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__Alaska in 1980 and a Report on an Exclusion Experiment of Sub-Ice Fauna__

__from the Ice__

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Sea ice provides an unique habitat for marine organisms in polar
and subpolar regions. Large numbers of invertebrates were collected
from the lower layer of fast ice in the nearshore Beaufort Sea, off
the northern coast of Alaska in the spring of 1980. Although the
density within the ice was low compared to that typically found in
sediments, it was much higher than had previously been reported from
sea ice. Nematodes were the numerically dominant group, but copepods
and turbellarians were also abundant. The life-histories of the two
most numerous copepods were examined and found to be very different.
Cyclopina gracilis appeared to reproduce continuously during the study,
while Harpacticus sp. mated in the ice but did not appear to undergo a
complete reproductive cycle there. An experiment was carried out to
test the hypothesis that pelagic organisms prey on ice fauna, but the
results were inconclusive.

Succession of the Under-Ice Fauna on Fast Ice
off Narwhal Island, Alaska in 1980 and a
Report on an Exclusion Experiment
of Sub-Ice Fauna from the Ice

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SUCCESSION OF THE UNDER-ICE FAUNA ON FAST ICE OFF NARWHAL ISLAND, ALASKA IN 1980 AND A REPORT ON AN EXCLUSION EXPERIMENT OF SUB-ICE FAUNA FROM THE ICE

INTRODUCTION

An unique habitat exists within the lower layers of polar and subpolar sea ice. The bottom ice layer has been described as being soft (Horner, 1976), or loose (Andriashev, 1968) in composition, in contrast to the hard ice above. It has relatively constant temperatures (-3 to 0°C), enough nutrients to support algal growth, variable osmotic pressure, and a probable abundance of organic material (Meguro et al., 1967). Seasonal ice is generally 2.0 to 2.5 m thick, yet sufficient light of adequate quality passes through it to support photosynthesis within the ice habitat (Maykut and Grenfell, 1975). Multi-year (pack) ice is generally thicker, but the presence of chlorophyll within the lower ice layers (English, 1961) is evidence that photosynthesis also occurs in this ice. Pack ice is present all year, and therefore provides a permanent environment in which ice organisms can survive. Seasonal ice breaks up each year in late spring, so that organisms within the lower layers of this ice exist in an ephemeral habitat. Despite the temporary nature of the seasonal ice environment, an abundance of life can be found there.

Early studies of the ice biota concentrated on the taxonomy of the algal species (reviewed by Horner, 1977). Recently, investigations of the amount of primary production occurring in the ice have been performed in the Arctic (Clasby et al., 1972), the Bering Sea (McRoy and Goering, 1974), and the Antarctic (Bunt and Lee, 1970). Standing stocks have been assessed in the Antarctic (Ackley et al., 1979), the

Arctic (Hsiao, 1980), and the Gulf of St. Lawrence region (Dunbar and Acreman, 1980). The possibility of a heterotrophic metabolism by ice algae during the period of 24 hour darkness has also been studied (Horner and Alexander, 1972). It is now known that low densities of algae are present in Arctic nearshore (or fast) ice from its formation in the fall until April, when a bloom occurs (Horner, 1977). By late May, the peak of the bloom, the algae have formed several centimeters of colored ice. Estimates of annual production by ice algae range up to 5 gC/m^2 (Alexander, 1974).

Invertebrates inhabit the sea ice environment, but in contrast to the ice flora, little is known about these organisms. Heliozoans, ciliates, nematodes, copepods, polychaete larvae, turbellarians, and amphipods have been collected from the ice (Andriashev, 1968; Horner, 1976), but quantitative estimates are unavailable. There is evidence suggesting that the ice fauna grazes on the algae within the ice (Horner, 1977). However the trophic connection of the ice faunal assemblage to the rest of the polar marine ecosystem is not understood. Some of the organisms probably fall to the bottom, either during the ice season (Andriashev, 1968), or, in areas where the ice is not present all year, when the ice breaks up. Upon reaching the bottom, the organic material from the ice could enter the benthic food web. Alternatively, ice organisms could be utilized by animals in the water column feeding in the ice. Some authors have speculated on this potential interaction (Andriashev, 1968, 1970; Horner, 1976; Alexander, 1980), but it remains largely unknown to what extent the fish and zooplankton found associated with the ice, termed the sub-ice fauna by Andriashev (1968), feed on the organisms within the ice.

This paper is the result of a study designed to answer some of the questions that have been raised as a result of the earlier work on sea ice organisms. The research undertaken had three goals. The first was to obtain quantitative estimates of the taxa found in the ice over most of the ice algal bloom by taking frequent samples in the same area. A second goal was to investigate the population structures of some of the dominant species found in the ice during the sampling period. The main question here was: Are the life-history strategies of the species living in this unique habitat different from those of related species in more typical environments? The third area of investigation was the possible trophic connection of the ice fauna to fish and zooplankton living in the water column beneath the ice. Connell (1975) regarded predation as being of primary importance in structuring most communities. A manipulative experiment was performed in which cages were used to exclude sub-ice fauna, which are potential predators of ice animals, from areas of the ice to see if, in their absence, significant changes in the density and structure of the ice assemblage would occur. This type of experiment has been used by many investigators (e.g. Menge, 1976; Virnstein, 1977; Buzas, 1978; Holland et al., 1980) in other environments to study the effects of predation.

MATERIALS AND METHODS

Sample Collection

The study site was located on a large ice pan in the Beaufort Sea approximately 0.4 km north of Narwhal Island, Alaska (Figure 1). A dive hole was cut through nearly two meters of ice, over a muddy sand bottom lying 6.5 m below its lower surface. A tent was placed over the dive hole.

Ice samples were collected following the program outlined in Table 1. Samples were collected on nine occasions from 14 April to 5 June. A 36 m^2 area, approximately 18 m from the tent, was staked out on the undersurface of the ice, and a rope marked every 0.5 m was placed around it. This divided the study area into a grid containing 144 0.25 m^2 quadrats. Sampling locations within this area were assigned using coordinates taken from a random numbers table. Samples from 24 April and 11 May were taken slightly outside the study grid. Ice samples collected on 14 April and 5 June were taken an unknown distance within 40 m of the study area.

Cages used in the sub-ice fauna exclusion experiment were round, 25 cm in diameter and 15 cm in height. They were constructed from two sizes of black plastic mesh. The sides had two layers of plastic: an inner coarse oval mesh with a largest dimension of 24 mm and an outer fine mesh with a largest dimension of three mm. Tops were constructed only of the fine mesh. Cages had small spherical plastic floats attached to the inside, near the top and were secured to the ice with aluminum pins. Deployment was within the study grid in randomly selected quadrats and took place on 5 May. Any amphipods visible on the ice were

removed before the cages were secured because these animals have been suggested as ones which might prey on ice organisms.

