/16 hour ($250\mu W/cm^2$) /night cycle and the remaining half were maintained under simulated summer conditions (10 C, 16/8 h day/night). It was possible, subsequently to make comparisons with respect to feeding preferences under two environmental conditions. Under both conditions, salinity was maintained at 31%.

b)   Culture of Food Sources

Bacteri and diatom species used in the food preference experiments were isolated from the detritus and from blade scrapings. Bacterial species were isolated in standard Petri dishes containing Difco Marine Broth and 1.0% Difco Bacto Agar. The cultures were maintained at room temperature on a 12/12 hour day/night light cycle. Four bacterial species were isolated from these blades by standard microbiological techniques and then maintained on liquid and solid media at 10 C on a 16/8 hour day/night cycle (Table 1).

Eight marine distom species were isolated by hand from blade scrapings using elongated Pasteur Pipettes (Table 1). These species were incubated in sterile "S" medium (Lee et al. 1970) at 22 C on a 16/8 hour day/night cycle. Every

Table 1: Diatom (D1-D8) and bacteria (B1-B4) species isolated from Macrocystis integrifolia blades and used in the feeding preference experiments.

Experiment I

				Size (μm)	
				Length	Width
D1	-	*	Gramatophora marina (Lyngb.) Kutz	35 - 40	6 - 7
D2	-	*	Rhoicosphenia curvata (Kutz) Grunow	35 - 40	8 - 10
D3	-		Navicula jamalinensis Cleve	25 - 50	15 - 25
D4	-	*	Synedra tabulata (Ag.) Kutz	25 - 140	3 - 6

Experiment II

D5	-		Gomphanema olivaceum (Lyngb.) Kutz	35 - 40	5 - 7
D6	-	*	Cocconeis scutellum Ehr.	25 - 50	10 - 40
D7	-	*	Achnanthes longissipes Ag.	15 - 25	6 - 9
D8	-		Amphora acutiuscula Kutz	25	10

Experiment III, IV and V

B1	-	rod, Gram negative	round, white colony
B2	-	coccoid, Gram positive	round, yellow colony
B3	-	rod, Gram neagtive	round, orange colony
B4	-	coccoid, Gram positive	round, dark yellow colony

* species associated with M. integrifolia from Roland (1980).

week these cultures of diatom species were checked for the presence of bacteria and marine fungi in the culture tubes by subculturing on Petri dishes containing Difco Marine Broth. Cultures with high populations of bacteria and/or marine fungi (> 5 colonies) were re-isolated and new cultures were initiated. Under this checking system, diatom cultures containing low bacterial and/or fungal populations were maintained.

c) Experimental Design

Experiments were designed to demonstrate the feeding preferences of the three most abundant nematode species found on M. integrifolia. The "cafeteria" design as described by Lee et al. (1977) was employed with the following modifications. Twenty-four hours prior to the feeding experiment, adult male and female nematodes of each species were isolated by hand from the cultures. They were washed in autoclaved, filtered seawater containing 100 units of the bactericidal Polymyxin B, for 6 hours. The individual species were then separated by sex and placed in culture flasks containing only autoclaved filtered seawater for 18 hours.

The nematodes were transferred one at a time into wells, made by a sterilized #13 cork borer (2 cm diam), in a Petri plate (150 x 25 mm) containing 40 ml of 0.4% sea-water agar. The well pattern was such that a central and eight equidistant peripheral wells were located on the plate. Subsequently, 0.7 ml of bacteria or diatom

suspension were placed in each of four alternate peripheral wells and the remaining peripheral wells were filled with 0.7 ml of sterile culture media. Large coverslips (29 x 50 mm) were then placed over each well. Control plates had eight wells filled with sterile culture media.

Diatom populations of $1.0 \times 10^5 \pm 1.0 \times 10^3$ individuals/ml were inoculated into the designated food wells. Bacterial food wells were inoculated with 1.0×10^6/ml $\pm 1.0 \times 10^4$/ml (Hobbie et al., 1977).

One hundred adult nematodes (1:1 sex ratio) of one of the three species were placed in seawater in the central well and covered with a coverslip. The agar plate was then carefully covered with a 0.5 cm deep layer of sterile sea-water after which all the coverslips were carefully removed. Four replicate plates and one control plate for each of the diatom or bacteria feeding preference experiments were established for each nematode species. Two additional experiments were done using Monhystera disjuncta Bastian under simulated summer conditions. They involved exposing this nematode species to either all rod or coccoid bacteria species under the same "cafeteria" design.

Each of the four experimental plates were oriented at right angles to the plate to its left or right and the control plate was placed in the center of the group of four experimental plates. The experiments were conducted under simulated summer (10 C, 16/8 h day/night cycle) and winter (5 C, 8/16 h day/night cycle) conditions. The

nematode inoculated plates were left under these conditions for 72 hours and then the number of nematodes present in each well was counted and sexed.

Detailed observations on the life cycle were collected only for M. disjuncta.

d)   Statistical Treatment

The data from the nematode feeding preference experiments were analyzed by the X^2 test, two-level ANOVA and the Student-Newman-Keuls test (Sokal and Rohlf, 1969).

RESULTS I

a) Observations on Physical Parameters

Surface water temperature (Fig. 3) ranged from 6.1 C to 14 C and surface water salinity from 29.4‰ to 32.0‰. The lowest temperature occurred in January and the highest in July. The highest salinity occurred during the summer months.

b) Nematode Species Composition

Nine nematode species belonging to six families were found associated with M. integrifolia (see Table 2). They were identified and classified according to the system of Chitwood and Chitwood (1950) as modified by Gerlach and Rieman (1973). Three of these species constituted 91.0 - 99.1% of the total nematode population in the M. integrifolia samples. The most abundant species were Monhystera disjuncta, M. refringens and Prochromadorella neapolitana.

c) Seasonal Species Changes

i) Prochromadorella neapolitana

Most P. neapolitana were found in early and mid-summer (Fig. 4). The largest percent abundance levels occurred in July 1978 and 1979 (40.3% and 37.6% respectively). Low numbers of this species were recorded for the remainder of the year except for November 1978 and 1979, when there was an increased frequency to 24.3% and 22.4% respectively. The age structure for P. neapolitana, represented as the percentage of males, females and juveniles, is given in Fig. 4

Fig. 3: Temperature and salinity in Dodger Channel over the sampling period 1978 - 1979.

- 24 -
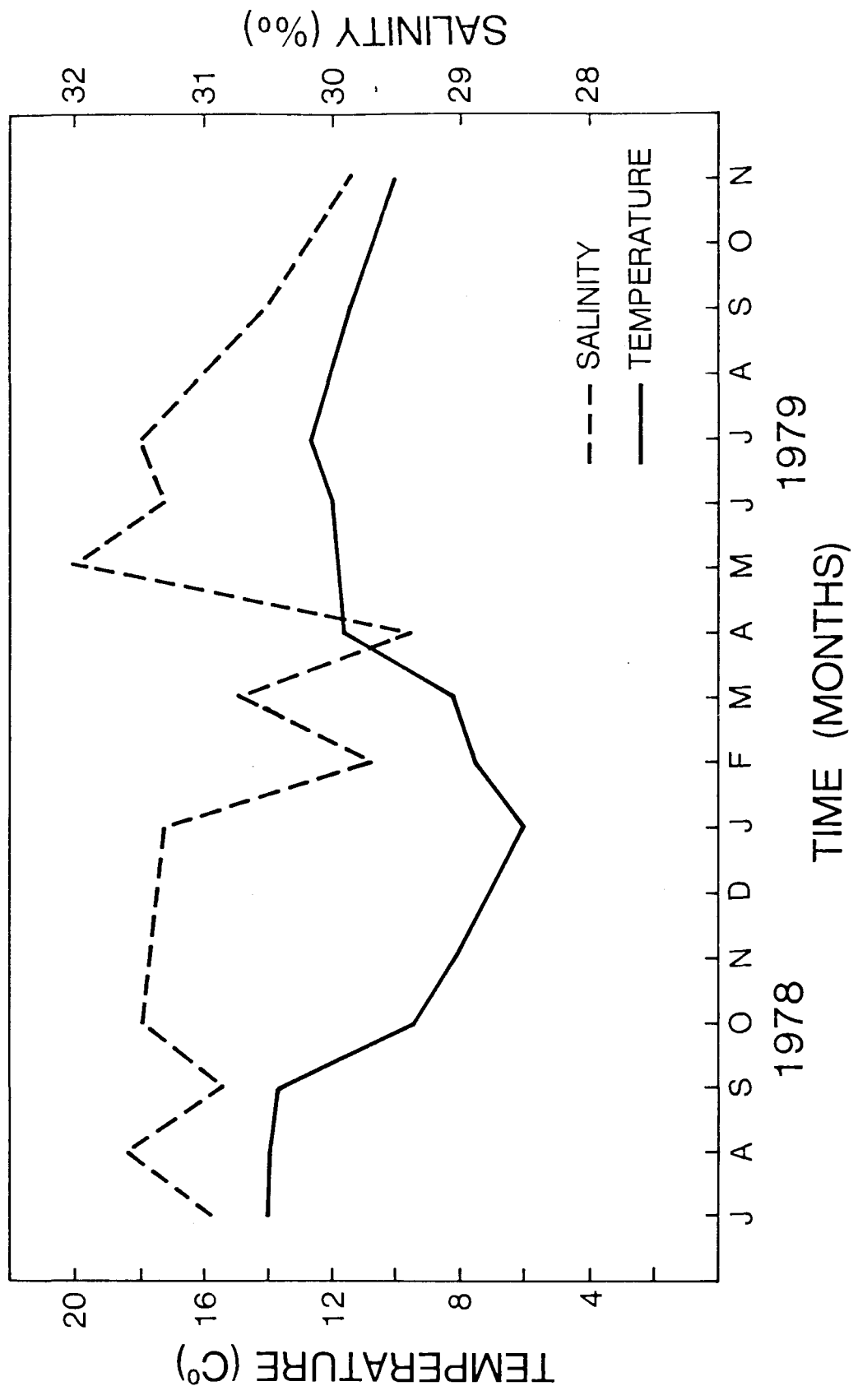
Table 2: Checklist of free-living nematodes found in
          blade samples of Macrocystis integrifolia.

Class Adenophorea

Order Araeolaimida

      Family Axonlaimidae
      Subfamily Diplopeltinae
      Araeolaimus
            A. elegans, DeMan, 1888

Order Monhysterida

      Family Monhysteridae
      Subfamily Monhysterinae
      Monhystera
            M. disjuncta, Bastian, 1865
            M. refringens, Bresslau & Stekhoven, 1935

Order Chromadorida

      Family Chromadoridae
      Subfamily Chromadorinae
      Chromadora
            C. nudicapitata, Bastian, 1865

      Chromadorina
            C. laeta, Micoletzky, 1924

      Prochromadorella
            P. neapolitana, Micoletzky, 1924

      Family Cyatholaimidae
      Subfamily Paracanthonchinae
      Parocanthonchus, Micoletzky, 1924
            Paracanthonchus sp.

Order Enoplida

      Family Anticomidae
      Anticoma
            A. acuminata, Bastian, 1865

      Family Oncholaimidae
      Subfamily Oncholaiminae
      Oncholaimus
            O. dujardini, DeMan, 1876

<u>Fig. 4</u>: Per cent distribution and age structure of <u>Prochromadorella neapolitana</u> over the sampling <u>period 1978 - 1979.</u>
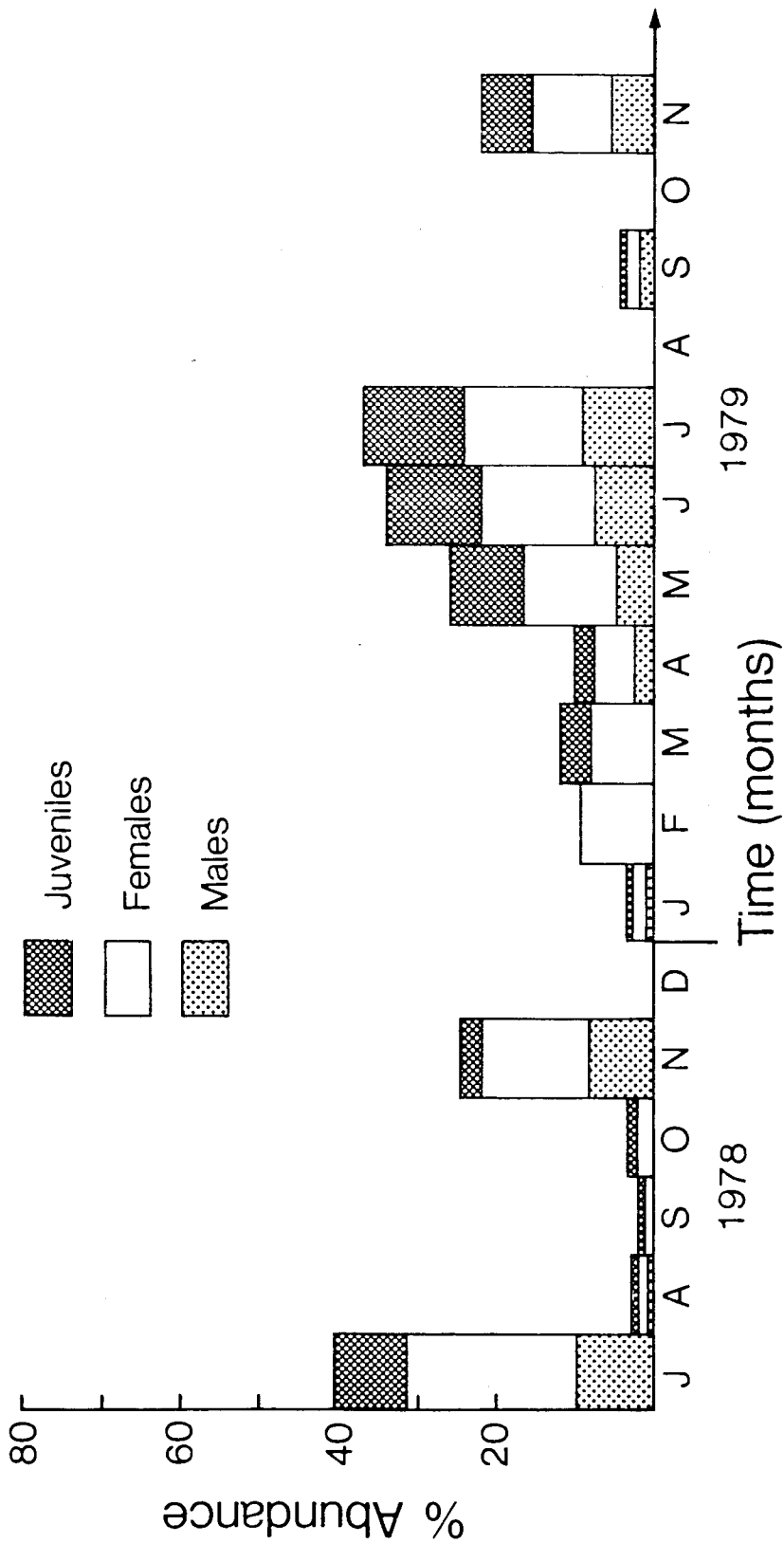
and Table 3. Their densities were found to be significant across the sampling period (see Appendix 21). Males were found in low frequencies except in June, July and November. In the months of September 1978, February and March 1979, none were found in the samples. Females were found in every month sampled and were very frequent except in September 1978, 1979, October 1978 and January 1979. There were low frequencies of juveniles in all the sampled months except those in the summer. No juveniles were recorded from the February 1979 samples.

ii) Monhystera refringens

Monhystera refringens occurred throughout the sampling years of 1978 and 1979 (Fig. 5). It had the highest frequency of occurrence during the early fall. The lowest frequency of occurrence was mid-winter and, thereafter, there was a gradual increase in population from January (11.0%) to September 1979 (44.1%). Densities of males, females and juveniles were found to be significant in all the sampled months (see Appendix 22). The age structure of this species, expressed as the percentage of males, females and juveniles, is given in figure 5 and Table 4. Males were less frequent in the population samples than either females or juveniles and exhibited little intersample variation with the exception of slight increases in the fall months. In particular, juveniles occurred most frequently during the early fall and contributed greatly to the increased overall fall frequencies for this species.

Table 3: Total number/0.5 m^2 and per cent abundance of males, females and juveniles of Prochromadorella neapolitana over sampling period 1978 - 1979.

Month	Total No.	Males		Females		Juveniles	
		#	%	#	%	#	%
July '78	108	26	24.1	59	54.6	23	21.3
Aug.	11	3	27.3	5	45.4	3	27.3
Sept.	6	0	0.0	4	66.7	2	33.3
Oct.	11	1	9.1	6	54.5	4	36.4
Nov.	69	23	33.3	38	55.1	8	11.6
Dec.	--	--	--	--	--	--	--
Jan. '79	11	2	18.2	7	63.6	2	18.2
Feb.	22	0	0.0	22	100.0	0	0.0
March	30	0	0.0	20	66.7	10	33.3
April	30	8	26.7	15	50.0	7	23.2
May	98	18	18.4	45	45.9	35	35.7
June	161	35	21.7	69	42.9	57	35.4
July	152	37	24.4	61	40.1	54	35.5
Aug.	--	--	--	--	--	--	--
Sept.	13	6	46.1	4	30.8	3	23.1
Oct.	--	--	--	--	--	--	--
Nov.	62	15	24.2	29	46.8	18	29.0
Mean	55.9	12.4	19.5	27.4	54.5	16.1	26.0
S.D.	±54.0	±13.3	±13.4	±23.2	±16.6	±19.3	±10.7

Fig. 5: Per cent distribution and age structure of
Monhystera refringens over the sampling period
1978 - 1979.
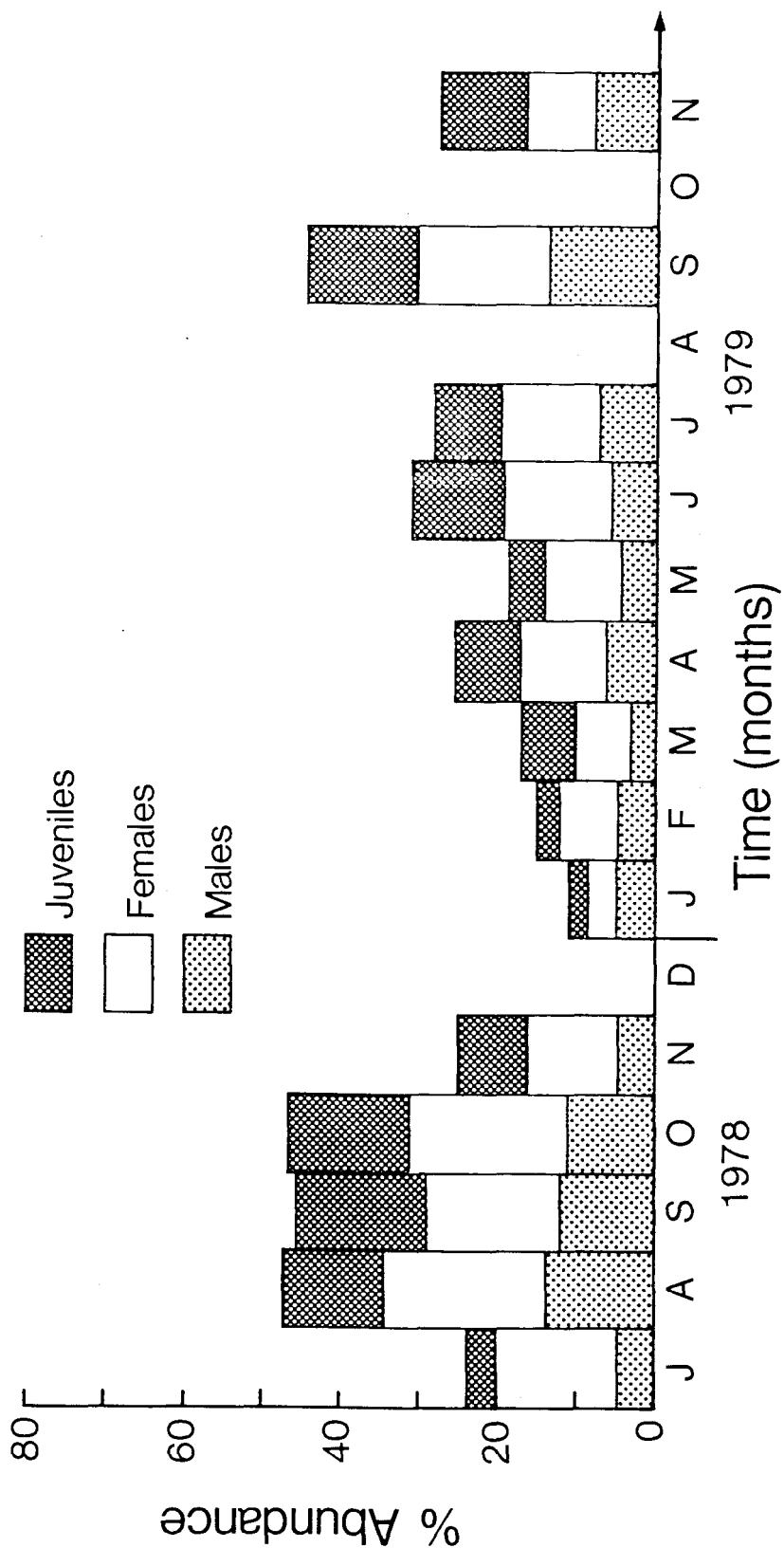
Table 4: Total number/0.5 m^2 and per cent abundance of males, females and juveniles of Monhystera refringens over sampling period 1978 – 1979.