Quadrats were sampled by a diver, using SCUBA, with a corer of 10.5 cm i.d. This sampled an 86.6 cm^2 area of the undersurface of the ice. One end of each corer was covered with 64 micron mesh. The open end was pushed into the undersurface of the ice until hard ice was reached. Cores were contained by sliding a spatula into the ice over the end of the corer, and then capped while underwater. Samples from cages were taken after the cages had been removed by cutting their sides at the ice surface. Caged and uncaged quadrats were never sampled more than once. Samples from 14 April and 5 June were collected using an ice scraper (Carey, 1981), rather than a corer, and cannot be compared quantitatively with cores.

Sample Treatment

Samples were placed in jars and transported to the lab where they were washed on a 64 micron sieve. Animals was preserved in ten percent buffered formalin and stained with rose bengal. Core samples were sorted into major taxonomic groups and enumerated under a dissecting microscope. Only taxa of sizes large enough to be consistantly retained on a 64 micron mesh were enumerated since the samples cannot be regarded as being quantitative for smaller organisms. Calanoid copepods, which were found infrequently in cores and always in low numbers, were also not counted since it is unclear whether they were present in the ice or caught in the corers prior to being inserted into the ice. Cyclopoid and harpacticoid copepods were identified to the species level. It

was not possible in the time available to identify each copepodite to its stage. Instead, all undamaged individuals belonging to the two dominant copepod species were measured to the nearest 24 microns using an ocular micrometer. Total length, excluding the terminal setae, of these organisms was measured. One hundred individuals of each of these species were randomly chosen from the ice scraper samples and measured. The presence of egg sacs and pre-copulatory clasping pairs was recorded for these species on all sampling dates. The gender of all individuals large enough to be sexed was recorded.

Data Analysis

Cores taken from uncaged ice were used for density estimates of the fauna, for collection of individuals belonging to species used for life-history studies, and as controls for comparison with cores from caged areas of the ice. Caged cores were used only for the sub-ice fauna exclusion experiment. Ice scraper samples were used only for the copepod life-history studies.

A one-way analysis of variance was used to test for changes over time in the density of major taxa and copepod species. A multi-variate analysis of variance (Cohen and Burns, 1977) was used to test for differences in the density of major taxa and copepod species between caged and uncaged ice. Data were $\log_{10}$ (x+1) transformed before the above tests were performed. The Kolmogorov-Smirnov test (Tate and Clelland, 1957) was employed to test whether the population size structures of the dominant copepod species changed over time. The size-frequency distribution at each sampling date was compared separately with

the distribution of the preceding date, as well as the following date. Since the same data set was tested several times, the chance of making an error by incorrectly rejecting the null hypothesis of no difference in population structure is increased. Therefore, to be conservative, the level of significance used to reject the null hypothesis was preset at 0.01.

RESULTS

Density and Succession of the Ice Fauna

Nematodes, copepods, turbellarians, polychaetes, and amphipods were collected from the undersurface of the ice. The mean number of individuals collected per 100 cm^2 for each group at all dates when corers were used, with the associated standard deviations, is given in Table 2. Nematodes dominated, comprising 47.0% of the fauna collected throughout the study. Copepods and turbellarians made up 28.8% and 16.1% of the fauna, respectively. Polychaetes and amphipods were minor members of the ice fauna, together representing less than ten percent of the total.

Each group showed a significant change in abundance over time (Table 2, right). In general, the number of individuals within each taxon increased as the ice algal bloom progressed. Polychaetes were the only exception to this pattern, with their greatest density occurring on 24 April. Nematode and turbellarian abundance increased rapidly from minimum values at 24 April to maximum on 2 June. Copepods exhibited a different trend in abundance (Figure 2). Instead of having a generally continuous increase in population like nematodes and turbellarians, copepod abundance appeared to decrease initially then increase, and finally decrease again. Since the standard deviations are high, it is possible that this pattern is not real. Amphipod density grew slowly to a maximum on 26 May and then decreased sharply.

Seven species of cyclopoid and harpacticoid copepods were identified from the ice. The mean number of individuals collected per 100 cm^2 for

each of the five dominant species, and the associated standard deviation
is given, for each date on which cores were taken, in Table 3. Cyclopina
gracilis, a cyclopoid, was the dominant species, making up 55.0% of the
ice copepod fauna. Harpacticus sp. and Halectinosoma sp., two harpacti-
coids, comprised 23.0% and 19.8% of the copepods, respectively. The
cyclopoid Oncaea sp. represented 1.5% of all copepods and Dactylopodia
signata, a harpacticoid, less than one percent. Two copepodites were
collected that probably belonged to the species Cyclopina schneideri.
The seventh species was represented by a single individual that was
too young to identify.

Although there was a significant change in abundance over time for
total copepods, densities of two species, Halectinosoma sp. and D.
signata, did not change significantly. The abundance of C. gracilis
and Harpacticus sp. did change significantly through the study (P<.002),
as well as that of Oncaea sp. (P<.05). The three dominant species
displayed similar patterns in abundance over time (Figure 3). Densities
appeared to decrease initially, reach a maximum in the second half of
May, and then decrease toward the end of the study.

Life-Histories of Cyclopina gracilis and Harpacticus sp.

Data on the life-history characteristics recorded for the two
dominant copepods, C. gracilis and Harpacticus sp., are given in
Table 4. Cyclopina gracilis adults were present at all dates. Only
copepodites of Harpacticus sp. were collected before 11 May. Harpacticus
sp. males were more abundant than females until the final three sampling

dates. The reverse trend occurred with C. gracilis where females out-numbered males initially, but were generally less numerous after 5 May. Gravid C. gracilis females were collected on five of the sampling dates, but were never a large percentage of the adult female population. No gravid Harpacticus sp. females were found in the ice, but pre-copulatory clasping pairs were present on 26 May and 2 June. Adult males clasped late copepodite females on the prosome with their modified antenules.

The size-frequency distribution of Harpacticus sp. indicates than the population structure changed greatly during the course of the study (Figure 4). Over 95% of the Harpacticus sp. individuals could be measured. Initially the population was composed entirely of copepodites. By 15 May, however, a mode appeared at appxoimately 840 microns that was composed of adult males and late copepodite females. This feature remained in later samples because the adult males had reached their maximum size. Females continued to grow and a broad mode corresponding to adult females was seen beginning 19 May. Significant differences in population structure were indicated by the Kolmogorov-Smirnov test in the second and third comparisons (24 April-5 May and 5 May-11 May), and the last three (19 May-26 May, 26 May-2 June, and 2 June-5 June). Only 29 individuals were measured from 5 May and this sample size is inade-quate to calculate the test statistic where the sample sizes are unequal (Tate and Clelland, 1957). To make comparisons between this date and the preceding and following sampling dates, the smaller sample size was used alone to determine the test statistic.

The population structure of C. gracilis (Figure 5) changed greatly during the study, but most of the change occurred in the early samples.

Over 92% of all individuals could be measured. The Kolmogorov-Smirnov
test indicates that significant changes in the size-frequency structure
of the population occurred between the first two sampling dates (14
April-24 April), the second and third dates (24 April-5 May), the
fifth and sixth dates (15 May-19 May), and the eighth and ninth dates
(2 June-5 June). The earliest samples contained mostly juveniles. In
the cores taken 15 May, and in all following samples, three major modes
were evident in the size-frequency distributions. The first mode,
centered at around 260 microns, was composed of young copepodites. The
second, located at approximately 520 microns, was largely made up of
adult males and late female copepodites. Adult females had a much greater
size range than males, and had a broad peak centered near 700 microns.
The presence of these three modes in the size-frequency distributions
of C. gracilis from 15 May until the end of the sampling is an indication
that the population structure was stable throughout this period. The
change that was detected by the Kolmogorov-Smirnov test between the
population structures of 15 May and 19 May are due to differences in the
height of the peaks, and not in their location. The size-frequency
structure of C. gracilis on 5 June had these three modes, but they were
broader and had shifted to larger sizes relative to the previous dates.

Sub-Ice Fauna Exclusion Experiment

The presence of cages produced lower densities of all major taxa
compared to areas without cages (Figure 6). This difference was statis-
tically significant for polychaetes, copepods, and amphipods (P<.01).
At the species level, all copepods except Oncaea sp. were less abundant

in caged ice than uncaged ice (Figure 7). _Oncaea_ sp. had significantly greater abundances inside cages (P<.04), while signiciantly fewer individuals were found inside cages for _Harpacticus_ sp. (P<.0001), _C_. _gracilis_ (P<.004), and _Halectinosoma_ sp. (P<.06). There were no readily visible alterations in the ice inside cages as revealed by diver observations (Ron Poirot, pers. comm.) or photographs.

DISCUSSION

Density and Succesion of the Ice Fauna

The large numbers of animals found within the ice of the Beaufort

Sea is surprising. Andriashev (1968) provided the only data in the

literature that can be used for quantitative comparisons, and his data

were from the Antarctic. He found solitary polychaete individuals,

cyclopoids up to several hundreds/m^2, harpacticoids (including species

of Harpacticus and Dactylopodia) up to hundreds/m^2, and amphipods up to

3040/m^2. No information was given for turbellarians, or for nematodes

which was the dominant group in my samples. The mean number of indi-

viduals/100 cm^2 for the taxa collected from the Beaufort Sea ice

(Table 2) can be converted to number/m^2 by multiplying the values given

by 100. When this is done (Table 5), it is apparent that the overall

abundance of the ice fauna is much greater in the samples collected

from the Arctic. Amphipods were the only group which had a greater

density in the Antarctic. It is possible that the Beaufort Sea site was

an unusually productive one, but there is no evidence to support this

idea. The study area was visually indistinguishable from surrounding

ice pans when viewed from a helicopter. Chlorophyll a values measured

in the ice close to my study grid (Horner and Schrader, 1981) are

similar to those recorded elsewhere (Apollonio, 1965). Further

sampling in other areas is required to test this hypothesis.

While the density of the ice fauna was greater than expected,

it was only around five percent of typical benthic meiofaunal density

(Coull and Bell, 1979). This may be due to the ephemeral nature of

the fast ice habitat. Ice is only present in the Beaufort Sea from
September or October until around June (Barnes and Reimnitz, 1975).
Populations must recolonize the lower layer of the ice each year.
There is evidence, using artificial substrates suspended over the bottom,
that some meiofaunal groups can rapidly develop large populations in
abiotic sediments (Scheibel, 1974). Nematodes and copepods, the most
abundant taxa in Beaufort Sea ice, were also the dominant groups colo-
nizing the suspended substrates. This is not surprising since these two
groups are typically the most abundant in normal sediments (McIntyre,
1969). At least some of the increase in density in Scheibel's study
was due to continued immigration of animals after the sediments had
initially been colonized. It is also possible that animals migrated
to the ice from underlying sediments during the sampling period.
However nematodes are not able to swim large distances (Scheibel, 1974),
and continued movement of these organisms to the ice would depend on
passive transport from the bottom by advection. Reproduction was
responsible for at least part of the increase in abundance observed in
the ice. At least one gravid female was collected in three ice copepods,
Cyclopina gracilis, Halectinosoma sp., and Dactylopodia signata. A few
nematodes were examined, and gravid individuals were observed (E. W.
Hogue, pers. comm.). Laboratory studies have shown that the time
required for marine nematodes to complete one life cycle varies greatly,
from less than two weeks (Gerlach and Schrage, 1971) to almost two years
(Gerlach and Schrage, 1972). It may be possible that the rapid increase
in abundance found for nematodes could largely be due to reproduction
rather than passive transport, if the ice species have short life cycles.

Grazing by ice fauna may be important in regulating standing stocks of ice algae. It had previously been suggested that ice algae were free from grazing and that the entire season's production was released into the water column at breakup (Meguro et al., 1967). Nematodes collected from fast ice in the Beaufort Sea had guts filled with diatoms. Most benthic harpacticoids have been found to feed extensively on diatoms (McIntyre, 1969). The large densities of these organisms in the ice suggests that at least some of the algal production may be utilized _in situ_. Further work is required to determine the extent of grazing by ice fauna.

Environmental conditions within the ice were not recorded in this study so it is not possible to try to relate variations in faunal density between sampling dates to changes in their environment. One interesting finding was the similarity in the abundance trends exhibited by the three dominant copepod species (Figure 3). These species displayed the same relative changes in density throughout the study. This suggests that the same factor or factors might be affecting these species in similar ways. Total copepod and amphipod abundance appeared to decline around 2 June. They might have been responding before other groups to changes in the ice associated with breakup. By 9 June, although the ice remained solid, there was a layer of low salinity (2.8 ppt) at the water-ice interface, where no salinities lower than 28.9 ppt were recorded before (Carey, 1981).

There was a large around of spatial variability in the ice fauna. Standard deviations were commonly greater than 50% of the mean for some taxa. Ice fauna apparently had a patchy distribution. Although

determining the scale of aggregations was not a goal of this study, and the sampling program was not designed to examine this problem, it is evident that the size of faunal patches varied in the study area. Some pairs of cores were virtually identical in the abundance of each of the major taxa, and of copepod species. The patch size in these instances must have minimally been larger along one axis than twice the core diameter (21 cm). Other pairs of cores differed greatly, indicating that these patches were smaller. Patchiness of ice flora has been found to be correlated with light attenuation due to snow depth (Clasby et al., 1976). This could not have been a factor in determining the patchiness of the ice fauna in this study since the snow cover over the sampling site was of uniform thickness at any one time.