Month	Total No.	Males		Females		Juveniles	
		#	%	#	%	#	%
July '78	64	12	18.8	43	67.2	9	14.0
Aug.	160	47	29.4	70	43.7	43	26.9
Sept.	137	36	26.3	51	37.2	50	36.5
Oct.	168	42	25.0	71	42.3	55	32.7
Nov.	69	13	18.9	31	44.9	25	36.2
Dec.	--	--	--	--	--	--	--
Jan. '79	34	15	44.1	11	32.4	8	23.5
Feb.	34	10	29.4	17	50.0	7	20.6
March	42	7	16.7	18	42.8	17	40.5
April	75	17	22.7	33	44.0	25	33.3
May	67	16	23.9	36	53.7	15	22.4
June	147	27	18.4	63	42.8	57	38.8
July	112	28	25.0	49	43.8	35	31.2
Aug.	--	--	--	--	--	--	--
Sept.	134	40	29.8	51	38.1	43	32.1
Oct.	--	--	--	--	--	--	--
Nov.	74	21	28.4	23	31.1	30	40.5
Mean	94.0	23.6	25.5	40.5	43.8	29.9	30.7
S.D.	±47.5	±13.1	± 7.0	±19.6	± 9.0	±17.6	± 8.1

iii) Monhystera disjuncta

Seasonal variations in the relative abundance of males, females and juveniles of this species are shown in figure 6. M. disjuncta was present throughout the year but was most abundant in the winter months (January to March). The population of this species was lowest in the summer months, and in particular in June 1979 and July 1978, 1979 when it showed 30.0% and 28.7% relative abundance respectively. The relative abundance in successive fall periods for 1978 and 1979 were closely similar with a range of 44.0% to 50.0% of the total population. Densities of males, females, and juveniles exhibited no significant monthly variation (see Appendix 23). Examination of the age structure of M. disjuncta from July 1978 to November 1979 showed that females were the predominant component of the population (Fig. 6, Table 5). With the exception of the mid-summer months, (June and July), the male and female populations exhibited little relative variation between months. The percentage frequency of the juvenile component in the population was less, particularly in July 1978, 1979, in comparison to the fall.

iv) Other species

Seasonal variations in the relative abundance of all other species found on M. integrifolia are shown in Fig. 7. These species comprised no more than 9.0% of the total population in any one month sampled. Fluctuations in the age structure of the population were not usually determined

Fig. 6: Per cent distribution and age structure of
Monhystera disjuncta over the sampling period
1978 - 1979.
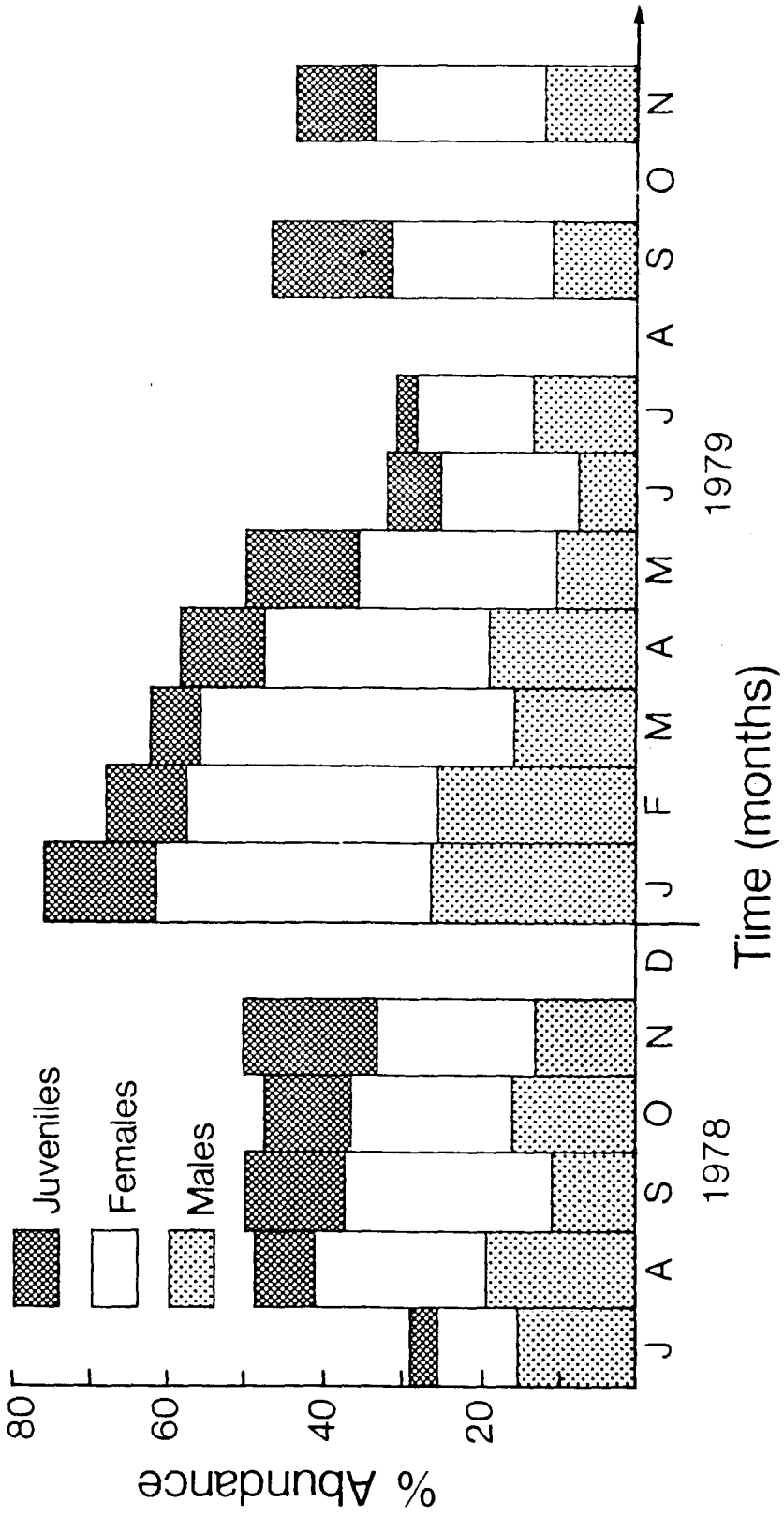
Table 5: Total number/0.5 m^2 and per cent abundance of males, females and juveniles of Monhystera disjuncta over sampling period.

Month	Total No.	Males #	Males %	Females #	Females %	Juveniles #	Juveniles %
July '78	77	41	53.2	27	35.1	9	11.7
Aug.	163	66	40.5	72	44.2	25	15.3
Sept.	152	33	21.7	81	53.3	38	25.0
Oct.	171	58	33.9	74	43.3	39	22.8
Nov.	138	36	26.1	56	40.6	46	33.3
Dec.	--	--	--	--	--	--	--
Jan. '79	237	82	34.6	110	46.4	45	19.0
Feb.	155	59	38.1	73	47.1	23	14.8
March	155	40	25.8	100	64.5	15	9.7
April	174	58	33.3	86	49.4	30	17.3
May	189	39	20.6	97	51.3	53	28.1
June	142	33	23.3	79	55.6	30	21.1
July	116	50	43.1	56	48.3	10	8.6
Aug.	--	--	--	--	--	--	--
Sept.	142	32	22.5	63	44.4	47	33.1
Oct.	--	--	--	--	--	--	--
Nov.	122	33	27.0	60	49.2	29	23.8
Mean	152.4	47.1	31.7	73.9	48.1	31.4	20.2
S.D.	±37.0	±15.4	±9.6	±21.3	±7.1	±14.0	±8.0

Fig. 7: Per cent distribution of the non-predominant
         nematode species over the sampling period 1978 -
         1979.
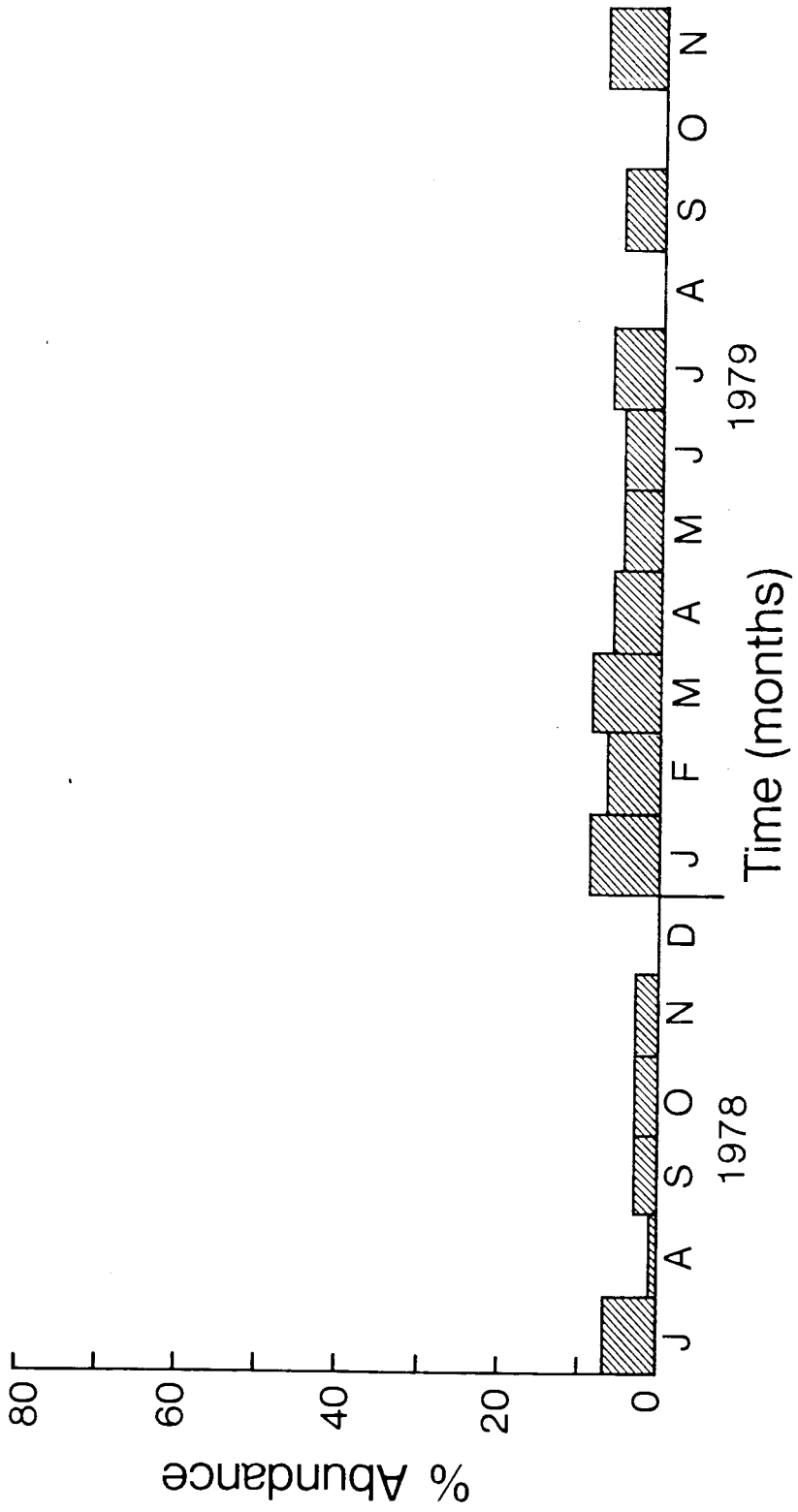
because of the low total numbers of these species.

d)   Species Distribution on Kelp

The distribution over the surface of M. integrifolia
of the three most abundant species of marine nematodes is
shown in figures 8-19 and of the remaining species in the
population in figures 20-23. Most individuals of each of
the three predominant species were located on the lower
blades. Significantly fewer nematodes of each species
occurred on the mid-blades and very few on the upper ones.
Spot samples and ad hoc observations showed that the nema-
todes were distributed evenly along the length and only
on the top surface of the blade.

The number of individuals on M. integrifolia increased
with depth of water and this was especially so with the
number on the mid and lower blades. A two-way ANOVA was
done of the data from each of the twelve grid points along
the transect line arranged into three groups, each of four
points. This showed that for the three predominant nematode
species, blade position was a significant factor ($P < 0.005$)
in their distribution (Tables 6-8). Further, for most of
the sampling times, the distribution of most of the nema-
todes was related to blade position on the stipe ($P < 0.005$)
and only rarely significantly to depth (Table 9).

These generalizations hold true for M. disjuncta with
only July 1978, 1979 exhibiting a deviation from these above
trends (Fgis. 16 and 18).

M. refringens exhibited these general distribution
patterns primarily in the late summer and early fall months.

Fig. 8:   Density of Prochromadorella neapolitana (nematodes/
0.5 m^2) on top, middle and bottom blade samples
of Macrocystis integrifolia along a depth transect
gradient from July 1978 to October 1978 (from deep
to shallow depth).

No. of Nematodes/0.50 m²

Distance (m)

Fig. 9: Density of Prochromadorella neapolitana (nematodes/ 0.5 m²) on top, middle and bottom blade samples of Macrocystis integrifolia along a depth transect from November 1978 to March 1979 (from deep to shallow depth).
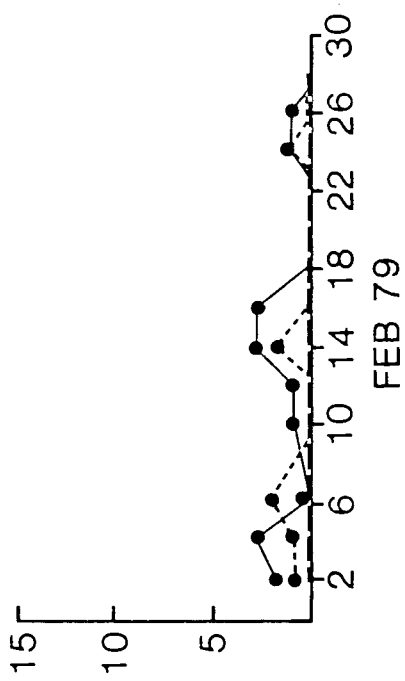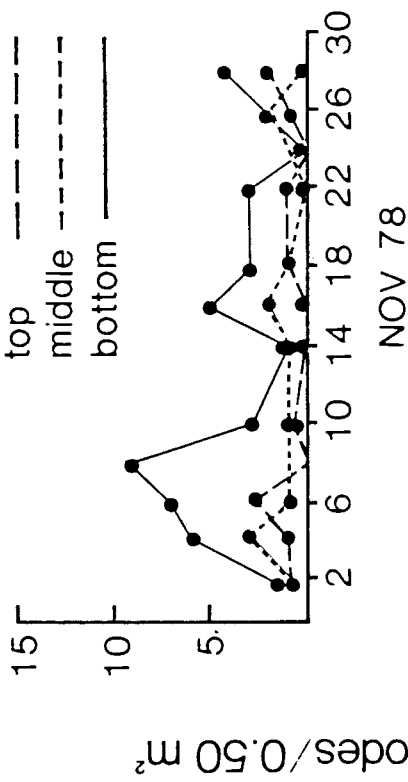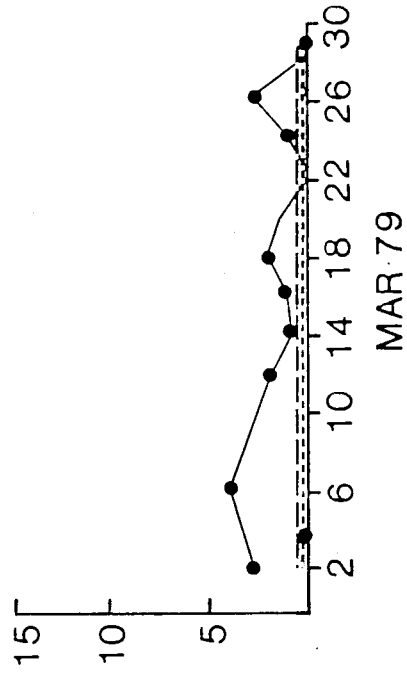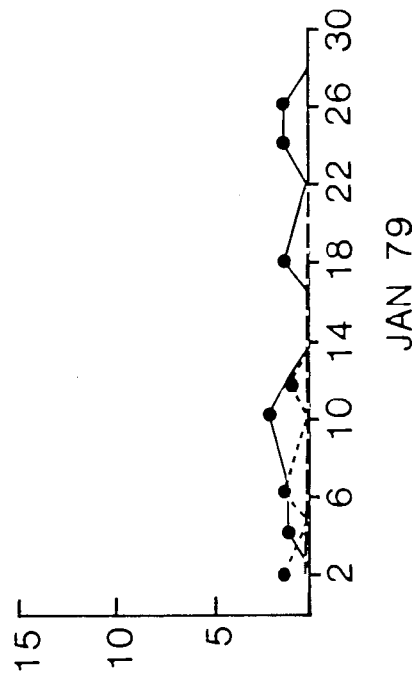
Fig. 10: Density of Prochromadorella neapolitana (nematodes/
0.5 m²) on top, middle and bottom blade samples
of Macrocystis integrifolia along a depth transect
from April 1979 to July 1979 (from deep to shallow
depth).

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Fig. 11:   Density of Prochromadorella neapolitana (nematodes/
0.5 m^2) on top, middle and bottom blade samples
of Macrocystis integrifolia along a depth transect
for September and November 1979 (from deep to
shallow depth).
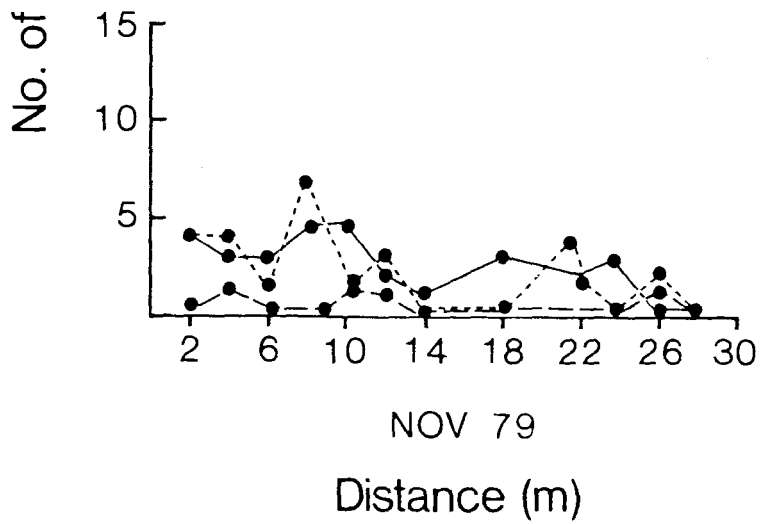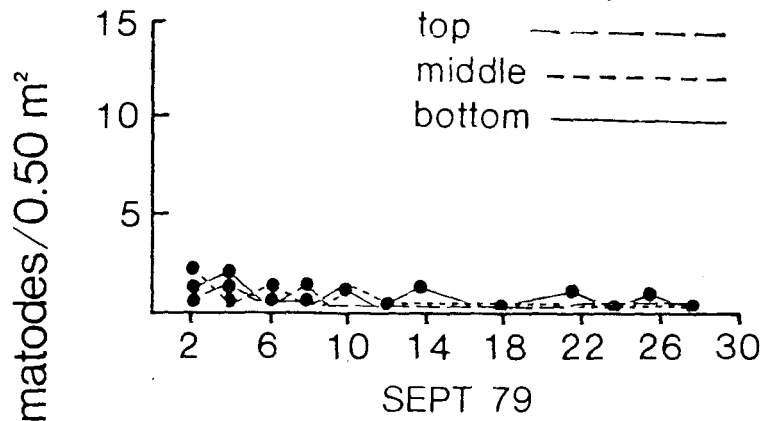
Fig. 12: Density of Monhystera refringens (nematodes/
0.5 m^2) on top, middle and bottom blade samples
of Macrocystis integrifolia along a depth transect
from July 1978 to October 1978 (from deep to
shallow depth).

No. of Nematodes/0.50 m²

Distance (m)

JULY 78

AUG 78

SEPT 78

OCT 78

top
middle
bottom

Fig. 13:   Density of Monhystera refringens (nematodes/
0.5 m²) on top, middle and bottom blade samples
of Macrocystis integrifolia along a depth transect
from November 1978 to March 1979 (from deep to
shallow depth).

Fig. 14:   Density of Monhystera refringens (nematodes/
0.5 m^2) on top, middle and bottom blade samples
of Macrocystis integrifolia along a depth transect
from April 1979 to July 1979.(from deep to shallow
depth).

Fig. 15: Density of <u>Monhystera</u> <u>refringens</u> (nematodes/
0.5 m^2) on <u>top, middle and bottom</u> blade samples
of <u>Macrocystis</u> <u>integrifolia</u> along a depth transect
for September and November 1979. (from deep to
shallow depth).

Fig. 16: Density of Monhystera disjuncta (nematodes/0.5 m^2)
on top, middle and bottom blade samples of
Macrocystis integrifolia along a depth transect
from July 1978 to October 1978 (from deep to
shallow depth).