Life-Histories of Cyclopina gracilis and Harpacticus sp.

Life-history studies of marine benthic copepods are rare, with most of the work done on harpacticoids living in tide pools (Fraser, 1936; Harris, 1973), in littoral sediments (Rao, 1967; Barnett, 1970; Lasker et al., 1970; Harris, 1972; Jewett and Feder, 1977; Fleeger, 1979; Feller, 1980a), and on algae (Hicks, 1977). These studies have shown that there are many reproductive patterns in harpacticoids, and that even closely related, sympatric species may have markedly different life-histories. Barnett (1970) investigated the life cycles of two congeneric species inhabiting the same mudflat and found that each species had a distinct life-history. Despite these variations, Hicks (1979) has shown that reproductive strategies of harpacticoid copepods tend to differ more between habitats than within habitats. He suggests

that factors such as food resource availability and environmental stability are important in determining the evolution of specific life-history strategies. Therefore, it might be expected that copepods inhabiting the ephemeral ice environment would show a different life-history pattern from those of copepods studied elsewhere.

It is evident that Harpacticus sp. and C. gracilis have different life-history strategies (Figure 4 and 5, Table 4). Cyclopina gracilis appears to reproduce continuously during the ice algal bloom. Gravid females were found on five of the nine sampling dates. Since the number collected on any sampling date tended to be low, it is possible that there were gravid females in the ice throughout the sampling period, but not collected on some occasions because of their low density. Egg sacs may also have been shaken loose when these samples were transferred. Continuous recruitment to the population is also indicated by the presence of young copepodites on all sampling dates. The location of modes in the size-frequency distributions of C. gracilis was similar from 15 May to the end of the study (Figure 5). Fleeger (1979) gave size-frequency distributions of Enhydrosoma propinquum that showed a pattern of constant peak locations for an extended period. He suggested that the stable population structure was brought about by continuous recruitment of nauplii. Cyclopina gracilis has been found associated with macro-algae (Sars, 1918) and described as a phytophile (Ceccherelli, 1976). Its continual reproduction, at least while in the ice, fits the strategy of continual or protraced reproduction utilized by most phytal harpacticoids (Hicks, 1979).

Harpacticus sp. did not appear to reproduce in the ice. Since the sampling period coincided with the annual ice algal bloom (Horner, and Schrader, 1981), when food resources are highest, the lack of gravid females is surprising. Pre-copulatory clasping, which is typical of harpacticoids, occurred among individuals collected on 26 May and 2 June. Fraser (1936) suggested that the clasping of females, usually copepodites, by adult males precedes spermatophore transfer. The reproductive cycle of Harpacticus sp. could be similar to that of some sediment-dwelling copepods. Jewett and Feder (1977) showed that Harpacticus uniremis around Port Valdez, Alaska had a single distinct reproductive period. Males clasped females most often in April and gravid individuals began to appear approximately nine months later. The intertidal copepod Platy-chelipus laophontoides had one generation per year and a distinct reproduction period with gravid females being absent for half of the year (Barnett, 1970).

No life-history data for Harpacticus sp. are available for the rest of the year so it is not possible to describe the complete life-history of the organism. Mating evidently takes place on the ice since clasping, which precedes spermatophore transfer, was observed there. Data from other habitats suggest that Harpacticus sp. probably has one or two generations per year (Jewett and Feder, 1977). The inseminated females probably migrate to the bottom when the ice breaks up in late May or early June. It is not known whether copepods recolonize the ice immediately after it reforms around October or later in the ice season. Low densities of diatoms are present in the ice from its formation and through the winter until around April (Clasby et al., 1972), so little

food is presumably available at that time. No Harpacticus sp. adults

were present in the April and early May samples indicating that either

colonization occurred shortly before by copepodites, or that gravid

females had migrated to the ice earlier. There are two possible

explanations as to how gravid females could colonize the ice during the

winter, in the near-absence of food, resulting in the population struc-

ture observed in my samples. First, they may produce resting eggs that

could overwinter in the ice. Overwintering resting eggs that hatch up

to five months after being laid have been found in calanoid copepods

(Grice and Gibson, 1975). Second, it has been shown that certain harpac-

ticoids have nauplii that undergo delayed development (Coull and Dudley,

1976), which could enable some offspring to survive under limited food

conditions. Delayed naupliar development might explain the sudden

influx of early copepodites on 2 June. Nauplii of benthic harpacticoids

cannot swim unlike adults and copepodites (Hauspie and Polk, 1973), so

colonization of the ice could not be by nauplii unless they were advected

to the ice from the sediments.

It is common for sex ratios to vary temporally in species of marine

copepods (Moraitou-Apostolopoulou, 1972; Hicks, 1977). This was true

for Harpacticus sp. and C. gracilis collected from the ice. There was

a general trend in which the percentage of Harpacticus sp. females

increased through the study. Since it appeared that the individuals

belonged to a single season's production of offspring, males may mature

earlier than females. Males reached sizes at which they could be sexed

before females did, as indicated by the initial low percentage of

females in th total sexable segment of the population. Earlier male

maturation has been noted for Huntemania jadensis (Feller, 1980a) and Harpacticus uniremis (Jewett and Feder, 1977). It is not possible to discuss the relative development rates of C. gracilis males and females since recruitment to the population appeared to be continuous; however, Smyly (1961) reported that the males of Cyclops leukarti, a freshwater cyclopoid, mature earlier than females. Females predominated early in the study when the population density was low. This has been found in other marine copepods (Moraitou-Apostolopoulou, 1972).

No life-history strategies unique to the ice environment are evident from the data collected in this study. These two copepod species are not very different in their reproductive activity from other copepods living on the bottom. Previous studies (Coull and Vernberg, 1975; Jewett and Feder, 1977) have shown that the dominant copepod species reproduce continuously, while rarer species in the same environment reproduce seasonally. This might also be true for ice copepods where the dominant species, C. gracilis, was found to reproduce continuously throughout the study, while the less abundant Harpacticus sp. showed seasonal reproduction.

It is not possible to describe the complete life-history of any species when sampling takes place only during one season. The ice scraper samples were used to extend the sampling period as much as possible, even though these samples were taken outside of the study area. The size-frequency distributions of Harpacticus sp. and C. gracilis in these samples generally fit the trends exhibited in the cores. The only exception to this agreement is with the size-frequency distribution of C. gracilis on 14 April. The population appears to be more

mature in this sample than in those collected on 24 April. Small-scale spatial heterogeneity in the population size-structures of benthic organisms has previously been observed (Curtis and Peterson, 1977), and may explain the apparent discrepancy in the size-frequency distributions between 14 April and 24 April. Sampling throughout the year, in the ice when the animals are there, and on the bottom when they inhabit the sediments, is required to fully describe the life-history strategies of these organisms.

This study has shown that frequent sampling is required to observe changes in the population structure of meiofauna. Significant changes in the size-frequency distributions for the two dominant ice copepods occurred on time scales of less than one week. Size-frequency distributions have previously been employed to study copepod life-histories (Lasker et al., 1970; Jewett and Feder, 1977; Fleeger, 1979), but not with samples taken as frequently as in this study. Many copepod species can undergo complete development in the lab, from hatch to hatch, in less than 30 days (Rosenfield and Coull, 1974), so frequent samples must be taken to observe the rapid changes in the populations. Feller (1980b) observed that the lengths of some copepodite stages of Huntemania jadensis overlapped. Although this was true to some extent for both ice species studied, the utilization of size-frequency distributions provided useful information in less time than would be required to identify each copepodite to its stage.

Sub-Ice Fauna Exclusion Experiment

The exclusion of large sub-ice fauna from the ice was expected to result in one or two outcomes. If the excluded organisms prey on ice

fauna, then densities of at least some of the ice species should have been higher inside the cages than outside. Alternatively, if the organisms living within the ice are not utilized as prey by those predators outside the ice, densities of ice species should not have differed between caged and uncaged ice. Some of the groups did not have significantly different abundances in caged ice compared to uncaged ice. This suggests that predation is not an important factor in the sea ice habitat. Other groups, and almost all of the copepod species, were significantly less numerous inside cages. This result is understandable for amphipods since the cages were designed to exclude them. Other taxa may have been less abundant inside cages because of the physical presence of the cages. Cage-effect controls, designed to allow predators access to the ice while simulating the physical presence of normal cages, were deployed but never sampled due to limitations in diver time. Therefore the hypothesis that cages changed the ice beneath them, resulting in lower densities compared to uncaged ice, cannot be tested.

Another complication is the unknown effects of releasing large volumes of air beneath the ice by divers. Most of the air was carried out of the area by the currents flowing directly beneath the ice. Irregularities in the ice undersurface captured some air. The diver was able to sample anywhere within the assigned 0.25 m^2 quadrat when not sampling cages. If the ice was air-damaged within cages, cores still had to be taken from them. The exclusion experiment must be regarded as failing to provide evidence for predation on ice fauna.

SUMMARY

1. The hypothesis that fish and zooplankton utilize ice fauna as food was not supported by this study. It is possible that the cages adversely affected the ice habitat beneath them. Therefore the results of this experiment cannot be regarded as providing strong evidence that the ice fauna are free from predation by animals in the water column.

2. Large densities of several invertebrate taxa, most notably nematodes, copepods, and turbellarians, were present in the fast ice of the Beaufort Sea in 1980. Although the density of the ice fauna was low compared to what is typically found in sediments, it was much greater than had previously been reported from the ice.

3. The life-histories of two copepods, C. gracilis and Harpacticus sp., while inhabiting the ice are similar to the life-histories of exclusively benthic copepods. The ice species were different from each other in terms of their life-histories, so it appears that there is not a life-history strategy unique to the ice. If this is the case, it is surprising that more species do not utilize the ice environment.

LITERATURE

Ackley, S. F., Buck, K. R., Taguchi, S. (1979). Standing crop of algae
    in the sea ice of the Weddell Sea region. Deep-Sea Research 26A:
    269-281.

Alexander, V. (1974). Primary productivity regimes of the nearshore
    Beaufort Sea, with reference to the potential role of ice biota.
    In: Sater, J. E. (ed.) The Coast and Shelf of the Bering Sea, Arctic
    Inst. North America, pp. 609-635.

Alexander, V. (1980). Interrelationships between the seasonal sea ice
    and biological regimes. Cold Regions Sci. and Technol. 2:157-178.

Andriashev, A. P. (1968). The problem of the life community associated
    with the Antarctic fast ice. In: Currie, R. I. (ed.) Symposium
    on Antarctic Oceanography, Scott Polar Research Institute,
    Cambridge, pp. 147-155.

Andriashev, A. P. (1970). Cryopelagic fishes of the Arctic and Antarctic
    and their significance in polar ecosystems. In: Holdgate, M. W.
    (ed.) Antarctic Ecology, Vol. I, Academic Press, London and New
    York, pp. 297-304.

Apollonio, S. (1965). Chlorophyll in Arctic sea ice. Arctic 18:118-122.

Barnes, P. W., Reimnitz, E. (1975). Sedimentary processes on Arctic
    shelves off the northern coast of Alaska. In: Reed, J. C. and
    Sater, J. E. (eds.) Proc. Sympos. Beaufort Sea Coast and Shelf
    Res., Arctic Instit. North America, Arlington, pp. 439-476.

Barnett, P. R. O. (1970). The life cycles of two species of Platy-
    chelipus Brady (Harpacticoida) on an intertidal mudflat. Int.
    Revue ges. Hydrobiol. 55:169-195.

Bunt, J. S., Lee, C. C. (1970). Seasonal primary production in Antarctic
    sea ice at McMurdo Sound in 1967. J. Mar. Res. 28:304-320.

Buzas, M. A. (1978). Foraminifera as prey for benthic deposit feeders:
    results of predator exclusion experiments. J. Mar. Res. 36:617-625.

Carey, A. G., Jr. (1981). The distribution, abundance, composition and
    variability of the western Beaufort Sea benthos. Annual Report of
    Research Unit 6 to the Outer Continental Shelf Environmental
    Assessment Program, NOAA, Boulder, pp. 1-287.

Ceccherelli, V. U. (1976). Preliminary observations on zooplankton
    communities of the "Valli di Comacchio": the copepods. Archivio
    di Oceanografia e Limnologia. 18:411-424.

Clasby, R. C., Alexander, V., Horner, R. (1976). Primary productivity of sea-ice algae. In: Hood, D. W. and Burrell, D. C. (eds.) Assessment of the Arctic Marine Environment, Inst. Mar. Science, University of Alaska, Fairbanks, Occasional Publ. No. 4, pp. 289-304.

Clasby, R. C., Horner, R., Alexander, V. (1972). An in situ method for measuring primary productivity of Arctic sea ice algae. J. Fish. Res. Bd. Can. 30:835-838.

Cohen, E., Burns, P. (1977). SPSS-MANOVA. Document No. 413 (Rev. A). Supplement to SPSS-Statistical Package for the Social Sciences. Volgelback Computing Center, Northwestern University.

Connell, J. H. (1975). Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody, M. L. and Diamond, J. M. (eds.) Evolution of Communities, Harvard University Press, Cambridge, pp. 460-490.