Fig. 17: Density of Monhystera disjuncta (nematodes/0.5 m^2)
on top, middle and bottom blade samples of
Macrocystis integrifolia along a depth transect
from November 1978 to March 1979 (from deep to
shallow depth).
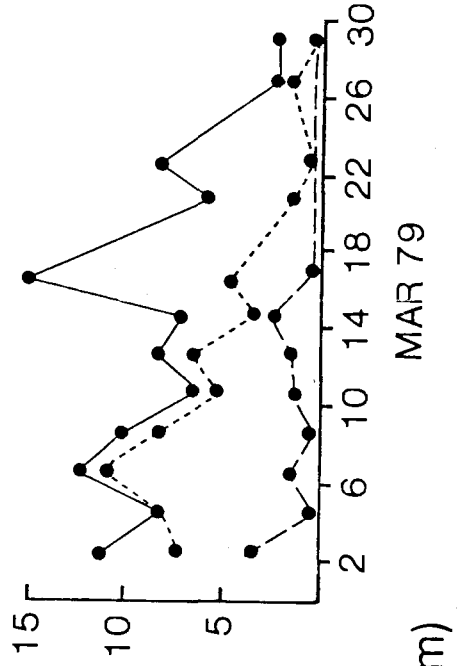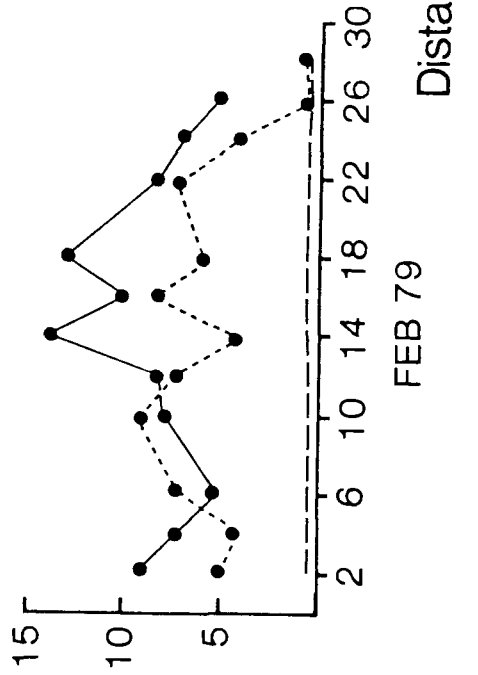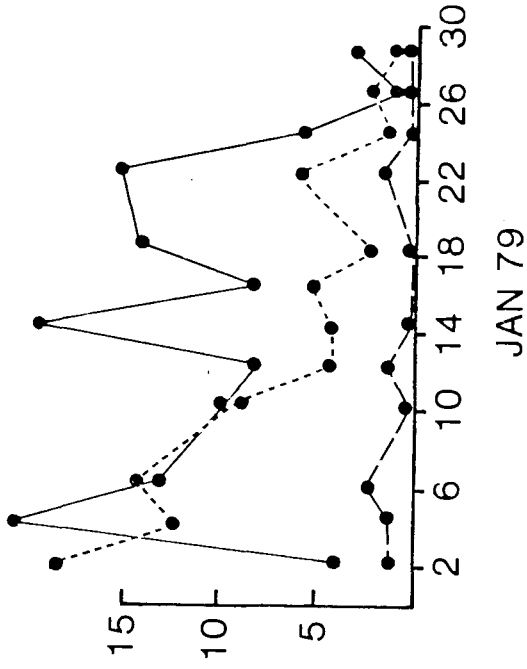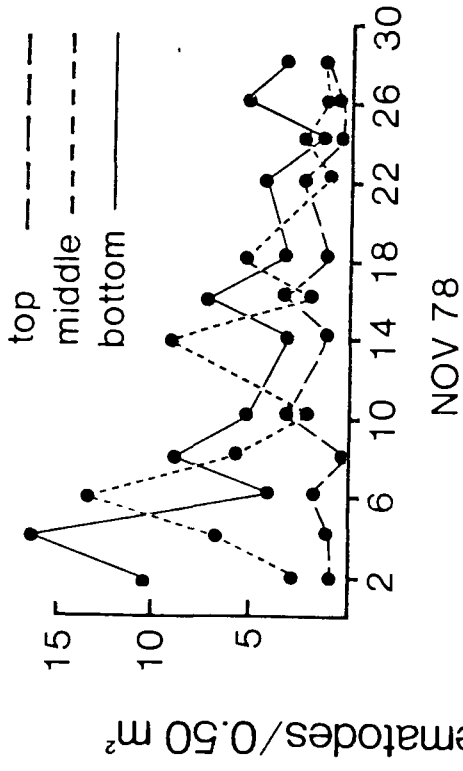
Fig. 18: Density of <u>Monhystera disjuncta</u> (nematodes/0.5 m^2) on top, middle and bottom blade samples of <u>Macrocystis integrifolia</u> along a depth transect from April 1979 to July 1979 (from deep to shallow depth).
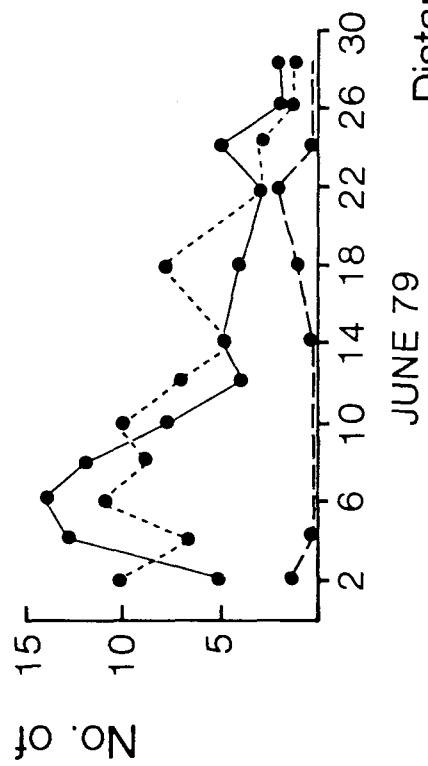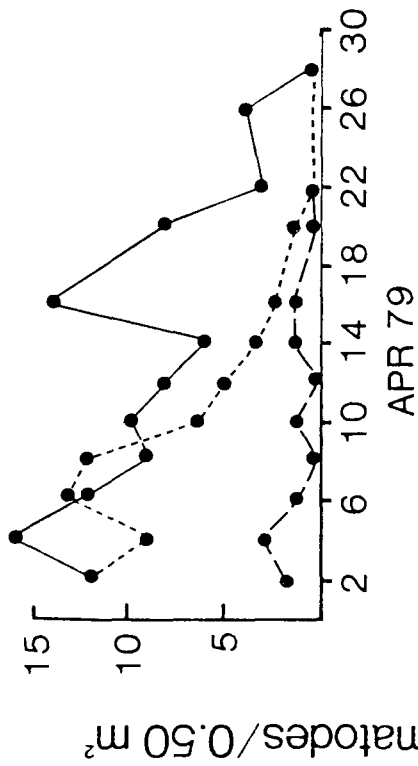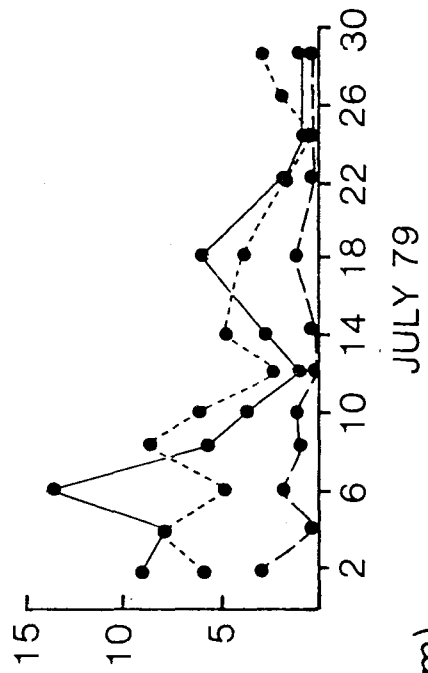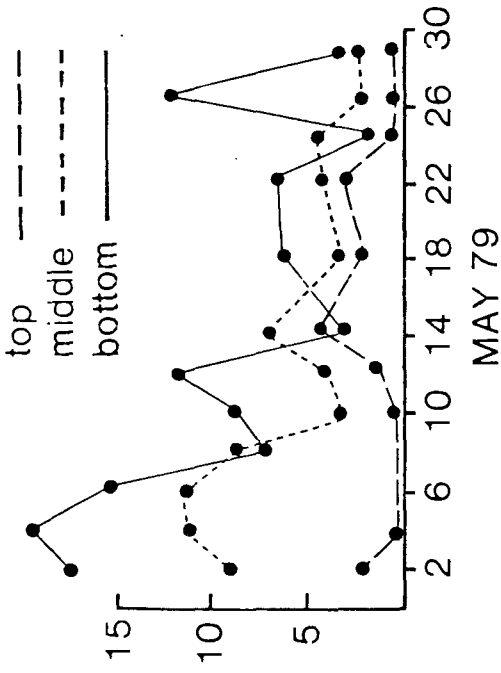
Fig. 19: Density of Monhystera disjuncta (nematodes/0.5 m^2) on top, middle and bottom blade samples of Macrocystis integrifolia along a depth transect for September and November 1979 (from deep to shallow depth).
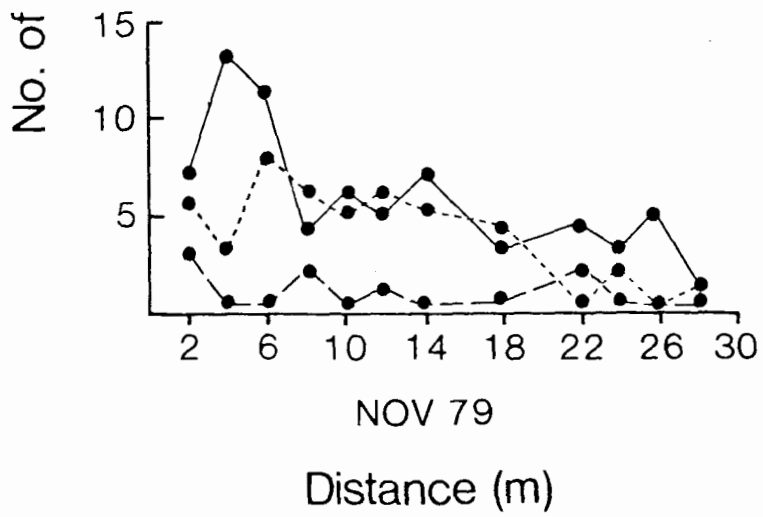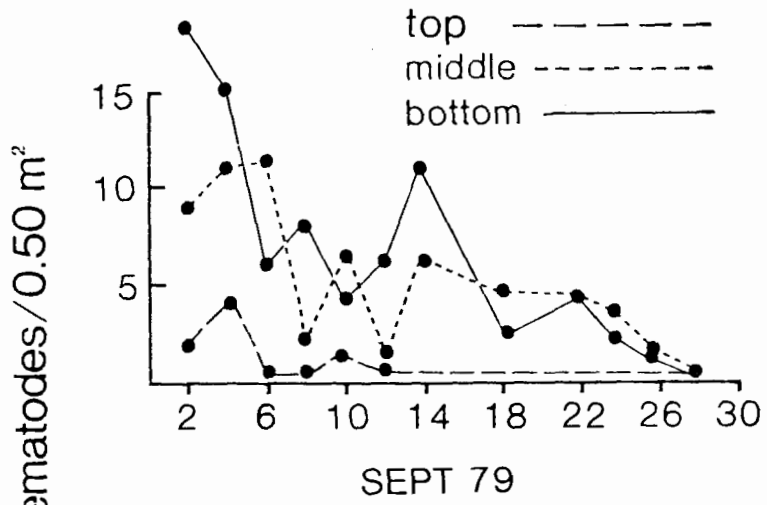
Fig. 20: Density of non-predominant nematode species (nematodes/0.5 m^2) on top, middle and bottom blade samples of Macrocystis integrifolia along a depth transect from July 1978 to October 1978. (from deep to shallow depth).
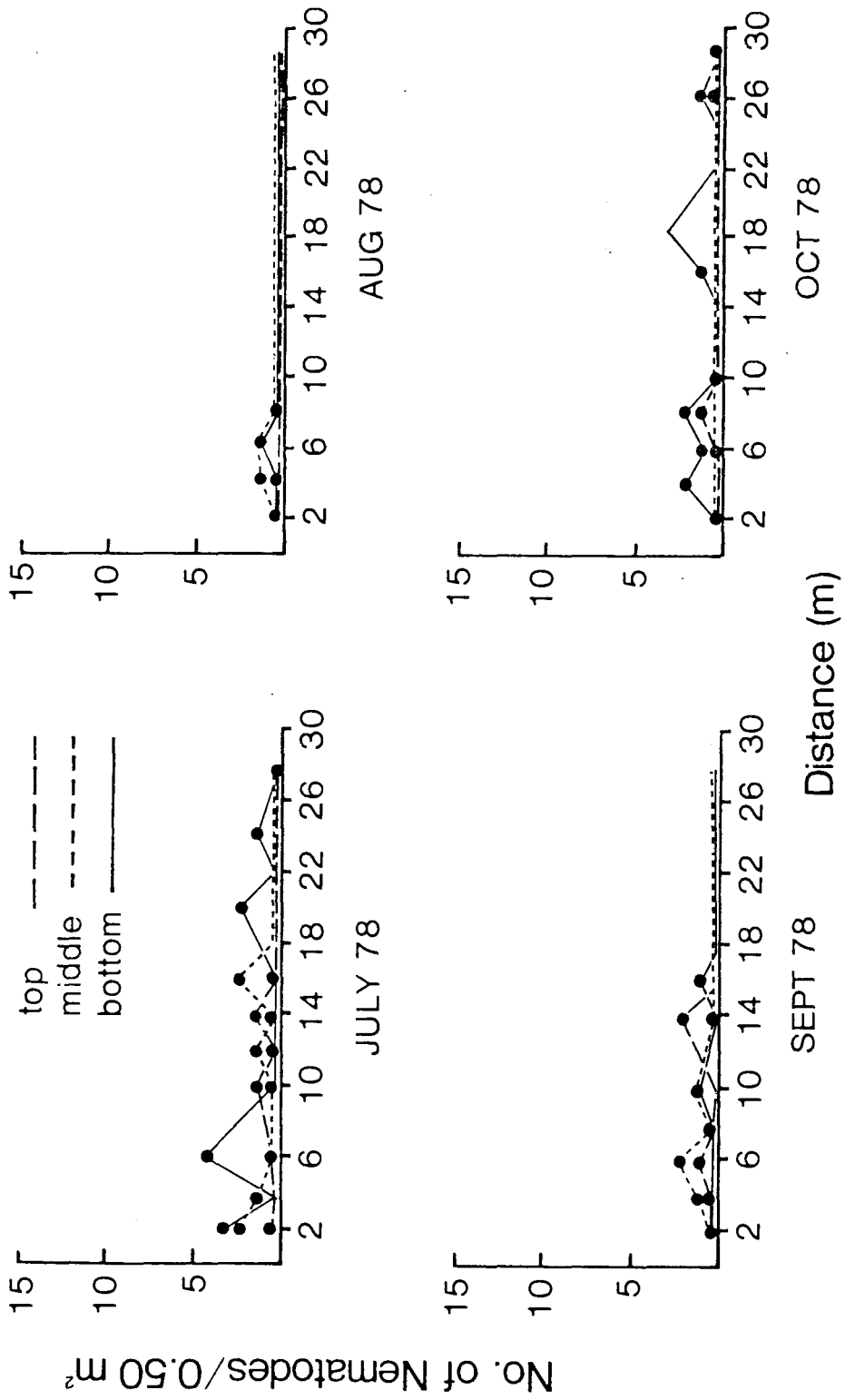
Fig. 21: Density of non-predominant nematode species (nematodes/0.5 m^2) on top, middle and bottom blade samples of Macrocystis integrifolia along a depth transect from November 1978 to March 1979 (from deep to shallow depth).
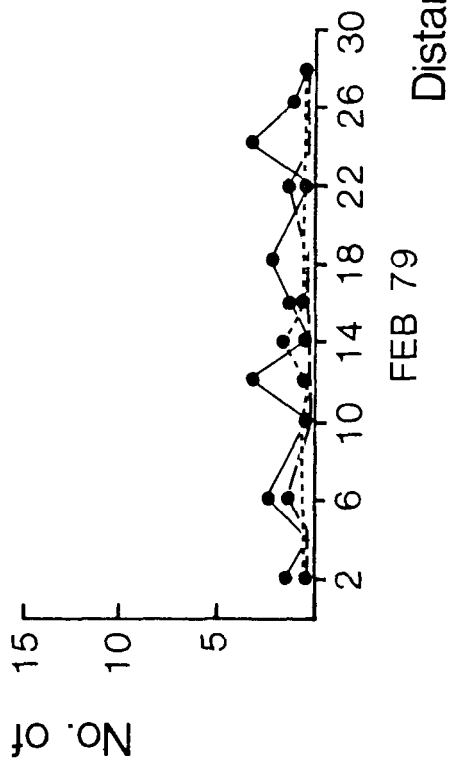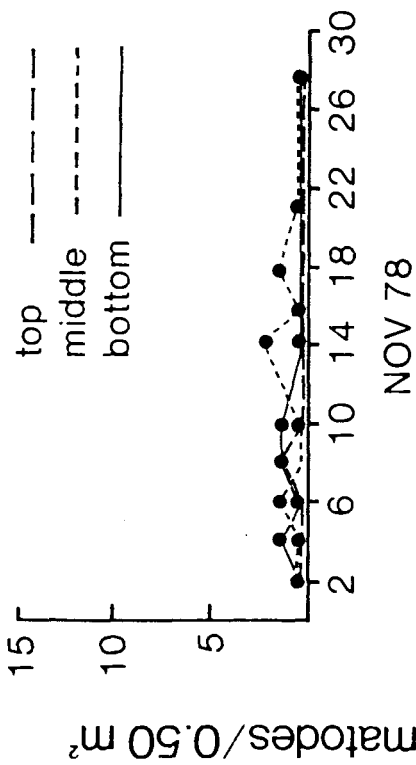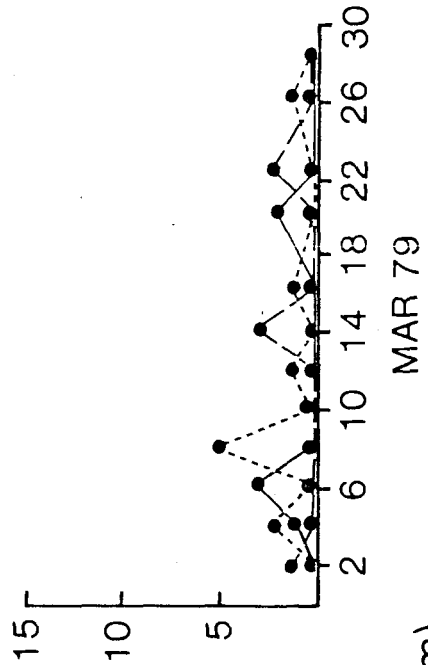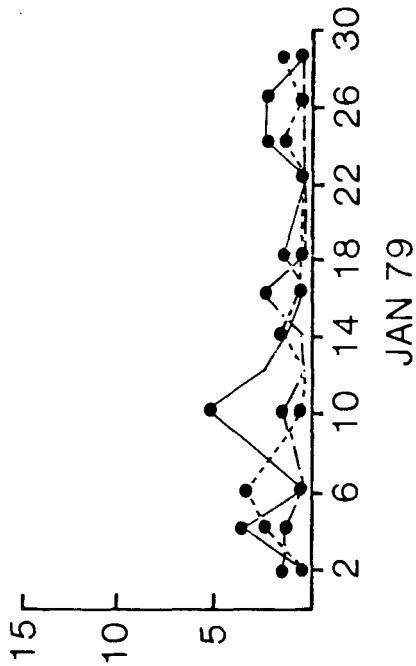
Fig. 22: Density of non-predominant nematode species
(nematodes/0.5 m^2) on top, middle and bottom blade
samples of Macrocystis integrifolia along a depth
transect from April 1979 to July 1979 (from deep
to shallow depth).
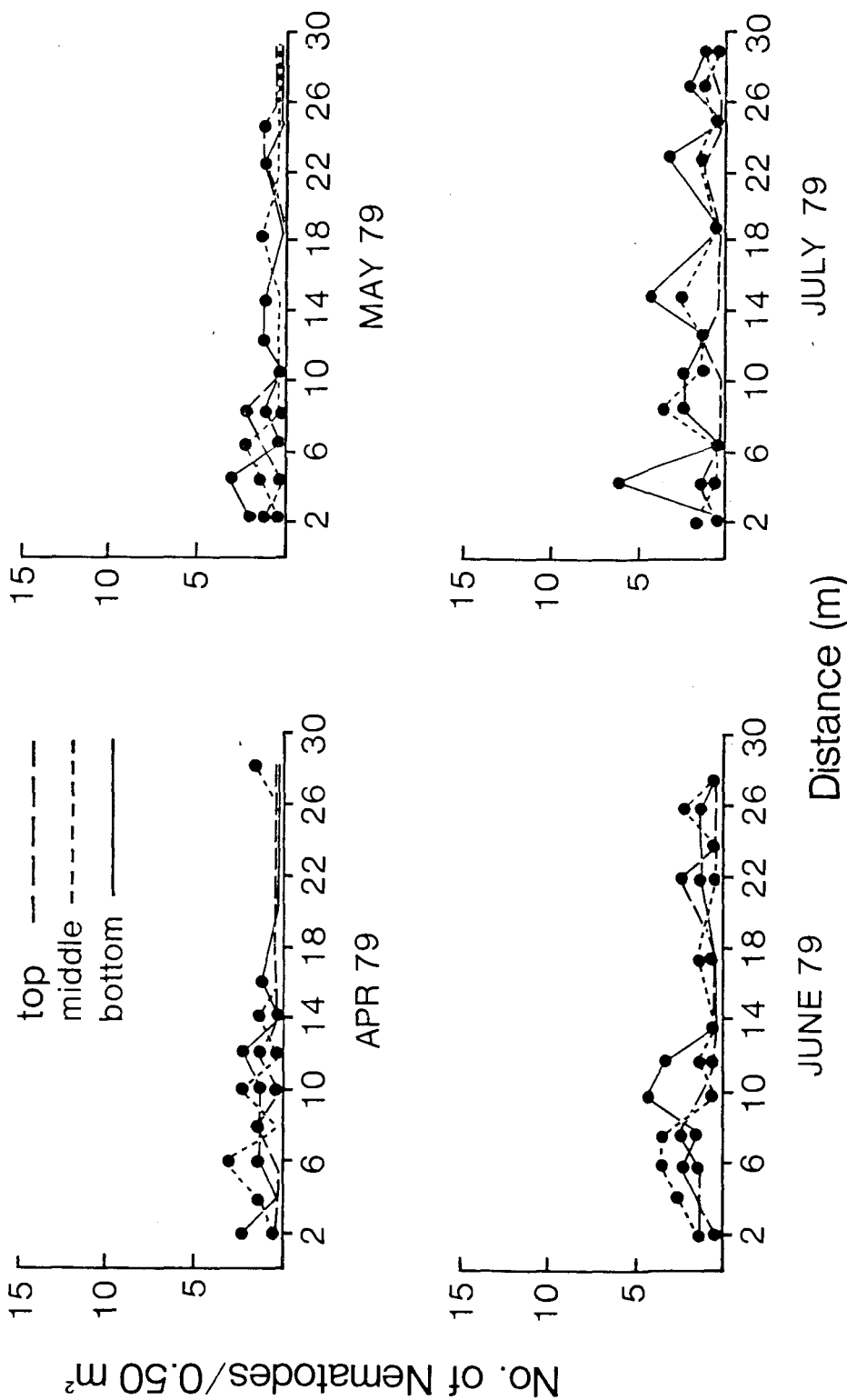
Fig. 23: Density of non-predominant nematode species
(nematodes/$0.5 \ m^2$) on top, middle and bottom
blade samples of Macrocystis integrifolia along
a depth transect for September and November 1979
(from deep to shallow depth).
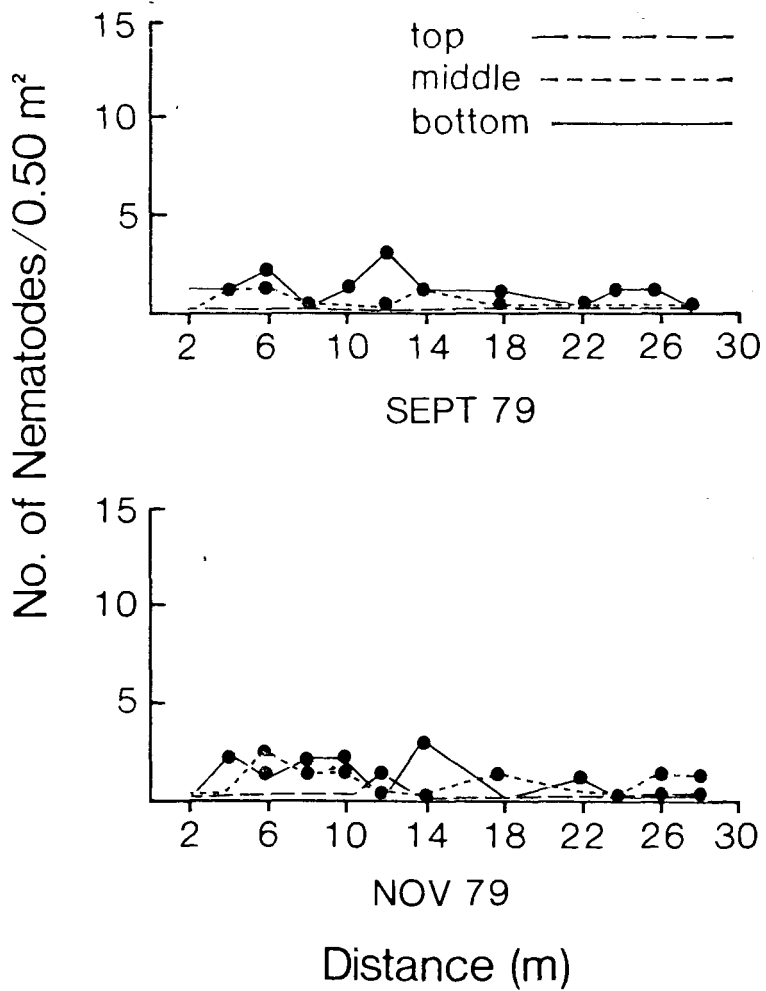
TABLE 6. Distribution of <u>Prochromadorella</u> <u>neapolitana</u> with reference to <u>Macrocystis</u> <u>integrifolia</u> blade position and depth F values for a grouped two-level ANOVA calculated on the number of nematodes/0.05m^2 for each sample month.