Coull, B. C., Bell, S. S. (1979). Perspectives of marine meiofaunal ecology. In: Livingston, R. J. (ed.) Ecological Processes in Coastal and Marine Systems, Plenum Publishing Corp., New York, pp. 189-216.

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

Coull, B. C., Vernberg, W. B. (1975). Reproductive periodicity of meiobenthic copepods: seasonal or continuous. Mar. Biol. 32: 289-293.

Curtis, M. A., Peterson, G. H. (1977). Size-class heterogeneity within the spatial distributions of subarctic marine benthic populations. Astarte 10:103-105.

Dunbar, M. J., Acreman, J. C. (1980). Standing crops and species composition of diatoms in sea ice from Robeson Channel to the Gulf of St. Lawrence. Ophelia 19:61-72.

English, T. S. (1961). Some biological oceanographic observations in the central north polar sea, Drift Station Alpha, 1957-1958. Arctic Inst. N. Am. Sci. Rep. 15. 79 pp.

Feller, R. J. (1980a). Quantitative cohort analysis of a sand-dwelling meiobenthic harpacticoid copepod. Estuar. cstl. mar. Sci. 2:459-476.

Feller, R. J. (1980b). Development of the sand-dwelling meiobenthic harpacticoid copepod Huntemania jadensis Poppe in the laboratory. J. exp. mar. Biol. Ecol. 46:1-15.

Fleeger, J. W. (1979). Population dynamics of three estuarine meiobenthic harpacticoids (Copepoda) in South Carolina. Mar. Biol. 52:147-156.

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

Gerlach, S. A., Schrage, M. (1971). Life cycles in marine meiobenthos.
    Experiments at various temperatures with Monohystera disjuncta
    and Theristus pertenuis (Nematoda). Mar. Biol. 9:274-280.

Gerlach, S. A., Schrage, M. (1972). Life cycles at low temperatures in
    some free-living marine nematodes. Veroff. Inst. Meeresforsch.
    Bremerh. 14:5-11.

Grice, G. D., Gibson, V. R. (1975). Occurrence, viability, and signiciance
    of resting eggs of the calanoid copepod Labidocera aestiva. Mar.
    Biol. 31:335-337.

Harris, R. P. (1972). Reproductive activity of the interstitial
    copepods of a sandy beach. J. mar. biol. Ass. U. K. 52:507-524.

Harris, R. P. (1973). Feeding, growth, reproduction and nitrogen
    utilization by the harpacticoid copepod, Tigriopus brevicornis.
    J. mar. biol. Ass. U. K. 53:785-800.

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

Hicks, G. R. F. (1977). Breeding activity of marine phytal harpacti-
    coid copepods from Cook Strait. N. Z. Journal of Marine and Fresh-
    water Research 11:645-666.

Hicks, G. R. F. (1979). Pattern and strategy in the reproductive
    cycles of benthic harpacticoid copepods. In: Naylor, E. and Hart-
    noll, R. G. (eds.) Cyclic Phenomena in Marine Plants and Animals,
    Pergamon Press, Oxford and New York, pp. 139-147.

Holland, A. F., Mountford, N. K., Hiegel, M. H., Kaumeyer, K. R.,
    Mihursky, J. A. (1980). Influence of predation on infaunal abun-
    dance in Upper Chesapeake Bay, U.S.A. Mar. Biol. 57:221-235.

Horner, R. A. (1976). Sea ice organisms. Oceanogr. Mar. Biol. Ann.
    Rev. 14:167-182.

Horner, R. A. (1977). History and recent advances in the study of ice
    biota. In: Dunbar, M. J. (ed.) Polar Oceans, Arctic Inst.
    North America, pp. 269-283.

Horner, R., Alexander, V. (1972). Algal populations in Arctic sea ice:
    an investigation of heterotrophy. Limnol. Oceanogr. 17:454-458.

Horner, R. A., Schrader, G. C. (1981). Beaufort Sea plankton studies:
    winter-spring studies in Stefansson Sound and off Narwhal Island,
    Nov 1978-Jun 1980. Final Report of Research Unit 359 to the Outer
    Continental Shelf Environmental Assessment Program, NOAA, Boulder,
    pp. 1-138.

Hsiao, S. I. C. (1980). Quantitative composition, distribution, community structure and standing stock of sea ice microalgae in the Canadian Arctic. Arctic 33:768-793.

Jewett, S. C., Feder, H. M. (1977). Biology of the harpacticoid copepod, Harpacticus uniremis Kroyer on Dayville Flats, Port Valdez, Alaska. Ophelia 16:111-129.

Lasker, R., Wells, J. B. J., McIntyre, A. D. (1970). Growth, reproduction, respiration and carbon utilization of the sand-dwelling harpacticoid copepod, Asellopsis intermedia. J. mar. biol. Ass. U. K. 50:147-160.

Maykut, G. A., Grenfell, T. C. (1975). The spectral distribution of light beneath first-year sea ice in the Arctic Ocean. Limnol. Oceanogr. 20:554-563.

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

McRoy, C. P., Goering, J. J. (1974). The influence of ice on the primary productivity of the Bering Sea. In: Hood, D. W. and Kelley, E. J. (eds.) Oceanography of the Bering Sea, Institute of Mar. Sci., Fairbanks, pp. 403-421.

Meguro, H., Ito, K., Fukushima, H. (1967). Ice flora (bottom type): a mechanism of primary production in polar seas and the growth of diatoms in sea ice. Arctic 20:114-133.

Menge, B. A. (1976). Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecol. Monogr. 46:355-393.

Moraitou-Apostolopoulou, M. (1972). Sex ratio in the pelagic copepods Temora stylifera Dana and Centropages typicus Kroyer. J. exp. mar. Biol. Ecol. 8:83-87.

Rao, G. C. (1967). On the life-history of a new sand dwelling harpacticoid copepod. Crustaceana 13:129-136.

Rosenfield, D. C., Coull, G. C. (1974). Adult morphology and larval development of Paramphiascella fulvofasciata n. sp. (Copepoda, Harpacticoida). Cahiers de Biologie Marine 15:295-317.

Sars, G. O. (1918) Crustacea of Norway, Vol. VI. Bergen Museum, Bergen, 225 pp.

Scheibel, W. (1974). Submarine experiments on benthic colonization of sediments in the western Baltic Sea. II. Meiofauna. Mar. Biol. 28:165-168.

Smyly, W. J. P. (1961). The life-cycle of the freshwater copepod _Cyclops leukarti_ Claus in Esthwaite Water. J. anim. Ecol. 30:153-169.

Tate, M. W., Clelland, R. C. (1957). Nonparametric and shortcut statistics. Interstate Printers and Publishers, Inc. Danville, 171 pp.

Virnstein, R. W. (1977). The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58:1199-1217.

APPENDIX

Table 1. Sampling program used in 1980 sea ice fauna study.