Month	Blade Position $F_{2,24}$	Significance	Depth $F_{3,24}$	Significance	Blade Position X Depth $F_{2,24}$	Significance
July, 1978	20.54	***	1.83	n.s.	0.30	n.s.
August	1.90	n.s.	0.63	n.s.	0.19	n.s.
September	0.50	n.s.	1.11	n.s.	1.24	n.s.
October	1.90	n.s.	1.17	n.s.	0.77	n.s.
November	9.02	***	0.63	n.s.	0.29	n.s.
December	-	-	-	-	-	-
Jan., 1979	6.12	**	0.12	n.s.	1.02	n.s.
February	8.05	**	3.37	n.s.	2.22	n.s.
March	3.47	*	1.54	n.s.	0.57	n.s.
April	3.31	n.s.	0.44	n.s.	0.08	n.s.
May	7.54	***	0.77	n.s.	1.06	n.s.
June	10.33	***	0.91	n.s.	0.14	n.s.
July	13.27	***	0.11	n.s.	1.18	n.s.
August	-	-	-	-	-	-
September	1.73	n.s.	1.55	n.s.	0.41	n.s.
October	-	-	-	-	-	-
November	6.27	**	1.14	n.s.	0.89	n.s.

*** P<0.005

TABLE 7   Distribution of <u>Monhystera</u> <u>refringens</u> with reference to
<u>Macrocystis</u> <u>integrifolia</u> blade position and depth F values for
a grouped two-level ANOVA calculated on the number of
nematodes/0.5m^2 for each sample month.

Month	Blade Position		Depth		Blade Position X Depth	
	$F_{2,24}$	Significance	$F_{3,24}$	Significance	$F_{2,24}$	Significance
July, 1978	5.75	**	0.20	n.s.	0.30	n.s.
August	11.46	***	0.64	n.s.	0.19	n.s.
September	15.97	***	2.84	n.s.	1.24	n.s.
October	21.25	***	1.34	n.s.	0.77	n.s.
November	6.37	**	0.61	n.s.	0.29	n.s.
December	-	-	-	-	-	-
Jan., 1979	6.68	***	1.05	n.s.	1.02	n.s.
February	16.22	***	3.33	*	2.22	n.s.
March	7.34	***	1.44	n.s.	0.57	n.s.
April	8.50	***	0.13	n.s.	0.08	n.s.
May	11.73	***	0.70	n.s.	1.06	n.s.
June	9.26	***	0.06	n.s.	0.14	n.s.
July	13.62	***	1.23	n.s.	1.18	n.s.
August	-	-	-	-	-	-
September	7.36	***	0.69	n.s.	0.41	n.s.
October	-	-	-	-	-	-
November	7.97	***	1.32	n.s.	0.89	n.s.

*** $P < 0.005$

TABLE 8.   Distribution of <u>Monhystera</u> <u>disjuncta</u> with reference to
<u>Macrocystis</u> <u>integrifolia</u> blade position and depth F values
for a grouped two-level ANOVA calcuated on the number
of nematodes/0.05m^2 for each sample month.

Month	Blade Position $F_{2,24}$	Significance	Depth $F_{3,24}$	Significance	Blade Position X Depth $F_{2,24}$	Significance
July, 1978	9.25	***	0.16	n.s.	0.62	n.s.
August	23.15	***	0.80	n.s.	0.75	n.s.
September	5.74	**	1.23	n.s.	0.84	n.s.
October	21.62	***	0.72	n.s.	0.33	n.s.
November	4.94	*	0.20	n.s.	0.38	n.s.
December	-	-	-	-	-	-
Jan., 1979	7.50	***	1.17	n.s.	1.42	n.s.
February	20.80	***	0.21	n.s.	0.30	n.s.
March	11.87	***	0.01	n.s.	0.17	n.s.
April	8.46	***	0.20	n.s.	0.06	n.s.
May	10.46	***	0.70	n.s.	0.27	n.s.
June	16.29	***	1.16	n.s.	1.02	n.s.
July	5.61	**	0.39	n.s.	0.13	n.s.
August	-	-	-	-	-	-
September	5.91	**	1.16	n.s.	0.22	n.s.
October	-	-	-	-	-	-
November	11.61	***	0.70	n.s.	0.89	n.s.

*** P<0.005

TABLE 9. Distribution of the three predominant nematode species with reference to Macrocystis integrifolia blade position and depth F values for an unreplicated three-level ANOVA calculated on the number of nematodes/0.5m² for each sample month.

Month	Blade Position $F_{2,52}$	Depth $F_{13,52}$	Nematode sp. $F_{2,52}$	Blade Position X Depth $F_{26,52}$	Blade Position X Nematode sp. $F_{4,52}$	Nematode sp. X Depth $F_{26,52}$
July, 1978	53.67 ***	4.50 ***	6.75 ***	1.37 n.s.	4.73 ***	1.40 n.s.
August	43.17 ***	3.05 ***	34.65 ***	0.89 n.s.	9.97 ***	0.81 n.s.
September	34.54 ***	6.44 ***	47.82 ***	1.40 n.s.	8.84 ***	2.75 ***
October	57.18 ***	1.98 *	55.12 ***	1.13 n.s.	12.11 ***	1.21 n.s.
November	28.88 ***	5.06 ***	12.69 ***	2.02 *	2.35	0.53 n.s.
December	-	-	-	-	-	-
January, 1979	10.10 ***	1.63	21.82 ***	0.95 n.s.	6.59 ***	1.31 n.s.
February	62.34 ***	3.00 ***	80.87 ***	1.68 n.s.	23.25 ***	1.84 *
March	39.27 ***	4.63 ***	56.44 ***	1.32 n.s.	15.45 ***	1.91 *
April	42.11 ***	6.03 ***	46.10 ***	1.52 n.s.	11.22 ***	2.40 ***
May	34.12 ***	4.00 ***	17.20 ***	1.33 n.s.	3.48 *	0.84 n.s.
June	62.37 ***	5.83 ***	0.54 n.s.	1.82 *	0.39 n.s.	0.72 n.s.
July	39.28 ***	5.03 ***	2.67 n.s.	1.20 n.s.	0.60 n.s.	0.65 n.s.
August	-	-	-	-	-	-
September	31.88 ***	5.93 ***	35.88 ***	1.47 n.s.	6.69 ***	2.86 ***
October	-	-	-	-	-	-
November	29.74 ***	2.91 ***	7.36 ***	0.83 n.s.	1.63 n.s.	0.71 n.s.

*** P≤0.005

The remainder of the year, mid and bottom blade samples had few individuals and there were very low or no individuals associated with the top blades (Figs. 12-15).

The distribution of P. neapolitana was similar to that of M. disjuncta and M. refringens for the months of July and November 1978 and May to July 1979 (Figs. 8-11). For the remainder of the year distribution was difficult to ascertain because of low numbers.

Distribution of the remaining nematode species is shown in Figures 20-23. However, due to their low numbers and to combined grouping of the species, no distribution trends on the blades could be confidently established.

DISCUSSION I

Although the area of nematode/algal associations is not well documented, published studies show that certain nematode taxa are commonly found in association with a variety of marine algae (Colman, 1940; Hopper, 1970; L'Hardy, 1962). All the fully identified nematode species recorded on the kelp in the present study have been recorded previously as being associated with algae (Wieser, 1953). The three most abundant nematode species have been recorded as being associated with algal species ranging from members of the Laminariales (Chitwood and Murphy, 1964; Moore, 1971, 1973a, 1973b; Wieser, 1952a) to Zostera marina (eelgrass) beds (Hopper and Meyers, 1967a, 1967b). The other species that have been recorded as seaweed associates include Araeolaimus elegans, Paracanthanchus sp., Anticoma acuminata and Oncholaimus dujardinii on Laminaria hyperborea (Moore, 1971) and O. dujardinii on turtle grass (Hopper and Meyers, 1967a) and some intertidal algae (Wieser, 1952b). The other two species, Chromadora nudicapitata and Chromadorina laeta have not been recorded as algal associates in any studies other than the Chilean survey by Wieser (1953). Generally, chromadorids appear to be the dominant group of nematodes associated with algae. In fact, Hopper and Meyers (1967a) found that two chromadorids, Chromadora macrolaimoides and Chromadorina epidemos Filipjev, in two separate Thalassia beds, comprised over 60% of the nematode

fauna. Wieser (1952b), studying the microfauna inhabiting intertidal seaweeds on rocky coasts, and Tietjen and Lee (1973), observing estuarine nematode populations on Enteromorpha intestinalis Link and Z. marina, found chromadorids to be the dominant group. Moore (1971, 1973a, 1973b) found that enoplids were predominant in the holdfasts of Laminaria hyperborea. In the present study on M. integrifolia, the chromadorids represented the largest single number of species, four of nine. However, the monhysterids were the most abundant.

Investigators have sometimes tried to associate nematode feeding strategies, based on Wieser's (1952) classifications, with nematodes found on marine algae. They have found that the epigrowth feeders are generally the dominant group (Hopper and Meyers, 1967a, 1967b; Tietjen and Lee, 1973). In the present study, chromadorids are considered to be equivalent to Wieser's (1952a) epigrowth feeders, the monhysterids equivalent to the nonselective feeders, the oncholaimid as omnivores and the araeolamids and anticomid as selective deposit feeders. As chromadorids are very abundant in algal habitats the dominance of the epigrowth feeding type is supported. Hopper and Meyers (1967b) found the epigrowth feeders to comprise 58% - 85% of the total nematode fauna. However, in the present study as monhysterids are the most abundant species on Macrocystis, there is an overall dominance of the

non-selective feeding type except during the summer months (see Figs. 4-6).

The most striking aspect of nematode distribution on the kelp is the marked seasonal differences in the nematode populations. In particular, the three most abundant species show distinct seasonal variations in their abundance (Figs. 4-6 and Tables 3-5). The most distinct pattern is exhibited by the chromadorid, P. neapolitana, which Wieser (1953) considered to be an epigrowth feeder. For most of the year, P. neapolitana ranges from 2% - 12% of the total nematode population but in the late spring, the population increases greatly to a maximum in mid-summer (see Fig. 4). The increase is characterized by the addition of substantially more juveniles and males. Hopper and Meyers (1967a) found similar results, in that populations of epigrowth feeders were lowest during the early spring and increased to a maximum during the summer.

Observations on two other chromadorids, Chromadora macrolaimoides and Chromadorina germanica Butschli, both associated with Enteromorpha intestinalis (L.) Link, exhibited their highest abundance during the early and mid-summer months respectively (Tietjen and Lee, 1973, 1977). Some researchers have suggested that these large increases in population of epigrowth feeders during the summer months may, in part, be associated to a corresponding increase in the epiflora, especially diatoms, which are a major food source for the species (Hagerman, 1966; Tietjen and Lee, 1973). It has

been suggested that the species diversity of the epiphytes
on the alga has a greater effect than does the specificity
of the nematodes on the alga itself (Hopper and Meyers,
1967a; Ott, 1967).

In addition to food availability, the influence of
temperature was probably an important parameter
affecting the reproductive potential of P. neapolitana.
Tietjen and Lee (1977a) observed that C. germanica had the
shortest generation times, 12-15 days, at 26 ^{O}/oo and 20-30 C.
Chromadorina germanica was most abundant in July and August
when the average temperature and salinity was 24 C and 25 ^{O}/oo
respectively. At temperatures below 20 C, the generation
time increased to nearly 100 days. It may be that the low
winter and spring temperatures in Dodger Channel lengthen
the generation time of P. neapolitana and thus, in part,
explain the low abundance levels.

The two monhysterids found in the M. integrifolia
blade samples exhibit different seasonal variations from
P. neapolitana. Both species are over 20% of the relative
abundance for most of the year, particularly M disjuncta
which was observed as high as 76% in January 1979. M.
disjuncta was the predominant species for most of the year
(Fig. 6, Table 5).

M. refringens was in greatest abundance during the
late summer and early fall (Fig.5, Table 4). Both monhy-
sterids have been classified as non-selective deposit
feeders (Chitwood and Murphy, 1964). Hopper and Meyers
(1967a) observed the increased abundance of non-selective

deposit feeders (Monhystera spp.) primarily in the spring. The seasonal abundance pattern described by Hopper and Meyers (1967a) closely fits my observations on M. disjuncta (see Fig. 6, Table 5). However, M. refringens did not correspond to this pattern and this may reflect different food preferences (see Section V).

M. disjuncta and M. refringens exhibited little variation in the male, female and juvenile population structure between July 1978 and November 1979, except for M. refringens during the early fall. However, as with P. neapolitana, temperature and salinity probably contribute to the variation in seasonal abundance. Observations by Gerlach and Schrage (1971) on the life cycle of M. disjuncta isolated from Laminaria in the North Sea, and reared at various temperatures correspond to my observations (Table 20) that the seasonality may be related to temperature (Zaika and Makarova, 1979). Generally, life cycles and generation times shorten with increasing temperature (Hopper et al., 1973).

Similar results were observed with another monhysterid, Monhystera denticulata Timm, isolated from Z. marina with the average generation time of 18 days at 26‰ and 15 C while it was 180 days at 5 C (Tietjen and Lee, 1972). M. refringens reflects quite well these trends. However, M. disjuncta exhibits a quite different response in the field. The data on M. disjuncta from the blade samples of Macrocystis indicated large numbers of this species occurring

throughout the year. This likely reflects the fact that little variation in the age' structure has been observed. The temperature and salinity effects on M. disjuncta generation times are not reflected in the field data.

All three major species exhibited the same general distribution pattern on the blades of M. integrifolia. Most nematodes were found in the bottom, fewer in the middle and very few or none in the top blade samples (see Figs. 8-23). Nematode numbers increased with water depth, particularily on the middle and bottom blades. Exceptions to this pattern were observed in the late winter and spring months for M. refringens and P. neapolitana and this was probably due to their reduced levels of abundance (Figs. 8-15). A variety of factors have been suggested that may affect distribution, namely algal shape, surface area, degree of encrustation and degree of silt or detritus deposits (Dahl, 1948; North, 1971; Ott, 1967; Wieser, 1952a, 1959c; Wing and Clendenning, 1971). In particular, increased levels of detritus cause large increases in nematode populations on heavily affected fronds (Wieser, 1952). Mukai (1971), studying epiphytic animals on Sargassum, observed large increases in nematode numbers in early spring which corresponded to the time of maximum degradation of the plant itself. Merrith (1973), studying deposit-feeding nematodes, observed the largest number of them to be at stations with the thickest layer of detritus. Wing and Clendenning (1971) observed that nematode populations were

much higher on blades of M. pyrifera that were totally
encrusted and deteriorating than on unencrusted, clean
growing blades. They also observed that the nematodes were
greatest on the deep rather than on the surface blades.
The deep blades are the oldest on the plant, and usually
carry the greatest amount of epiphytes (North,
1971). This is also true for M. integrifolia (Lobban, 1978;
Roland, 1980). Ott (1967) observed deposit feeders
to predominate   at the bases of two species of Cystoseria.
Also, monhysterids have been found to be good indicators on
an increased degree of sedimentation of detritus (Wieser,
1959). Hence, with a much more developed microenvironment
associated with the older blades of Macrocystis, which are
themselves the lower blade areas of the plant, and the
associated concentration of life forms associated with this
older tissue, then the distribution and seasonality of the
nematodes, particularly Monhystera spp., appear to be
closely tied.

RESULTS II

a)   Prochromadorella neapolitana

   i)   Summer conditions

Data for the "cafeteria" experiments are included in
Appendices 1-6 and the analyses are presented in Table 10
and 11.   Individuals of this species accumulated signifi-
cantly (P > 0.005) more around food wells than around the
non-food interwells or, around the wells of the control
plate.   Observations from the three experiments indicated
that P. neapolitana was attracted in greater numbers to
diatom   than to bacteria sources.   In experiment I,
nematodes accumulated in the greatest numbers and were
equally attracted to diatom species G. marina and R.
curvata.   Diatom species N. jamalinensis and S. tabulata
showed equivalent accumulations of P.
neapolitana.   Values obtained from wells containing
N. jamalinensis were very close to nematode numbers observed
from the control wells.

   In experiment II, almost 50% of the nematodes were
found   to accumulate in food wells containing C. scutellum.
Fewer nematodes accumulated around diatom species A.
longissipes and A. acutiuscula but did so equally ($\overline{X}$ = 19.0
and 16.75 respectively).   Nematode accumulations in food
wells containing G. olivaceum were not significantly
different from those around the control wells.   P.
neapolitana did not accumulate significantly more around any

TABLE 10. Total, male and female mean recruitment of Prochromadorella neapolitana to diatom and bacteria species (see Table 1) under simulated summer conditions

Expt N=4	Species	Total $\overline{X}$	Total S.D.	Male $\overline{X}$	Male S.D.	Female $\overline{x}$	Female S.D.
I	D1	37.00	8.60	19.50	6.61	17.50	4.51
	D2	32.25	6.85	14.50	2.89	17.75	8.22
	D3	5.50	3.70	3.75	2.75	1.75	0.96
	D4	12.00	5.10	6.25	3.59	5.75	3.10
II	D5	3.25	2.22	2.50	2.38	0.75	1.50
	D6	48.00	5.72	23.00	6.98	25.00	4.90
	D7	19.00	4.90	9.75	0.96	9.25	4.99
	D8	16.75	4.99	7.00	3.56	9.75	2.75
III	B1	4.00	2.94	1.50	1.73	2.50	3.70
	B2	2.75	2.06	1.50	1.30	1.25	1.89
	B3	15.75	3.95	9.75	2.63	6.00	1.83
	B4	3.75	2.87	1.50	1.73	2.25	2.87
I	Outside	3.00	2.31	1.50	1.73	1.50	0.58
II	Outside	4.25	0.50	2.25	1.71	2.00	1.41
III	Outside	64.00	12.03	29.50	4.65	34.50	9.18
I	Interwell	2.56	2.50	1.13	1.15	1.44	1.75
II	Interwell	2.19	1.28	1.38	1.20	0.81	0.91
III	Interwell	2.44	2.22	1.56	1.63	0.88	1.02
I	Control	4.75	2.92	3.00	2.39	1.75	1.67
II	Control	3.13	3.04	2.25	2.60	0.88	1.13
III	Control	3.63	3.66	2.38	2.26	1.25	1.58

TABLE 11. Analysis of attractiveness and preference of Prochromadorella neapolitana to diatom and bacteria species (see Table 1) using Chi-square, two-level ANOVA and Student-Newman-Keuls testing under simulated summer and winter conditions.

	Diatom sp. D1-D4		Diatom sp. D5-D8		Bacteria sp. B1-B4	
	Summer	Winter	Summer	Winter	Summer	Winter
$x^2_{1,2}$	3960.78 ***	2681.96 ***	3969.73 ***	2527.95 ***	238.58 ***	115.15 ***
2 Level ANOVA						
$F_{3,9}$ (Plate Effect)	0.12 n.s.	0.08 n.s.	0.12 n.s.	1.29 n.s.	0.38 n.s.	1.37 n.s.
$F_{3,9}$ (Food Effect)	18.17 ***	6.50 *	49.39 ***	44.13 ***	22.67 ***	17.01 ***
Student-Newman-Keuls Test	D3 D4 D1 D2	D3 D4 D2 D1	D5 D8 D7 D6	D5 D7 D8 D6	B2 B4 B1 B3	B4 B2 B1 B3

*** P<0.005

one of three species of bacteria (namely B1, B2 and B4) than around interwells and 'control wells. However, significantly more accumulated around species B3 than around control wells and this species attracted nematodes significantly more ($P > 0.005$) than the other three species. In general, males and females accumulated with equal facility at any of the food sources.

ii) Winter conditions

Data for the "cafeteria" experiments are included in Appendices 1-6 and the analyses are presented in Table 11 and 12. P. neapolitana exhibited the same overall pattern of accumulations around particular food wells as found under simulated summer conditions, with a few exceptions. This nematode accumulated to a greater degree in food wells with diatoms but the mean number of nematodes found in a particular food well was proportionally lower than under summer conditions. Also, the number of nema-todes not associated with any particular well, food or control, was higher than those observed under summer condi-tions.

In experiments II and III, the only difference from the observations under summer conditions were changes in the mean accumulation of nematodes in wells containing diatom species, A. longispes and A. acutiuscula and bacteria species B4 and B2. The male/female ratio of those nematodes attracted to food wells was approximately 1:1.

TABLE 12. Total, male and female mean recruitment of Prochromadorella
neapolitana to diatom and bacteria species (see Table 1)
under simulated winter conditions.

Expt N=4	Species	Total $\overline{X}$	S.D.	Male $\overline{X}$	S.D.	Female $\overline{X}$	S.D.
I	D1	27.50	6.56	12.00	4.97	15.50	5.80
	D2	23.50	6.61	11.75	5.12	11.75	5.44
	D3	7.50	4.65	3.75	1.94	3.75	5.56
	D4	14.25	6.80	8.75	5.06	5.50	3.87
II	D5	4.50	2.08	2.00	1.41	2.50	2.65
	D6	36.75	3.59	19.00	7.53	17.75	8.10
	D7	14.25	6.70	7.75	5.91	6.50	2.65
	D8	15.00	3.16	7.25	2.99	7.75	2.63
III	B1	3.25	2.63	1.50	0.58	1.75	2.22
	B2	2.50	1.00	1.75	0.96	0.75	0.96
	B3	12.75	4.11	4.75	2.87	8.00	3.56
	B4	2.00	1.41	1.00	0.00	1.00	1.41
I	Outside	18.75	4.57	8.50	6.24	10.25	1.89
II	Outside	18.25	7.68	7.75	3.86	10.50	9.00
III	Outside	71.25	2.87	35.25	1.71	36.00	4.08
I	Interwell	2.13	1.26	1.44	1.41	0.69	0.79
II	Interwell	2.81	2.10	1.56	1.31	1.25	1.48
III	Interwell	2.06	1.77	1.38	1.31	0.68	0.95
I	Control	4.13	2.90	2.13	2.30	2.00	1.60
II	Control	2.88	2.59	1.63	2.07	1.25	1.67
III	Control	3.25	1.58	1.75	1.67	1.50	0.93

b)   Monhystera refringens

   i)   Summer conditions'

Data for the "cafeteria" experiments are included in Appendices 7-12 and the analyses are presented in Table 13 and 14.   This nematode species exhibited an equal accumulation   to both diatom and bacteria food wells.   In all three experiments, M. refringens was observed to exhibit a significant (P > 0.005) accumulation of individuals in food wells when compared with control wells. In experiment I, higher nematode numbers were found in association with only diatom species S. tabulata.   In comparison, the remaining three diatom species had low mean accumulations of nematodes (G. marina = 10.5, R. curvata = 11.5 and N. jamalinensis = 14.0).   Nematode attraction to wells containing S. tabulata exhibited the highest mean accumulation ($\overline{X}$ = 40.0) in comparison to all three experiments.

In experiment II, M. refringens exhibited higher mean accumulations in wells with A. acutiuscula and A. longissipes (22.5 and 21.75 respectively) as compared to the accumulations in wells containing diatom species C. scutellum and G. olivaceum (15.0 and 9.25 respectively).   In comparison, the nematode was found to show no significant accumulations to any single diatom species.   When presented bacterial food sources, M. refringens was found to be equally attracted to bacteria species B2, B3 and B4 with a significantly lower mean accumulation in B1 food wells.   In general, none of the

TABLE 13.   Total, male and female mean recruitment of Monhystera
            refringens to diatom and bacteria species (see Table 1)
            under simulated summer conditions.

Expt N=4	Species	Total X̄	S.D.	Male X̄	S.D.	Female X̄	S.D.
I	D1	10.50	5.20	6.75	4.65	3.75	2.63
	D2	11.50	6.24	3.00	0.82	8.50	6.76
	D3	14.00	4.55	5.50	3.70	8.50	6.19
	D4	40.00	8.29	21.75	6.18	18.25	12.53
II	D5	9.25	3.10	6.25	4.79	3.00	2.16
	D6	15.00	6.98	7.50	2.74	7.50	6.56
	D7	21.75	9.36	7.25	4.11	14.50	11.00
	D8	22.25	6.85	12.75	7.14	9.50	6.24
III	B1	9.25	3.50	5.00	2.71	4.25	2.50
	B2	21.50	4.93	10.25	3.40	11.25	6.08
	B3	24.00	5.29	8.00	2.94	16.00	5.94
	B4	17.25	2.63	10.75	3.69	6.50	6.03
I	Outside	10.00	3.37	7.00	2.45	3.00	1.41
II	Outside	12.50	2.65	6.50	3.87	6.00	4.24
III	Outside	13.00	3.92	8.00	3.74	5.00	3.46
I	Interwell	3.50	2.80	1.50	1.26	2.00	2.19
II	Interwell	4.81	2.40	2.44	1.79	2.38	2.06
III	Interwell	3.75	3.07	2.00	2.28	1.75	1.61
I	Control	3.25	3.11	2.00	2.51	1.25	1.49
II	Control	3.50	2.14	1.50	1.69	2.00	2.00
III	Control	4.50	3.21	2.38	2.07	2.13	2.30

TABLE 14. Analysis of attractiveness and preference of Monhystera refringens to diatom and bacteria species (see Table 1) using Chi-square, two-level ANOVA and Student-Newman-Keuls testing under simulated summer and winter conditions.

	Diatom sp. D1-D4		Diatom sp. D5-D8		Bacteria sp. B1-B4	
	Summer	Winter	Summer	Winter	Summer	Winter
$X^2_{1,2}$	3017.22 ***	2317.41 ***	2480.77 ***	2317.41 ***	2691.98 ***	1854.0 ***
2-Level ANOVA						
$F_{3,9}$ (Plate Effect)	0.10 n.s.	0.19 n.s.	0.06 n.s.	0.37 n.s.	0.32 n.s.	0.50 n.s.
$F_{3,9}$ (Food Effect)	15.83 ***	13.39 ***	2.42 n.s.	3.92 n.s.	7.98 **	2.88 n.s.
Student-Newman-Keuls Test	D1 D2 D3 D4	D3 D1 D2 D4	D5 D6 D7 D8	D5 D7 D6 D8	B1 B2 B3 B4	B1 B2 B3 B4

*** P<0.005

TABLE 15. Total, male and female mean recruitment of Monhystera
refringens to diatom and bacteria species (see Table 1)
under simulated winter conditions.

Expt N=4	Species	Total X̄	S.D.	Male X̄	S.D.	Female X̄	S.D.
I	D1	13.25	5.12	6.50	4.65	6.75	2.99
	D2	15.25	4.92	7.50	3.70	7.75	2.87
	D3	11.75	3.59	5.00	3.56	6.75	1.89
	D4	33.00	5.48	17.00	9.35	16.00	4.08
II	D5	11.25	4.79	6.50	7.33	4.75	2.63
	D6	19.25	3.95	6.50	3.32	12.75	3.50
	D7	16.75	6.65	11.75	7.41	5.00	2.16
	D8	20.50	5.00	8.50	4.36	12.00	6.48
III	B1	9.50	4.93	5.00	3.56	4.50	2.65
	B2	20.00	8.04	11.50	7.60	8.50	5.57
	B3	19.75	6.85	8.75	2.50	11.00	7.87
	B4	11.50	3.11	5.25	2.50	6.25	4.43
I	Outside	19.75	3.30	9.75	6.70	10.00	4.97
II	Outside	22.50	5.00	10.75	11.56	11.75	7.93
III	Outside	25.00	6.06	12.25	6.60	12.75	7.14
I	Interwell	1.75	1.06	1.06	0.85	0.69	0.95
II	Interwell	2.38	1.41	1.50	1.37	0.88	1.20
III	Interwell	3.56	1.79	1.81	1.60	1.75	1.73
I	Control	4.13	2.70	2.38	2.20	1.75	1.49
II	Control	2.25	1.67	1.125	0.99	1.125	1.25
III	Control	3.50	2.20	1.50	1.60	2.00	2.20

nematode accumulations in food wells was as low as those
found in the control wells. The male/female ratio of the
attracted nematodes was approximately 1:1.

ii)   Winter conditions

Data for the "cafeteria" experiments are included in
Appendices 7-12 and the analyses are presented in Table 14
and 15.   In experiments I and II, this nematode exhibited a
similar display of accumulation compared with summer except
that relatively fewer nematodes occurred in the food wells
and more of them occurred outside any particular well.
In experiment II, the mean number of nematodes in wells with
C. scutellum increased.   Nematode accumulations in A.
longissipes were observed to decrease.   In experiment III,
the mean accumulation of nematodes in all four bacteria
wells were not significantly different from each other.   A
1:1 ratio with respect to male/female accumulations in
wells was observed in all experiments.

c)   Monhystera disjuncta

i)   Summer conditions

Data for the "cafeteria" experiments are included in
Appendices 13-18 and the analyses are presented in Table 16
and 17.   In all three experiments, nematodes accumulated
in significant numbers (P < 0.005) in the food wells.   M.
disjuncta showed a marked attraction to bacteria as compared
to diatoms.   In experiment I, M. disjuncta exhibited a low
response to all diatom species except S. tabulata in which

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TABLE 16.   Total, male and female mean recruitment of Monhystera
            disjuncta to diatom and bacteria species (see Table 1) under
            simulated summer conditions.

Expt N=4	Species	Total $\overline{X}$	S.D.	Male $\overline{X}$	S.D.	Female $\overline{X}$	S.D.
I	D1	9.75	4.43	5.50	4.36	4.25	2.50
	D2	5.00	2.94	1.00	0.82	4.00	3.27
	D3	7.75	4.99	5.25	2.87	2.50	3.00
	D4	21.75	6.08	12.25	6.70	9.50	5.57
II	D5	8.75	3.30	5.25	3.31	3.50	3.00
	D6	9.50	5.45	7.25	5.00	2.25	1.26
	D7	0.50	0.58	0.25	0.50	0.25	0.50
	D8	5.50	2.52	3.00	4.08	2.50	2.38
III	B1	18.00	5.90	7.50	6.60	10.50	1.30
	B2	19.25	3.86	8.50	4.93	10.75	5.62
	B3	27.75	7.27	19.25	5.44	8.50	4.51
	B4	14.75	2.63	6.25	2.06	8.50	1.91
I	Outside	45.50	19.23	20.00	15.01	25.50	10.41
II	Outside	63.00	6.27	25.25	3.59	27.75	5.50
III	Outside	9.75	4.27	3.75	2.50	6.00	3.37
I	Interwell	2.56	2.16	1.50	1.46	1.06	1.53
II	Interwell	3.19	2.56	2.25	2.18	0.94	1.12
III	Interwell	2.63	1.78	1.19	0.66	1.44	1.55
I	Control	2.38	2.33	2.00	2.14	0.38	0.52
II	Control	3.38	2.83	2.00	2.07	1.38	1.41
III	Control	4.00	2.00	2.50	1.31	1.50	1.93

Table 17. Analysis of attractiveness and preference of Monhystera disjuncta to diatom and bacteria species (see Table 1) using Chi-square, 2 level ANOVA and Student-Newman-Keuls testing under simulated summer and winter conditions.

	Diatom sp. D1-D4		Diatom Sp. D5-D8		Bacteria Sp. B1-B4	
	Summer	Winter	Summer	Winter	Summer	Winter
$\chi^2_{1,2}$	875.22 ***	698.23 ***	213.53 ***	311.31***	3301.74 ***	2474.85 ***
2 level ANOVA						
$F_{3,9}$ (Plate Effect)	4.94 *	0.20 n.s.	0.41 n.s.	0.81 n.s.	0.63 n.s.	1.04 n.s.
$F_{3,9}$ (Food Effect)	19.24 ***	2.92 n.s.	4.85 *	1.70 n.s.	4.08 *	2.95 n.s.
Student-Newman-Keuls Test	D2 D3 D1 D4	D2 D3 D1 D4	D7 D8 D5 D6	D7 D5 D6 D8	B4 B1 B2 B3	B4 B1 B2 B3

*** P<0.005

the relatively high accumulations were later attributed to
bacterial contamination.

The accumulations of nematodes in the food wells
containing diatom species of experiment II (see Table 1)
were even lower than the values observed in experiment I.
The mean number of nematodes found in the wells containing
A. longissipes and A. acutiuscula had values comparable to the
control wells. The mean number of nematodes outside the
wells was relatively high ($\overline{X}$ = 63.0) compared to the other
two nematode species. In experiment III, the majority of
the nematodes were found to accumulate in the wells with rod-
shaped (B1 and B3) rather than with coccoid bacteria (B2 and
B4).

Data and analyses for the two additional "cafeteria"
experiments are presented in Appendices 19-20 and Table 18
respectively. The results indicated, as observed above, a
higher accumulation of nematodes in wells containing rod
as opposed to coccoid bacteria. The male/female ratio in
all experiments was approximately 1:1.

ii) Winter conditions

Few nematodes were attracted to diatom food sources
as measured by the accumulations at the food wells (Tables
17 and 19). The number of individuals not in food wells
was high. In experiments I and II, none of the diatom
sources showed any significant accumulations. In experiment
III, M. disjuncta showed a reduced response to bacterial
sources, such that it accumulated with relatively equal

TABLE 18. Total, male and female mean recruitment of <u>Monhystera</u>
<u>disjuncta</u> to rod and coccoid bacteria species (see Table 1)
under simulated summer conditions.

Expt N=8	Species	Total $\overline{X}$	S.D.	Male $\overline{X}$	S.D.	Female $\overline{X}$	S.D.
IV	B1	16.25	5.52	7.62	3.11	8.63	6.57
	B3	25.13	10.02	13.63	5.32	11.50	8.97
V	B2	14.75	5.68	9.38	5.90	5.37	2.96
	B4	10.63	6.28	5.25	3.37	5.38	4.34
IV	Outside	8.75	5.12	3.50	3.51	5.25	4.43
V	Outside	39.50	12.45	15.00	7.75	24.50	11.27
IV	Interwell	1.81	1.52	0.56	0.73	1.25	1.18
V	Interwell	2.44	2.00	1.44	1.03	1.00	1.86
IV	Control	3.38	4.69	2.38	3.07	1.00	1.77
V	Control	2.25	1.98	1.25	1.49	1.00	1.60

TABLE 19.   Total, male and female mean recruitment of Monhystera
             disjuncta to diatom and bacteria species (see Table 1) under
             simulated winter conditions.

Expt N=4	Species	Total X̄	Total S.D.	Male X̄	Male S.D.	Female X̄	Female S.D.
I	D1	10.50	7.19	4.50	2.87	6.00	4.83
	D2	5.75	3.50	3.75	3.59	2.00	2.00
	D3	6.25	4.57	3.50	3.51	2.75	1.89
	D4	17.25	6.24	6.75	6.29	10.50	7.00
II	D5	7.50	4.80	5.50	4.36	2.00	2.16
	D6	8.25	4.65	4.25	3.20	4.00	4.24
	D7	3.00	0.82	2.00	2.00	1.00	0.82
	D8	9.25	4.79	3.25	2.99	6.00	2.71
III	B1	16.25	4.79	7.75	5.06	8.50	2.89
	B2	18.00	3.83	8.50	3.70	9.50	3.32
	B3	22.75	6.80	10.50	2.52	12.25	5.85
	B4	12.75	3.30	5.25	3.77	7.50	5.20
I	Outside	47.75	6.50	24.75	2.75	23.00	8.37
II	Outside	58.50	14.20	28.25	5.74	30.25	8.77
III	Outside	18.50	8.74	10.50	6.34	8.00	4.97
I	Interwell	3.13	2.00	1.69	1.45	1.44	1.09
II	Interwell	3.38	3.03	1.69	2.09	1.69	1.82
III	Interwell	2.94	1.34	1.88	1.09	1.06	1.06
I	Control	2.50	2.33	0.75	0.71	1.75	1.91
II	Control	4.50	3.16	1.75	1.04	2.75	3.37
III	Control	3.38	2.26	1.63	1.19	1.75	2.19

attraction to all four bacteria species. Also, the mean
number of nematodes outside any particular well was
significantly greater than summer condition values. As
seen in all previous experiments, a 1:1 ratio of male/
female accumulations was observed in the food wells.

d)   Life Cycle Observations on Monhystera disjuncta

   M. disjuncta was the only one of the three species to
reproduce continuously in culture. P. neapolitana was
never observed to reproduce and so cultures could be main-
tained only by the continual supplement with new individuals.
M. refringens was observed only once to reproduce and so
the observations are scant and inconclusive.

   Observations on the life cycle of five female M.
disjuncta (A-E) and their progeny (N) are summarized in
Table 20. Under environmental conditions of 10 C ± 1 C,
30.8‰ and a 16/8 h day/night cycle, the mean number of days
from egg deposition of the original female to egg deposition
of the progeny was 23.25 days. A breakdown of this turnover
time indicates that on average 4.3 days were required from
egg deposition to hatching, 14.1 days from hatching to the
appearance of recognizable sexual characteristics and a
further 4.3 days for the appearance of the first egg in the
uterus. Development of the egg to its deposition was
observed to take an average of 2.3 days. Females
deposited, on the average, 14.4 eggs.

TABLE 20. Duration of development and generation time (in days) of Monhystera disjuncta in cultures maintained under simulated summer conditions.

		N=5 A	N=5 B	N=4 C	N=5 D	N=3 E	Mean
I	Development of eggs (egg deposition- hatching)	3-4 (3.5)	5-6 (5.5)	1-2 (1.5)	3-4 (3.5)	7-8 (7.5)	4.3
II	Postembryonic development (hatching - recognizable sexual characteristics)	13-14 (13.5)	12-13 (12.5)	14-15 (14.5)	14-15 (14.5)	15-16 (15.5)	14.1
III	Maturation (development of sexual characteristics - 1st egg in uterus)	2-3 (2.5)	3-4 (3.5)	3-4 (3.5)	4-5 (4.5)	7-8 (7.5)	4.3
IV	Development of eggs in uterus (1st egg in uterus - egg deposition)	1-2 (1.5)	2-3 (2.5)	2-3 (2.5)	2-3 (2.5)	-	2.25 (N=4)
	I + II + III	19-22 (20.5)	20-23 (21.5)	18-21 (19.5)	21-24 (22.5)	29-32 (30.5)	22.9
	I + II + III + IV	20-24 (22)	22-26 (24)	20-24 (22)	23-27 (25)	-	23.25 (N=4)
	Egg number	15	19	18	12	8	14.4

DISCUSSION II

Very little detail is known of the microbiological assemblages found on macrophytic algal species. Some researchers have endeavoured to characterize these relationships under laboratory conditions and extrapolate the results so as to understand subsequent field observations.

A variety of techniques have been developed to culture marine nematodes and their food sources (Lee and Muller, 1975; Tietjen et al., 1970). Some studies have tried to characterize feeding preferences by way of gut contents (Jennings and Colman, 1970) but this has proved to be unsuccessful as researchers have found nematodes to exhibit both selective ingestion and digestion (Meyers and Hopper, 1966; Tietjen and Lee, 1977b: Viglierchio et al., 1969).

The three dominant species in this study were cultured and subjected to food preference testing using a technique modified from Lee et al. (1977). The nematodes were exposed to eight diatom and four bacteria species isolated from M. integrifolia blades. The eight diatom species were all identified as benthic types (Lee et al., 1975; Rao and Lewin, 1976) and five of the species had previously been identified as associates of M. integrifolia (see Table 1) (Roland, 1980).

Each nematode species exhibited some distinct food preferences. P. neapolitana, classified as an epigrowth

feeder, selected primarily for diatom species, in particular, Cocconeis scutellum, Gramatophora marina, and Rhoicosphenia curvata (see Tables 10-13). The preferential response of P. neapolitana for bacteria was little different from the controls except for the rod-shaped bacteria species, B3. Chromadorina germanica responds similarly in that it is attracted to varying degrees to a variety of diatom species but only to one bacterium to any extent (Tietjen and Lee, 1977; Lee et al., 1977). Chromadora macrolaimoides was observed to effectively utilize eleven of the twenty species of microalgae presented but only five species were able to sustain growth indefinitely (Tietjen and Lee, 1973). Calorific content of the algae does not appear to be a factor governing food preference selection in nematodes but selective digestion and ingestion are evident such that a selective diet in conjunction with a particular set of digestive enzymes may, in fact, dictate selection (Tietjen and Lee, 1977b).