	Uncaged Ice Samples			Caged Ice Samples		
	# of quadrats sampled	# of cores per quadrat	Total # cores from umcaged ice	# of cages sampled	# of cores per cage	Total # cores from caged ice
Date						
4/14	$	—	—	—	—	—
4/24	3*	3	9	—	—	—
5/5	3	3	9	—	—	—
5/11	3*	2	6	—	—	—
5/15	3	2	6	3	2	6
5/19	3	2	6	3	2	6
5/26	3	2	6	3	2	6
6/2	3	2	6	3	2	6
6/5	$	—	—	—	—	—

$: Ice scraper samples taken within 40 m of study grid; used only for life-history studies.

*: Cores taken slightly outside study grid.

Table 2. Mean abundance per 100 cm^2 for major taxa collected on each sampling date. $\overline{X}$: Mean, SD: Standard deviation. The results of one-way ANOVA's are given at right.

Group	4/24 $\overline{X}$	SD	5/5 $\overline{X}$	SD	5/11 $\overline{X}$	SD	5/15 $\overline{X}$	SD
Nematoda	3.59	1.95	9.23	10.51	34.84	33.92	6.36	17.74
Copepoda	50.94	28.13	27.21	13.62	24.63	10.06	57.74	27.59
Turbellaria	2.96	2.53	2.06	2.15	4.82	3.45	6.16	4.42
Polychaeta	51.07	65.30	14.63	19.51	1.35	0.87	9.62	13.12
Amphipoda	2.82	2.09	2.18	2.34	2.31	1.63	6.54	4.04

Group	5/19 $\overline{X}$	SD	5/26 $\overline{X}$	SD	6/2 $\overline{X}$	SD	Significant Change over time? (P)	
Nematoda	175.34	129.66	186.71	145.44	250.22	76.63	Yes	(<.002)
Copepoda	109.71	56.63	125.11	81.39	69.87	36.51	Yes	(<.002)
Turbellaria	52.93	14.56	26.56	9.49	151.67	22.65	Yes	(<.002)
Polychaeta	7.89	6.42	18.10	21.86	8.08	5.89	Yes	(<.002)
Amphipoda	9.24	7.04	11.93	7.47	2.51	1.99	Yes	(<.002)

Table 3. Mean abundance per 100 cm^2 for the five dominant copepod species on each sampling date. $\overline{X}$: Mean, SD: Standard deviation. The results of one-way ANOVA's are given last.

Group	4/24 $\overline{X}$	SD	5/5 $\overline{X}$	SD	5/11 $\overline{X}$	SD	5/15 $\overline{X}$	SD
Cyclopina gracilis	22.97	13.26	15.27	9.43	10.20	5.99	29.65	18.00
Harpacticus sp.	10.39	7.96	6.55	4.65	5.58	3.13	11.74	6.83
Halectinosoma sp.	15.52	11.41	4.11	2.45	8.08	2.92	9.82	7.37
Oncaea sp.	0.51	0.84	0.25	0.51	0.38	0.60	2.51	2.36
Dactylopodia signata	0.77	1.15	0.13	0.38	0.0	-	0.0	-

Group	5/19 $\overline{X}$	SD	5/26 X	SD	6/2 X	SD	Significant change over time?	(P)
Cyclopina gracilis	60.78	34.24	76.99	40.73	34.65	27.27	Yes	(<.002)
Harpacticus sp.	31.56	15.16	17.90	10.65	20.59	13.45	Yes	(<.002)
Halectinosoma sp.	14.05	12.38	27.52	34.51	8.08	5.01	No	
Oncaea sp.	1.35	0.87	0.38	0.95	1.73	2.71	Yes	(<.05)
Dactylopodia signata	0.77	1.19	0.35	0.95	0.0	-	No	

Table 4. Summary of life-history data for <u>Harpacticus</u> sp. and
          <u>Cyclopina</u> <u>gracilis</u>.

<u>Cyclopina</u> <u>gracilis</u>

Date	% Females of Adults	% Females of all Sexable	% Adults	% Gravid Females of Adult Females
4/14	94.4	96.0	18.0	0.0
4/24	79.2	68.1	4.9	11.1
5/5	58.2	67.4	56.3	0.0
5/11	32.4	39.5	64.2	9.1
5/15	34.0	41.5	65.4	5.9
5/19	36.1	46.8	46.8	1.9
5/26	43.8	48.1	47.3	4.9
6/2	45.0	47.4	55.6	0.0
6/5	55.0	57.1	60.0	0.0

<u>Harpacticus</u> sp.

Date	% Females of Adults	% Females of all Sexable	% Adults	% Gravid Females of Adult Females
4/14	-	-	0.0	-
4/24	-	25.0	0.0	-
5/5	-	40.5	0.0	-
5/11	11.1	45.0	31.0	0.0
5/15	16.7	34.4	70.0	0.0
5/19	22.8	39.1	62.6	0.0
5/26	42.7	53.8	80.6	6.8
6/2	33.9	56.0	55.1	12.8
6/5	35.3	56.5	51.0	0.0

Table 5. Abundance of major taxa collected from sea ice in the Antarctic (Andriashev, 1968) and the Beaufort Sea. Values given are number per m^2. No values for Nematoda or Turbellaria were available from the Antarctic. The minimum densities for taxa collected from the Beaufort Sea were calculated using the lowest mean number per core; the maximum using the highest mean number per core.