The monhysterids, M. disjuncta and M. refringens, though both classified as non-selective deposit feeders, exhibited different feeding preferences from each other. M. disjuncta preferred particular species of bacteria rather than diatoms (see Table 18-22). Except for one species of diatom, Synedra tabulata, which was later found to be contaminated with bacteria, this nematode species showed no detectable pattern in relation to diatom food sources. Studies on Rhabditis marina, a bactivorous species,

indicated that it avoided some species of diatoms but otherwise was randomly distributed on both control and experimental plates (Lee et al., 1977). Food size was a significant factor for bactivorous nematodes (Tietjen and Lee, 1977). Hence, all the diatom species may well have been too large for M. disjuncta to successfully ingest.

M. refringens was observed to be attracted to both particular species of diatoms and bacteria (see Tables 14 - 17). However, M. refringens appears to be much more of a generalist than does M. disjuncta in its feeding preferences. Both species ingested rod and coccoid bacteria but the rod-shaped species were preferred over the coccoid forms.

Rhabditis marina fed heavily on Pseudomonas sp. and Flavobacterium sp., both rod bacteria, over the coccoid species, Micrcoccus sp. (Lee et al., 1970). Wilt et al. (1973) found that bacteriophagus nematodes preferentially migrated and fed on Vibrio sp. (rod) under various conditions. Comparison of the feeding strategies of two bacteria feeding nematodes showed them to be highly selective for particular bacterial species, primarily rod forms (Tietjen, 1967, 1969).

Thus, if all marine nematodes are as selective as the three predominant species from this study, then spatial and

seasonal variations in the abundance of microorganisms may account for variations in abundance and distribution (Lee et al., 1977; Tietjen and Lee, 1973, 1977b). However, caution must be used because data from such laboratory studies are not directly applicable to feeding conditions in the field because of different nutrient values of food sources, growth and reproduction rates, feeding rates (Duncan et al, 1974) and alternate feeding sources (Chia and Warwick, 1970; Tietjen and Lee, 1975).

However, food is still likely to be a main contributing factor governing the population dynamics of nematode species under field conditions (Schiemer et al., 1980).

GENERAL DISCUSSION

This study has contributed to our understanding of the spatial and temporal distribution of nematodes living on M. integrifolia and has initiated our appreciation of microbial food chains involved in the nutrition of these animals.

From the previous sections, the three dominant nematode species isolated from the blades of M. integrifolia exhibited distinctive patterns of abundance and distribution and specific feeding preferences on the epiflora associated with the blades of this kelp. From these observations and previous studies, a possible explanation of the variations observed for these three nematode species may be derived.

From Roland's (1980) study on the per cent occurrence of several diatom taxa on M. integrifolia blades and the feeding preference data from this study, it appears that the observed seasonal and spatial distributions of the three predominant nematode species may be related to the variation in availability of particular food sources. Kita and Harada (1962) observed that the abundance of animals on Zostera blades was related to the abundance of epiphytes and microalgae. P. neapolitana appears to prefer the diatom species C. scutellum (Tables 10-12). This diatom species occurs in high levels of abundance in April to July which is the time of increasing abundance of P. neapolitana (Fig. 4). The large decrease in the relative

occurrence of this diatom species in August corresponds
with the decreased abundance of P. neapolitana. The in-
creased per cent occurrence of the diatom Rhoicosphenia
curvata in October may be an explanation for the sudden
increase in P. neapolitana numbers found in the November
samples. P. neapolitana was observed to concentrate when
in high abundance in the bottom blades. Roland (1980) found
higher percentages of occurrence of diatoms on top blades
with smaller densities in subsequently lower blades of M.
integrifolia. It may be that only a particular level of
food availability can effectively maintain a large popula-
tion of this species. Above this level, the nematode
abundance does not alter substantially. Also, Roland's
(1980) study did not sample to the depth of senescent
blades, which are primarily the bottom blades and, hence,
the per cent occurrence of the food sources are unknown.
P. neapolitana showed little or no preference for bacteria
and thus did not utilize this food source though
Roland (1980) found that both the rod and coccoid
bacteria froms on the blades of Macrocystis exhibited no
seasonality.

In contrast, the high relative abundance of M. disjuncta
may, in part, be related to this unlimited unvaried
seasonality of the bacteria. Studies have indicated that
nematode numbers are directly related to decreases and
increases in bacteria population levels (Boucher and Chamroux,

1976; Chamroux et al., 1977). Thus, with M. disjuncta's
preference for bacteria, primarily the rod forms, and
little association with diatom species, the observed high
abundance of this species, in conjunction with its short
generation time, may explain its seasonal distribution. Many
investigators have observed large bacterial populations
associated with seaweed species and most have found the
bacteria in highest abundance on the older and deteriorating
parts of the plant and to be primarily of the rod type
(Kong and Kwong-yu Chan, 1979; Laycock, 1974; Mazure and
Field, 1980). Also, most investigators on nematode feeding
preference have observed the selective and non-selective
deposit feeders to survive and reproduce more readily on
rod-shaped bacterial sources (Hopper and Meyers, 1967a;
Tietjen, 1967; Tietjen and Lee, 1973, 1977b). Therefore,
the high abundance of M. disjuncta throughout the year and
on the older blades of Macrocystis may, in a good part, be
related to the bacterial populations. Studies have shown
that epiphyte population encrustations tend to increase
with tissue age (Ballantine, 1979; North, 1978) and that
most nematodes are found associated with deteriorating
heavily encrusted blades (Wing and Clendenning, 1971).
Thus, the relation between these two factors may contribute
substantially to nematode abundance and distribution.

M. refringens shows a more complex interaction between
food availability and abundance. In the food preference
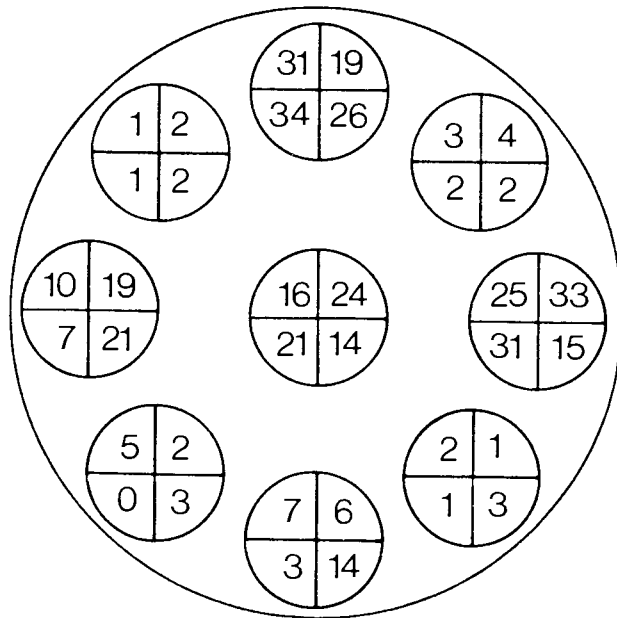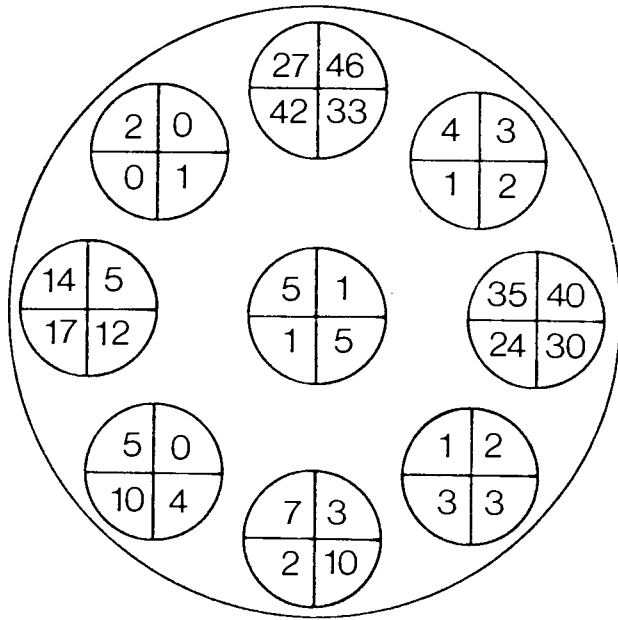experiments, M. refringens is preferentially associated with

both particular diatom and bacteria species (Tables 13-15).

Its most preferred diatom species, _Synedra tabulata_, is at

its greatest abundance during late summer and fall (Roland,

1980). This corresponds to the observed increases in

abundance of _M. refringens_ that reached their highest levels

in the fall. The remainder of the diatoms presented to

M. refringens reflected fairly similar responses of

attraction. These diatoms predominate primarily in the

mid- and late summer but in relatively low per cent

occurrence. The only exception is _Cocconeis scutellum_, which

was most abundant during mid-summer and was the preferred

food of _P. neapolitana_. In contrast, _M. refringens_ was

attracted to _C. scutellum_ only moderately and showed

little associated response to it in the field. With

respect to bacteria, _M. refringens_ exhibited almost the

same response as _M. disjuncta_ in terms of preference but

not to the same degree. As a result, the variations in

abundance of _M. refringens_ may be in part related to the

diatom food sources but its higher relative abundance

compared to _P. neapolitana_ through the year may be related

to its partial affinity for bacterial food sources.

Thus, if marine nematodes are as selective in their

feeding habits as this and other studies have indicated, then

spatial and temporal variations in the abundance of epiphytic

microorganisms could account for the spatial and seasonal

variations in abundance of marine nematodes. Hence,

selective feeding by different nematodes on different food sources may reduce or perhaps even eliminate competition for a few chosen food sources. This would enable cohabitation of a small area, like algal blades, by a variety of nematode species which, on the basis of buccal morphology, would appear to feed on the same foods. This may be the case for M. disjuncta and M. refringens and the dominance of species types with the epigrowth feeding classification. Thus quantification or even precise definition of competitive interactions between marine nematodes in relation to preferred food sources in association with seaweeds should be pursued.

APPENDICES

Appendix 1:   Selective accumulation of *Prochromadorella* *neapolitana* to alternating wells of diatom species D1-D4 (see Table 1). Diagram records four replicates for each condition.

Top figure (nine quartered circles):

- 2 | 0 / 0 | 1
- 27 | 46 / 42 | 33
- 4 | 3 / 1 | 2
- 14 | 5 / 17 | 12
- 5 | 1 / 1 | 5
- 35 | 40 / 24 | 30
- 5 | 0 / 10 | 4
- 7 | 3 / 2 | 10
- 1 | 2 / 3 | 3

Bottom figure (nine quartered circles):

- 1 | 2 / 1 | 2
- 31 | 19 / 34 | 26
- 3 | 4 / 2 | 2
- 10 | 19 / 7 | 21
- 16 | 24 / 21 | 14
- 25 | 33 / 31 | 15
- 5 | 2 / 0 | 3
- 7 | 6 / 3 | 14
- 2 | 1 / 1 | 3

Appendix 2: Accumulation of Prochromadorella neapolitana
to control wells.
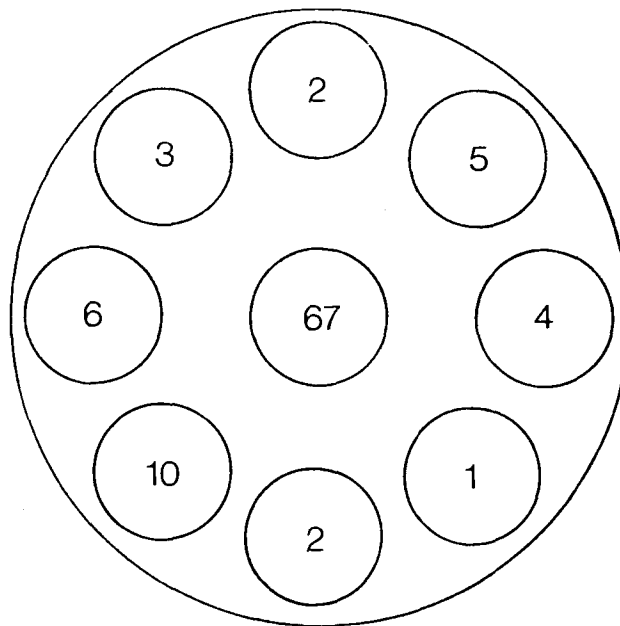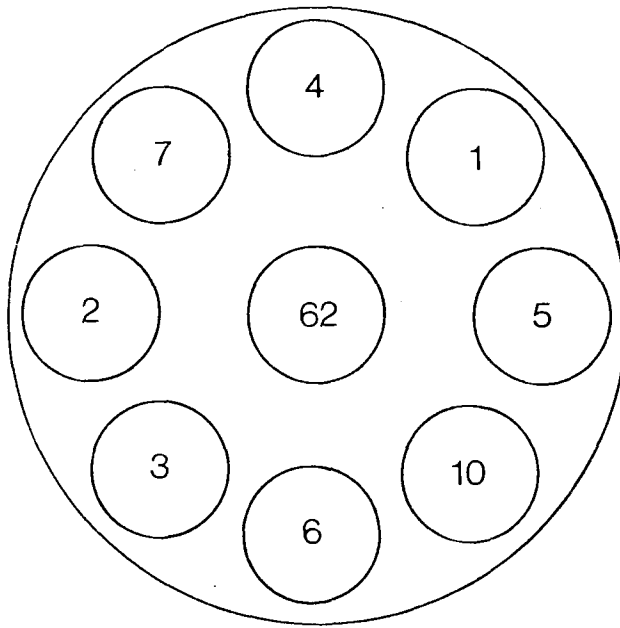
Appendix 3:   Selective accumulation of Prochromadorella
neapolitana to alternating wells of diatom
species D5-D8 (see Table 1).

Figure 1 (top circle):

- Top center: 2 | 4 / 6 | 1
- Upper left: 1 | 1 / 2 | 3
- Upper right: 2 | 3 / 1 | 1
- Left: 21 | 10 / 16 | 20
- Center: 5 | 4 / 4 | 4
- Right: 46 | 51 / 41 | 54
- Lower left: 1 | 3 / 3 | 1
- Bottom center: 17 | 23 / 23 | 13
- Lower right: 5 | 1 / 4 | 3

Figure 2 (bottom circle):

- Top center: 4 | 5 / 2 | 7
- Upper left: 2 | 1 / 1 | 3
- Upper right: 6 | 3 / 3 | 2
- Left: 12 | 16 / 19 | 13
- Center: 27 | 22 / 14 | 10
- Right: 36 | 32 / 39 | 40
- Lower left: 1 | 4 / 7 | 0
- Bottom center: 11 | 13 / 9 | 24
- Lower right: 1 | 4 / 6 | 1

Appendix 4: Accumulation of <u>Prochromadorella</u> <u>neapolitana</u> to
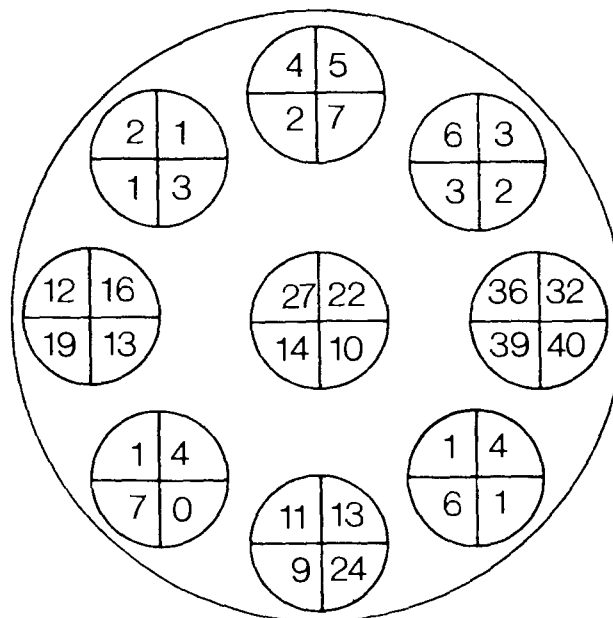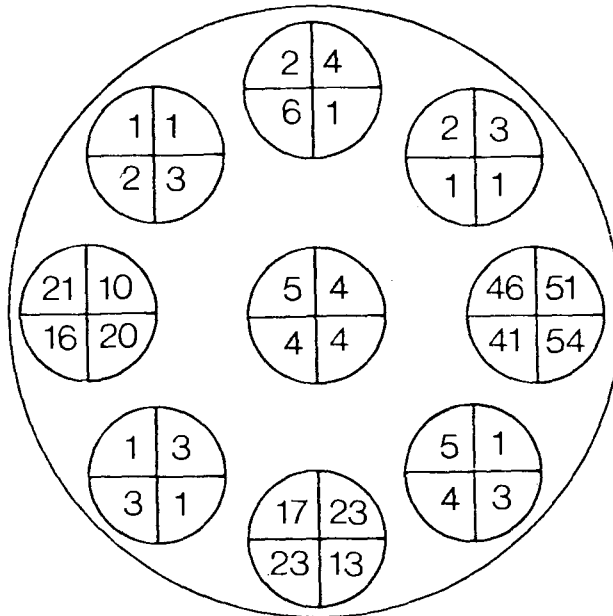   control wells.

Appendix 5: Selective accumulation of _Prochromadorella neapolitana_ to alternating wells of bacteria species B1-B4 (see Table 1). Diagram records four replicates for each condition.
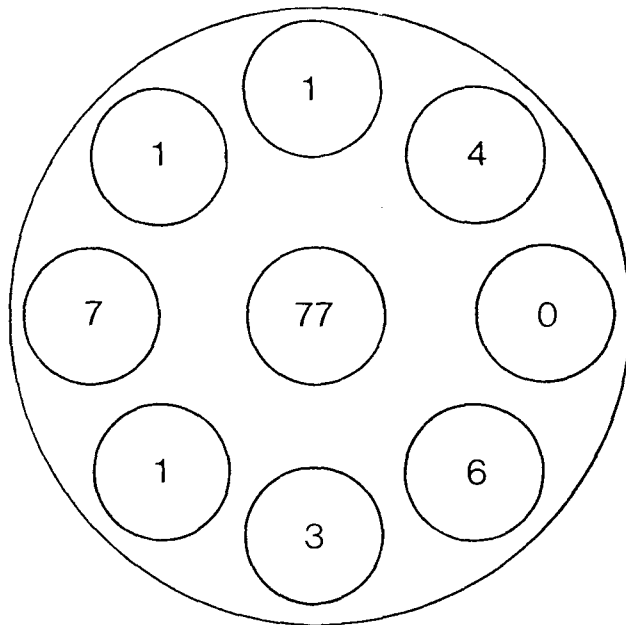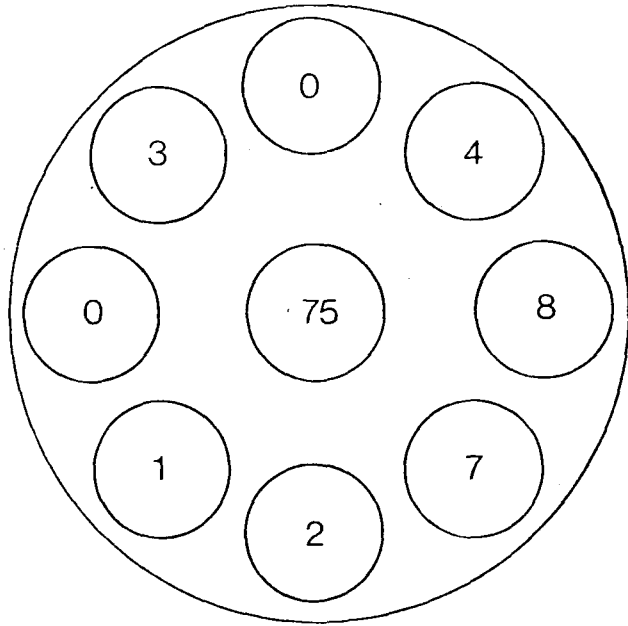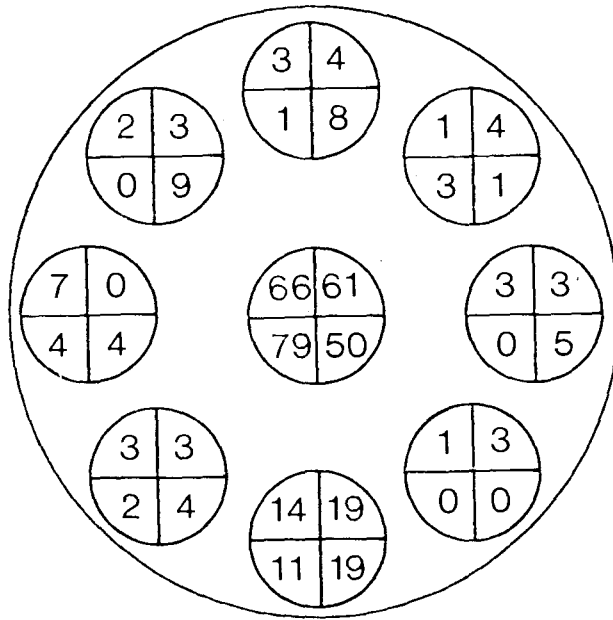
Appendix 6: Accumulation of _Prochromadorella neapolitana_
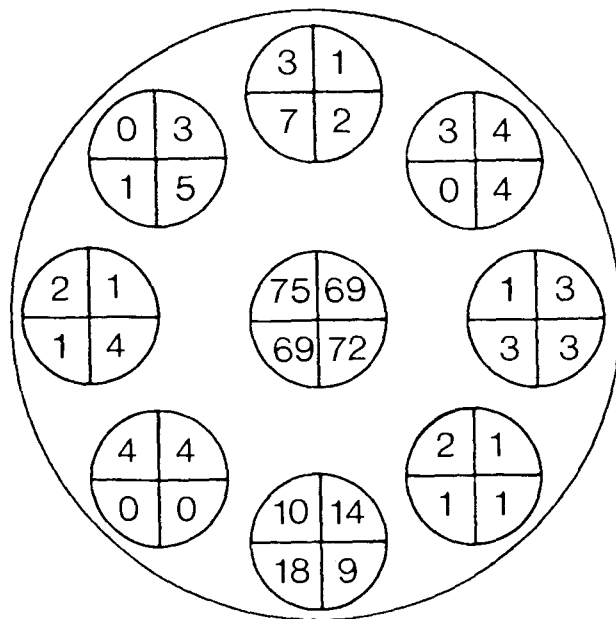to control wells.
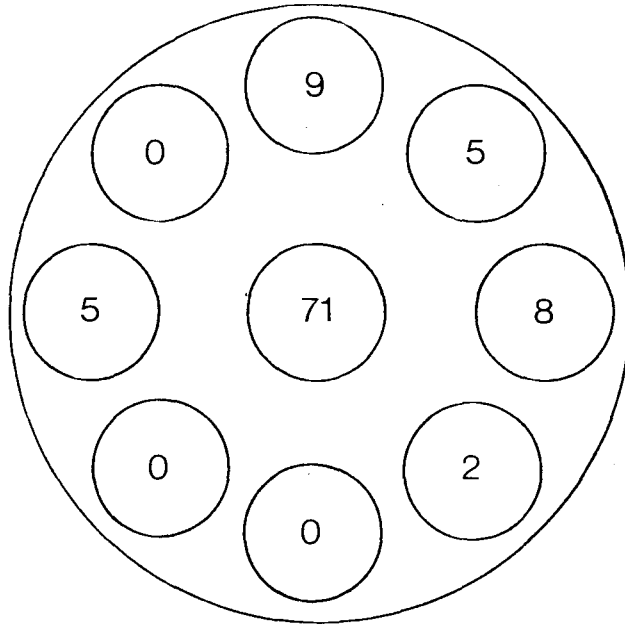
Appendix 7:   Selective accumulation of Monhystera refringens
              to alternating wells of diatom species D1-D4
              (see Table 1). Diagram records four replicates
              for each condition.

Top figure:

- 5 4 / 0 11
- 17 5 / 12 8
- 3 5 / 1 3
- 38 31 / 51 40
- 9 11 / 14 6
- 10 19 / 4 13
- 3 0 / 2 7
- 11 20 / 15 10
- 4 5 / 1 2

Bottom figure:

- 1 2 / 2 2
- 14 11 / 20 8
- 3 2 / 0 1
- 31 34 / 27 40
- 22 22 / 20 15
- 16 15 / 9 21
- 2 1 / 4 2
- 9 10 / 17 11
- 2 3 / 1 0

Appendix 8: Accumulation of Monhystera refringens to control wells.

Appendix 9:   Selective accumulation of Monhystera refringens
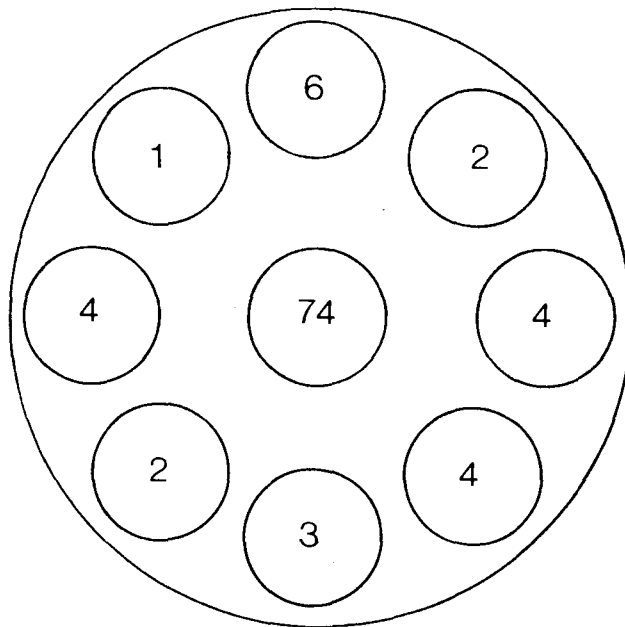   to alternating wells of diatom species D5-D8
              (see Table 1). Diagram records four replicates
              for each condition.

9	11
5	12

8	3
3	1

3	5
7	7

25	14
30	20

16	10
13	11

16	18
21	5

4	6
6	9

17	31
11	28

2	2
4	7

11	7
18	9

4	4
2	0

4	3
1	1

15	21
27	19

23	17
21	29

16	24
21	16

3	2
1	5

22	21
7	18

2	1
2	3

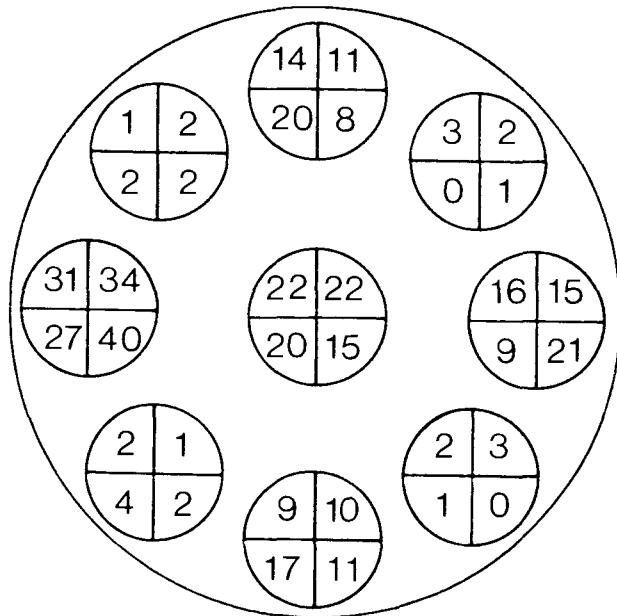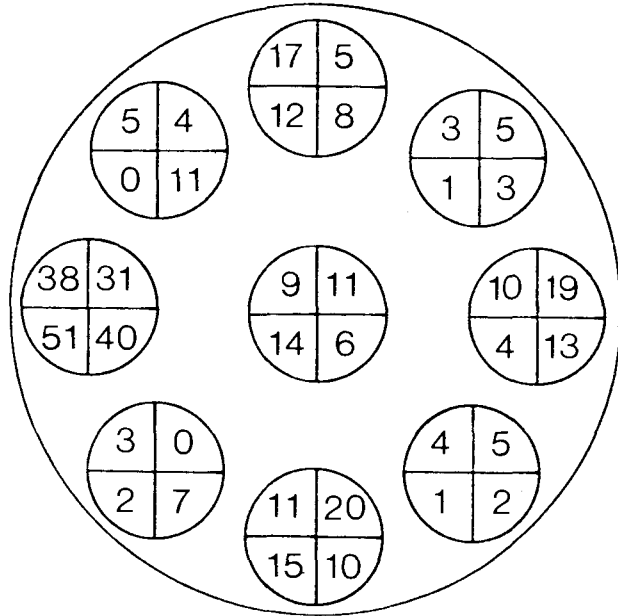Appendix 10:Accumulation of Monhystera refringens to
control wells.

Appendix 11:   Selective accumulation of <u>Monhystera refringens</u>
to alternating wells of bacteria species B1-B4
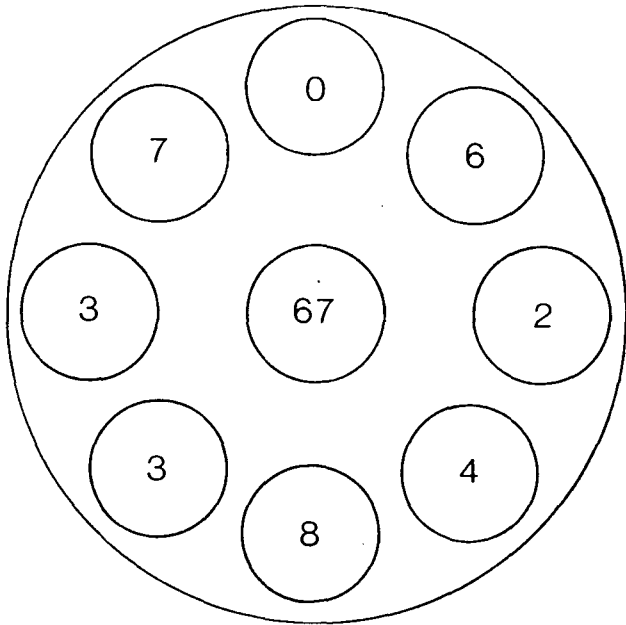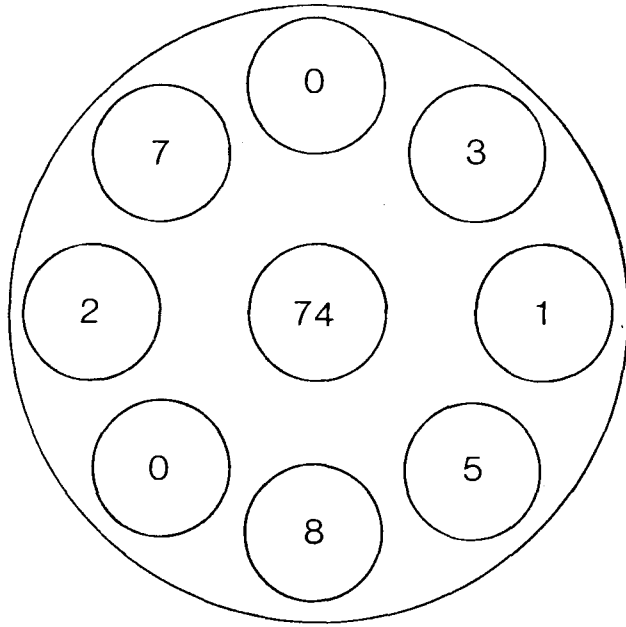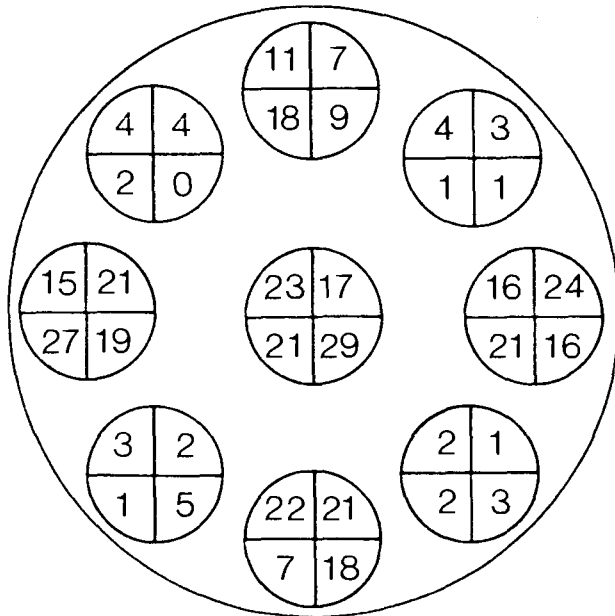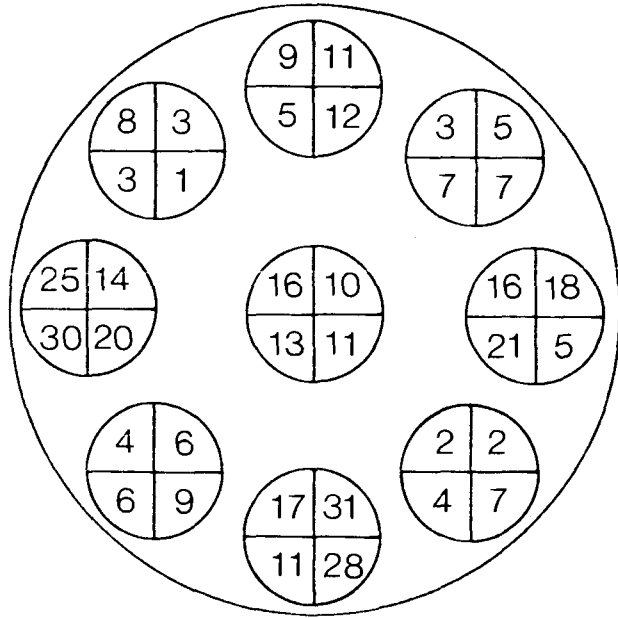(see Table 1).   Diagram records four replicates
for each condition.

Top figure:
- Top center: 5 | 13 / 11 | 8
- Upper left: 1 | 2 / 7 | 1
- Upper right: 3 | 4 / 1 | 3
- Middle left: 16 | 15 / 21 | 17
- Center: 12 | 17 / 15 | 8
- Middle right: 24 | 16 / 19 | 27
- Lower left: 4 | 7 / 0 | 5
- Bottom center: 31 | 21 / 25 | 19
- Lower right: 4 | 5 / 1 | 12

Bottom figure:
- Top center: 12 | 7 / 4 | 15
- Upper left: 3 | 5 / 1 | 2
- Upper right: 4 | 4 / 3 | 6
- Middle left: 16 | 10 / 11 | 9
- Center: 22 | 26 / 19 | 33
- Middle right: 20 | 12 / 31 | 17
- Lower left: 1 | 7 / 5 | 3
- Bottom center: 21 | 26 / 22 | 10
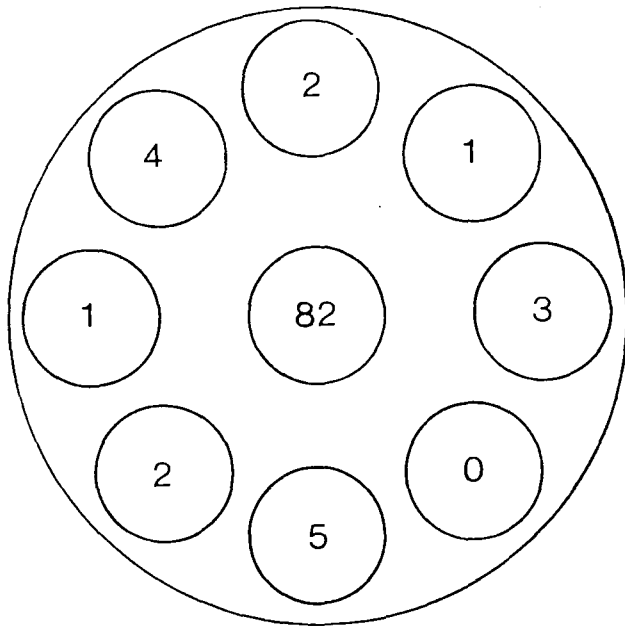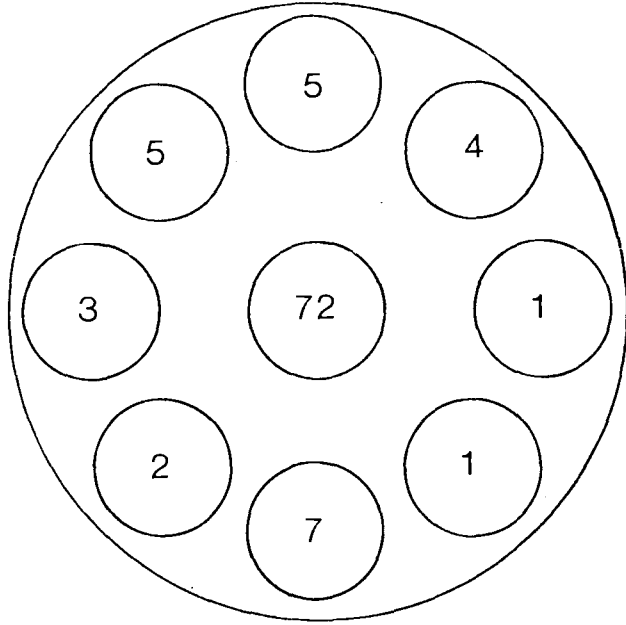- Lower right: 1 | 3 / 4 | 5

Appendix 12: Accumulation of <u>Monhystera</u> <u>refringens</u> to
            control wells.

Appendix 13:   Selective accumulation of <u>Monhystera disjuncta</u>
to alternating wells of <u>diatom species D1-D4</u>
(see Table 1).   Diagram records four replicates
for each condition.

Appendix 14: Accumulation of <u>Monhystera</u> <u>disjuncta</u> to
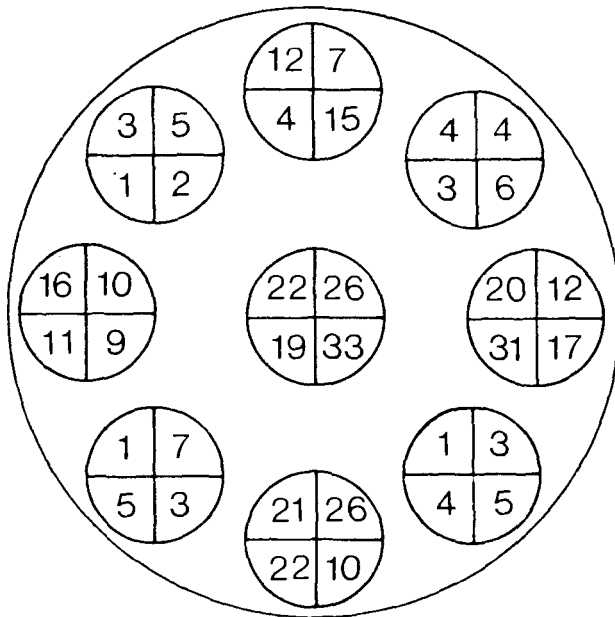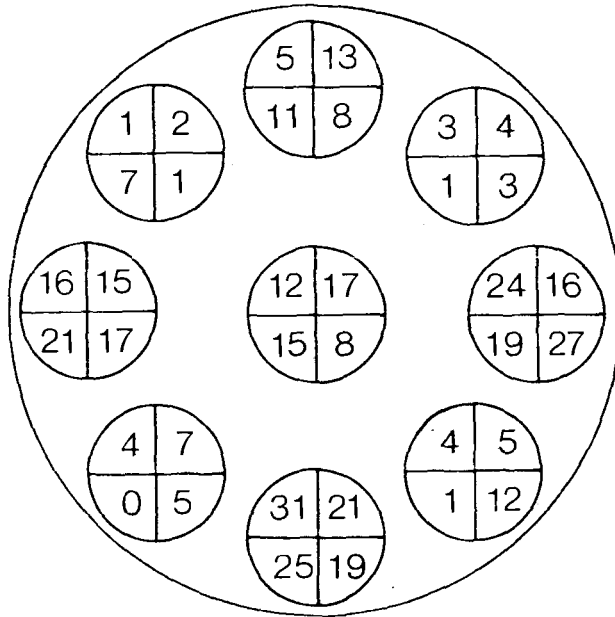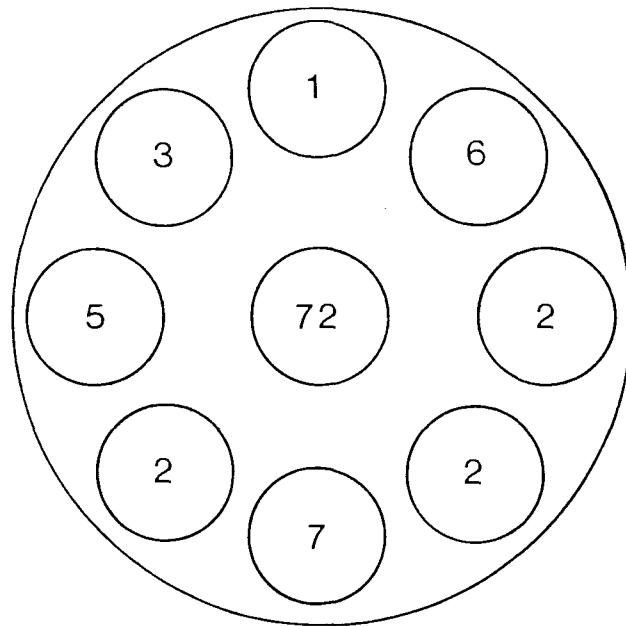control wells.

Appendix 15:   Selective accumulation of Monhystera disjuncta
to alternating wells of diatom species D5-D8
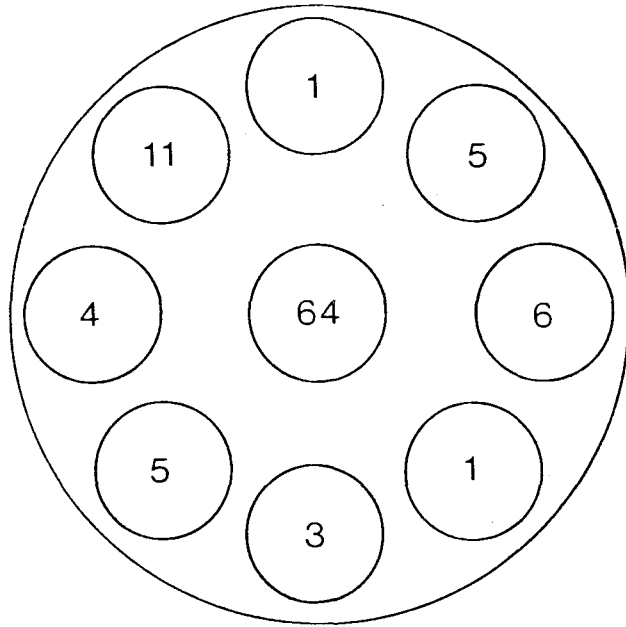(see Table 1).   Diagram records four replicates
for each condition.

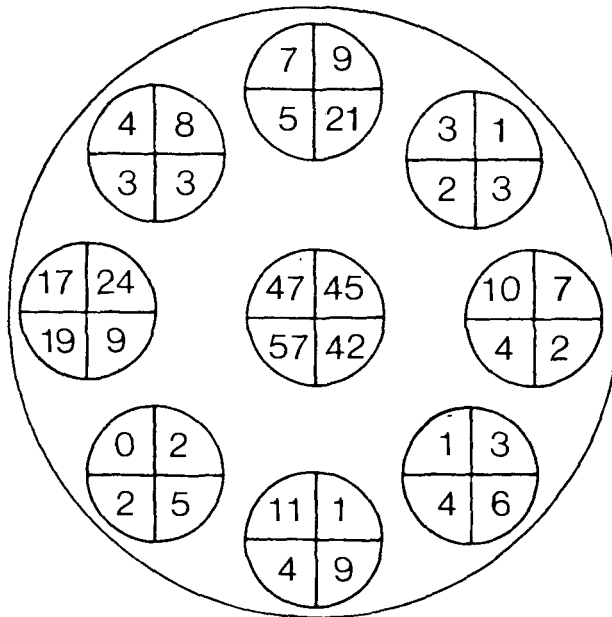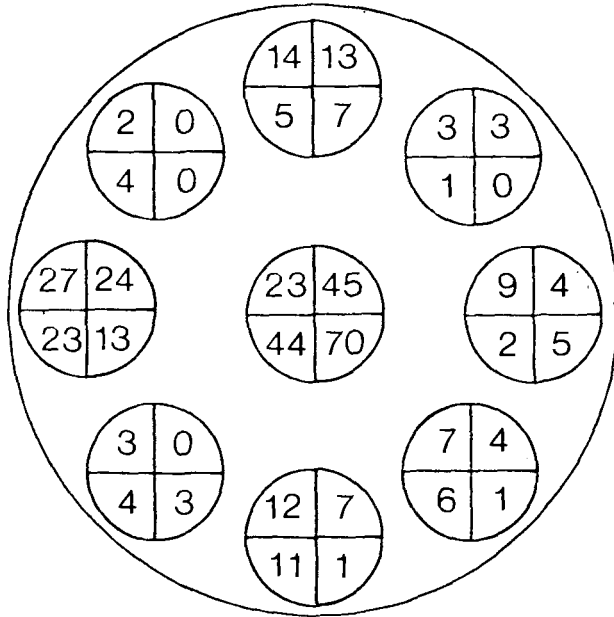Appendix 16: Accumulation of *Monhystera* *disjuncta* to
control wells.
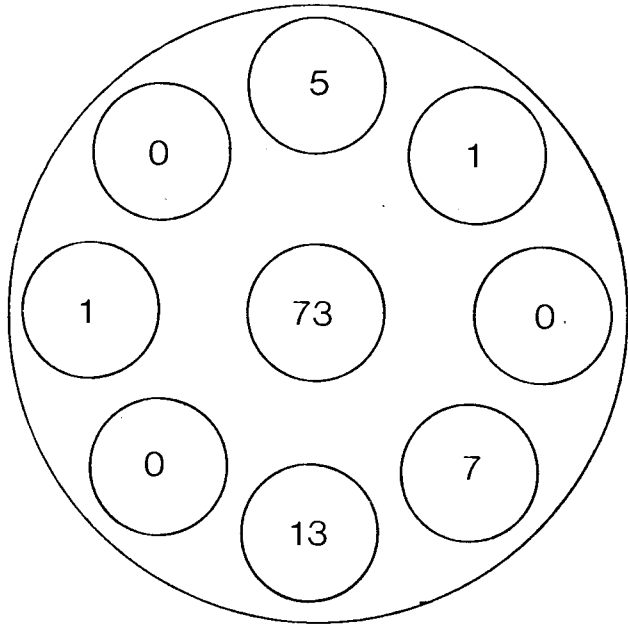
Appendix 17: Selective accumulation of Monhystera disjuncta
to alternating wells of bacteria species B1-B4
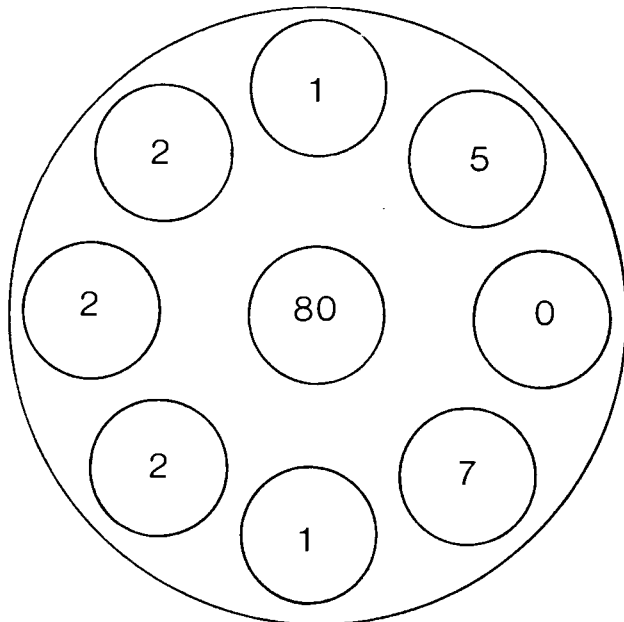(see Table 1). Diagram records four replicates
for each condition.

Top figure:

3 | 1 / 2 | 4	26 | 16 / 18 | 12	3 | 1 / 1 | 7
17 | 16 / 15 | 11	11 | 5 / 8 | 15	14 | 21 / 19 | 23
4 | 1 / 2 | 1	21 | 37 / 30 | 23	1 | 2 / 5 | 4

Bottom figure:

4 | 1 / 2 | 5	14 | 22 / 11 | 18	3 | 5 / 4 | 2
17 | 13 / 12 | 9	9 | 16 / 19 | 30	21 | 21 / 17 | 13
3 | 1 / 1 | 3	27 | 18 / 30 | 16	2 | 3 / 4 | 4
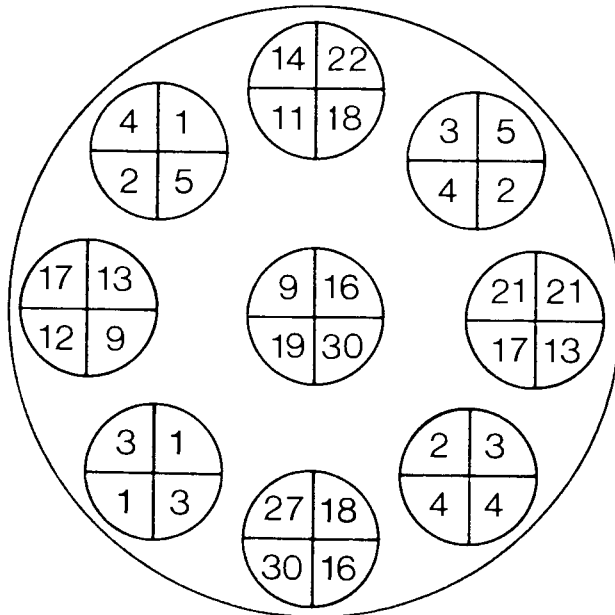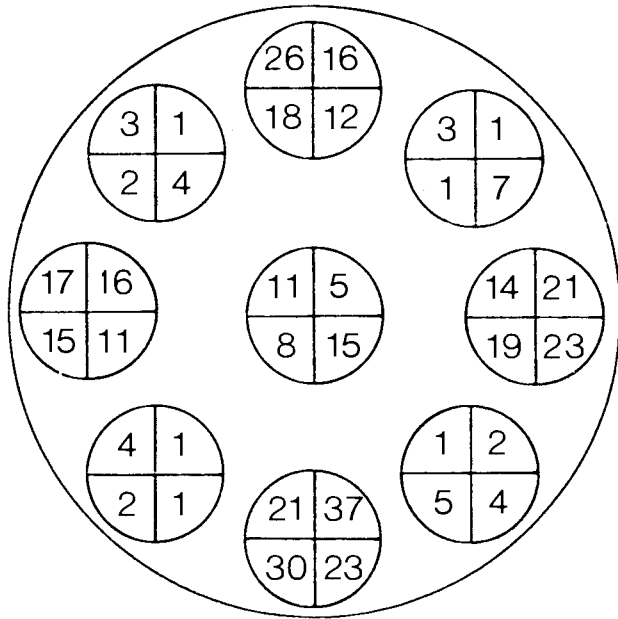
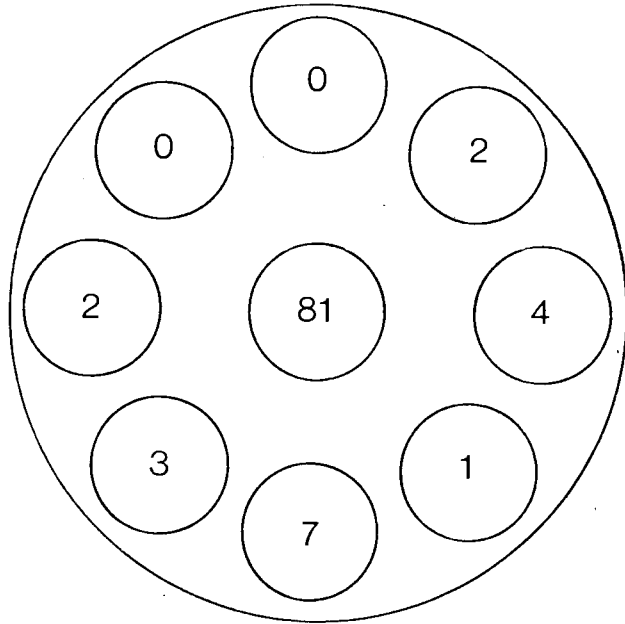Appendix 18: Accumulation of Monhystera disjuncta to control wells.
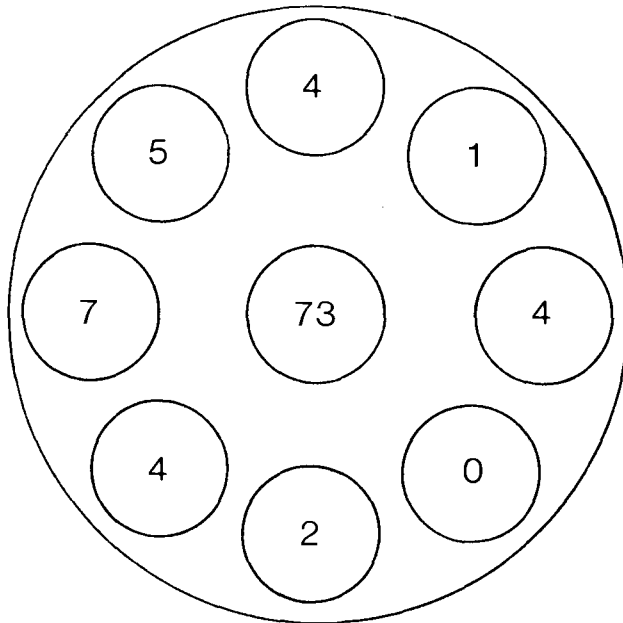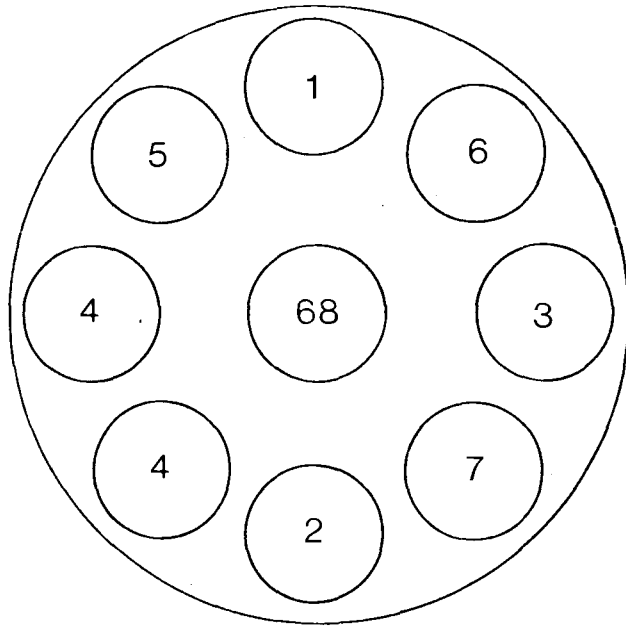
Appendix 19:   Selective accumulation of Monhystera disjuncta
                to alternating wells of (i) rod or (ii) coccoid
                bacteria species (see Table 1). Diagram
                records four replicates for each condition.

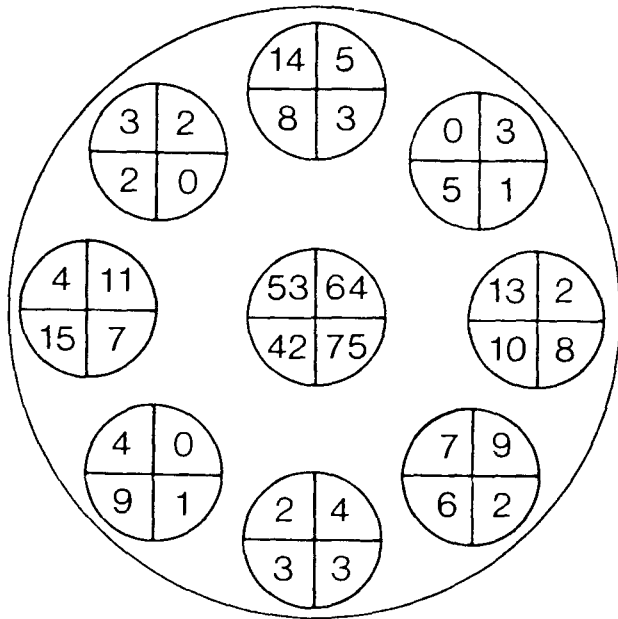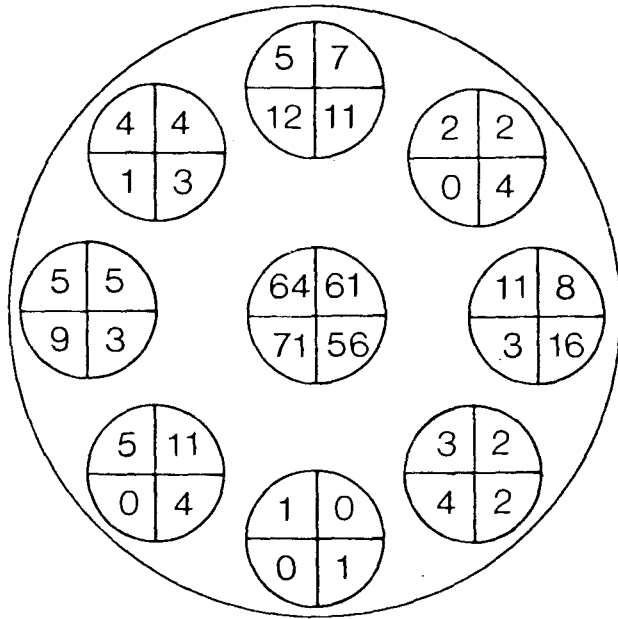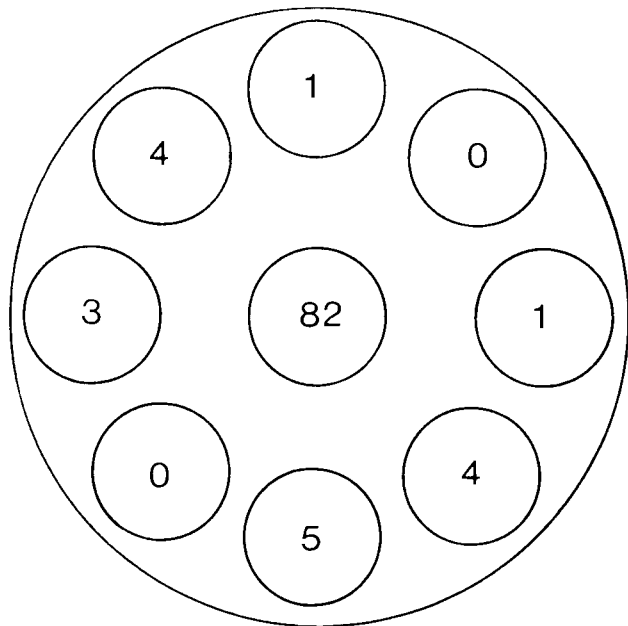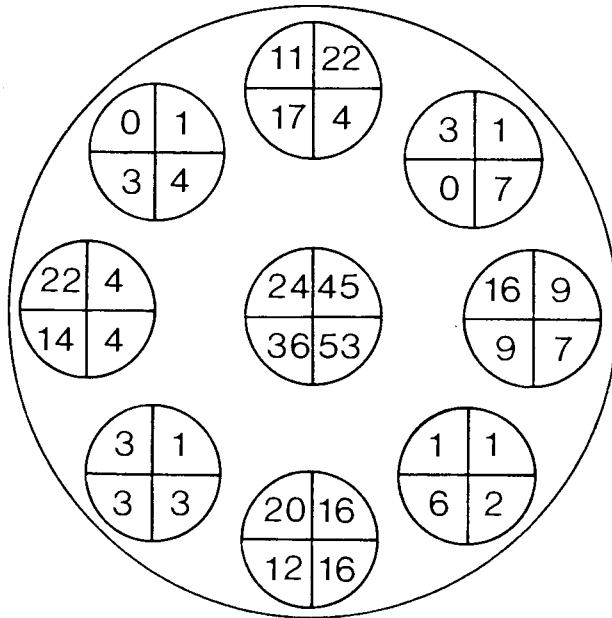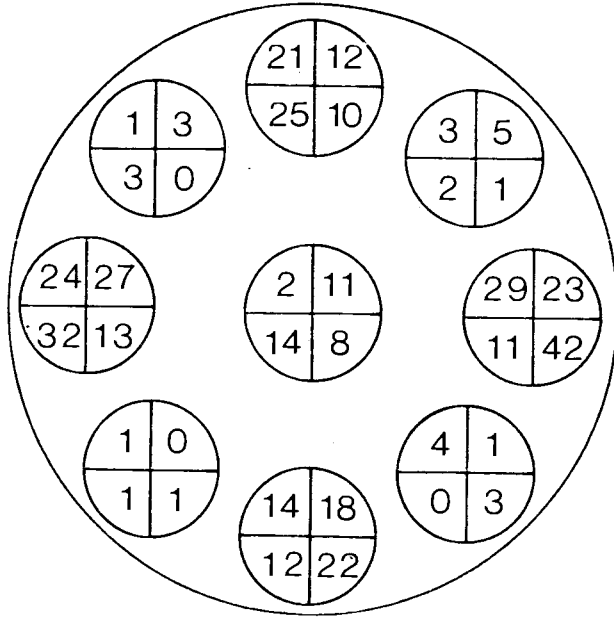Appendix 20: Accumulation of <u>Monhystera</u> <u>disjuncta</u> to control wells.
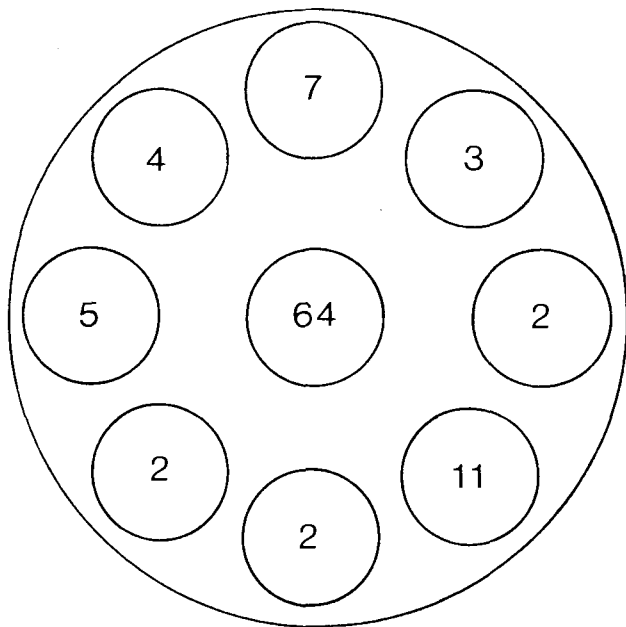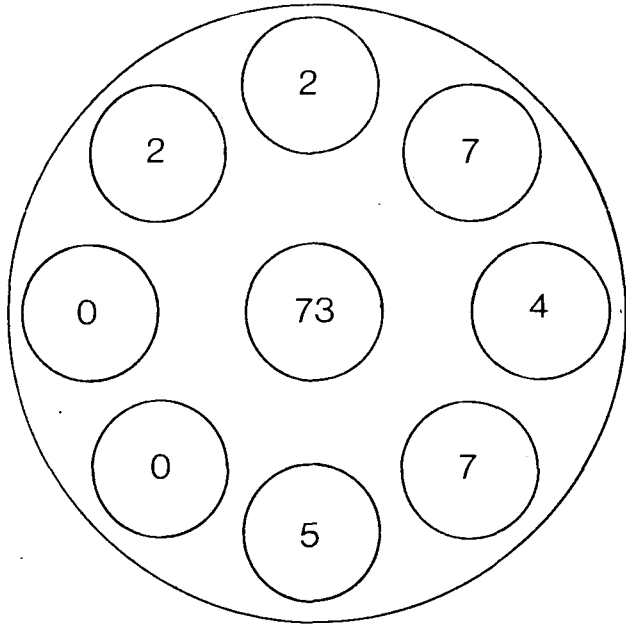
Appendix 21: Two level ANOVA calculated on age structure (males, females, juveniles/ 0.5 m²) densities of _Prochromadorella neapolitana_.

Source of Variance	Degrees of Freedom	Sum of Squares	Mean Square	F	Significance
Age Structure	2	1708.8	854.3	14.56	***
Time	13	12615.3	970.4	16.54	***
Residual	26	1525.2	58.7		
Total	41	15849.3			

Appendix 22: Two level ANOVA calculated on age structure (males, females, juveniles/ 0.5 m^2) densities of Monhystera refringens.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F	Significance
Age Structure	2	2032.0	1016.0	17.92	***
Time	13	9777.4	752.1	13.27	***
Residual	26	1473.9	56.7		
Total	41	13283.6			

Appendix 23: Two level ANOVA calculated on age structure (males, females, and juveniles/0.5 m^2) densities of Monhystera disjuncta.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F	Significance
Age Structure	2	12922.4	6461.2	30.05	***
Time	13	5931.1	456.2	2.12	N.S.
Residual	26	5589.6	215.0		
Total	41	24443.1			

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