Group	Antarctic	Beaufort Sea Minimum	Maximum
Polychaeta	Solitary Individuals	135	5,107
Cyclopoida	Up to Several Hundreds	1,058	7,737
Harpacticoida	Scores to Hundreds	1,079	4,638
Amphipoda	Up to 3040	218	1,193
Nematoda	-----------	359	25,022
Turbellaria	-----------	206	15,167
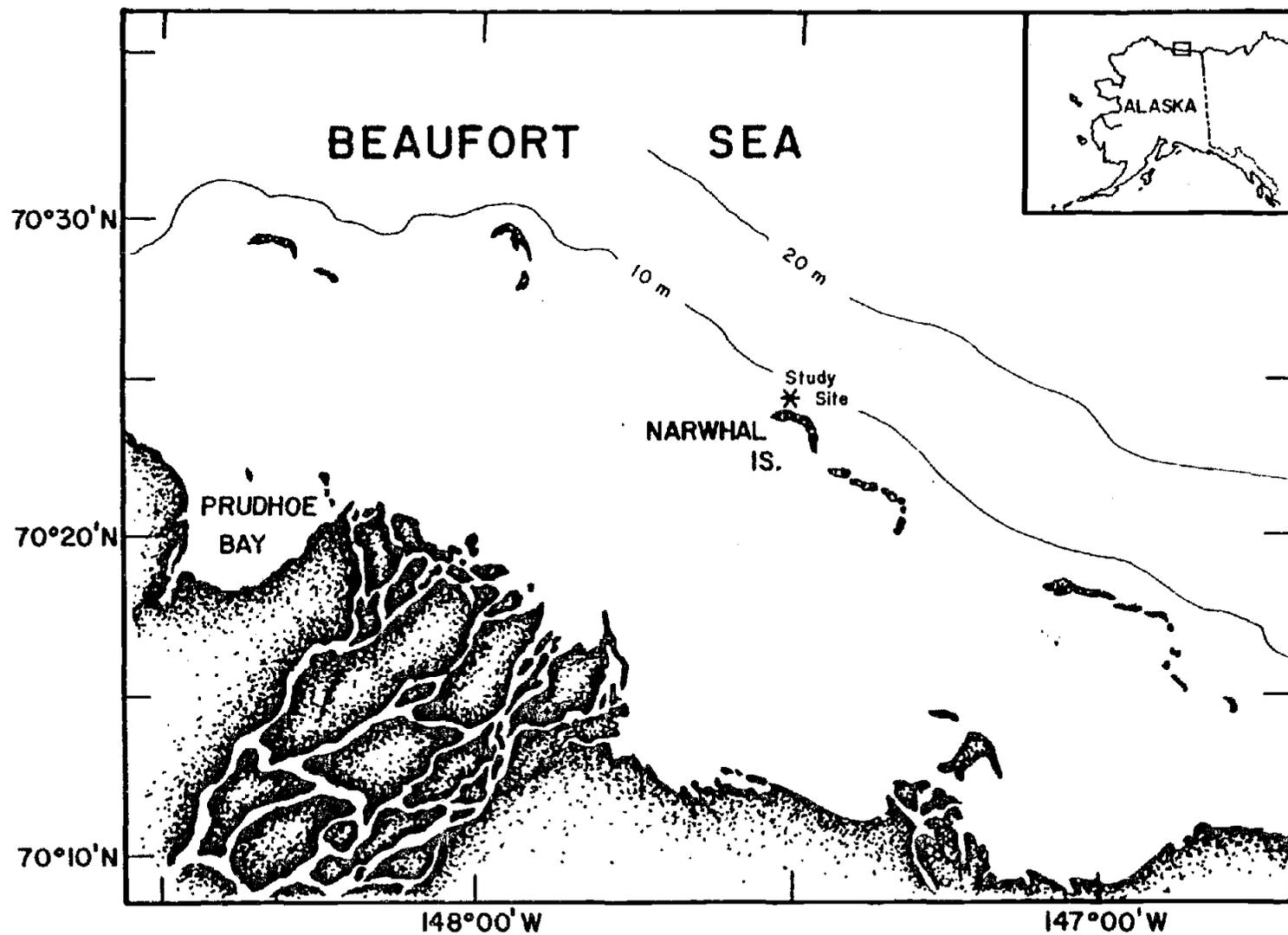
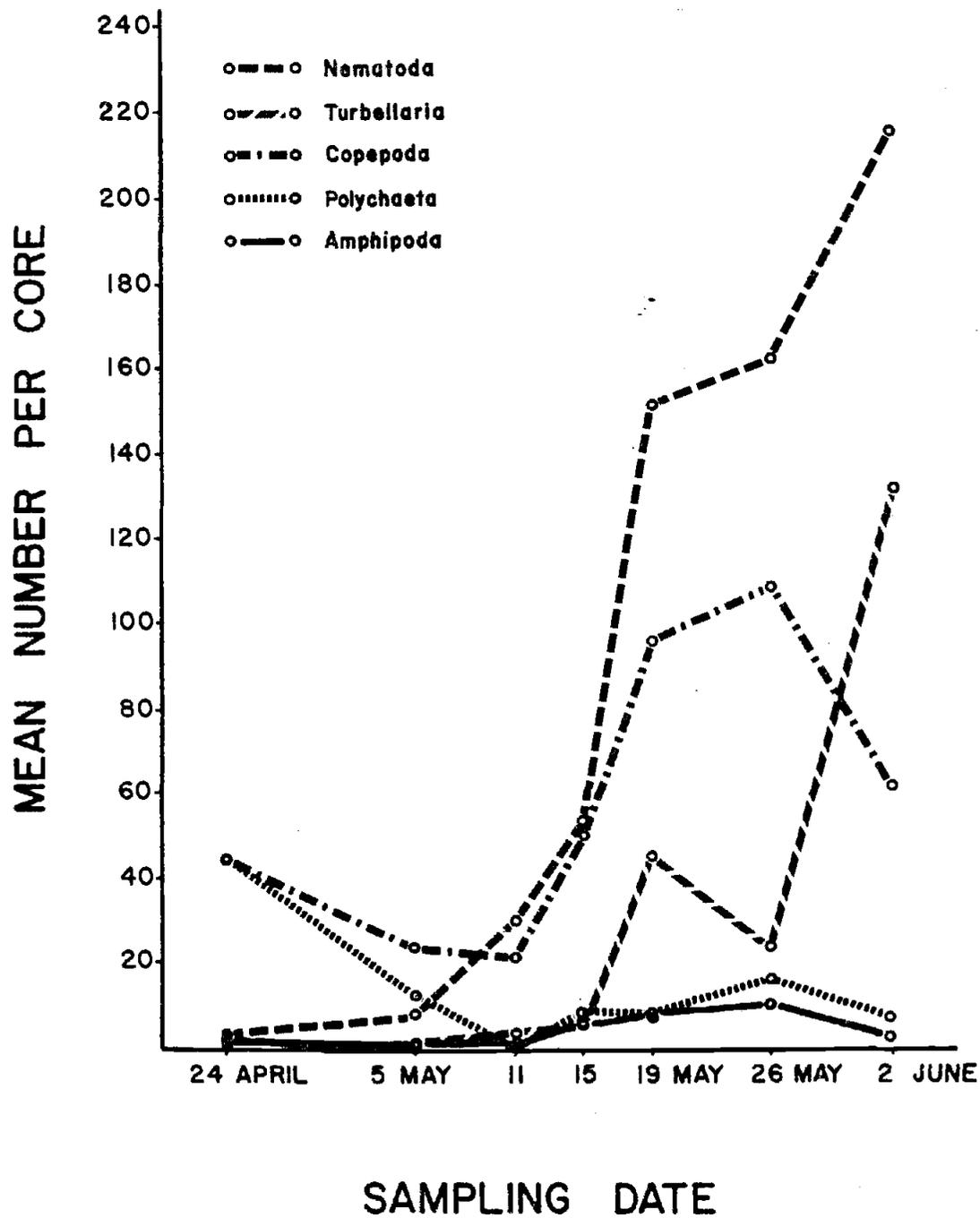Figure 1. Location of the Narwhal Island study site.

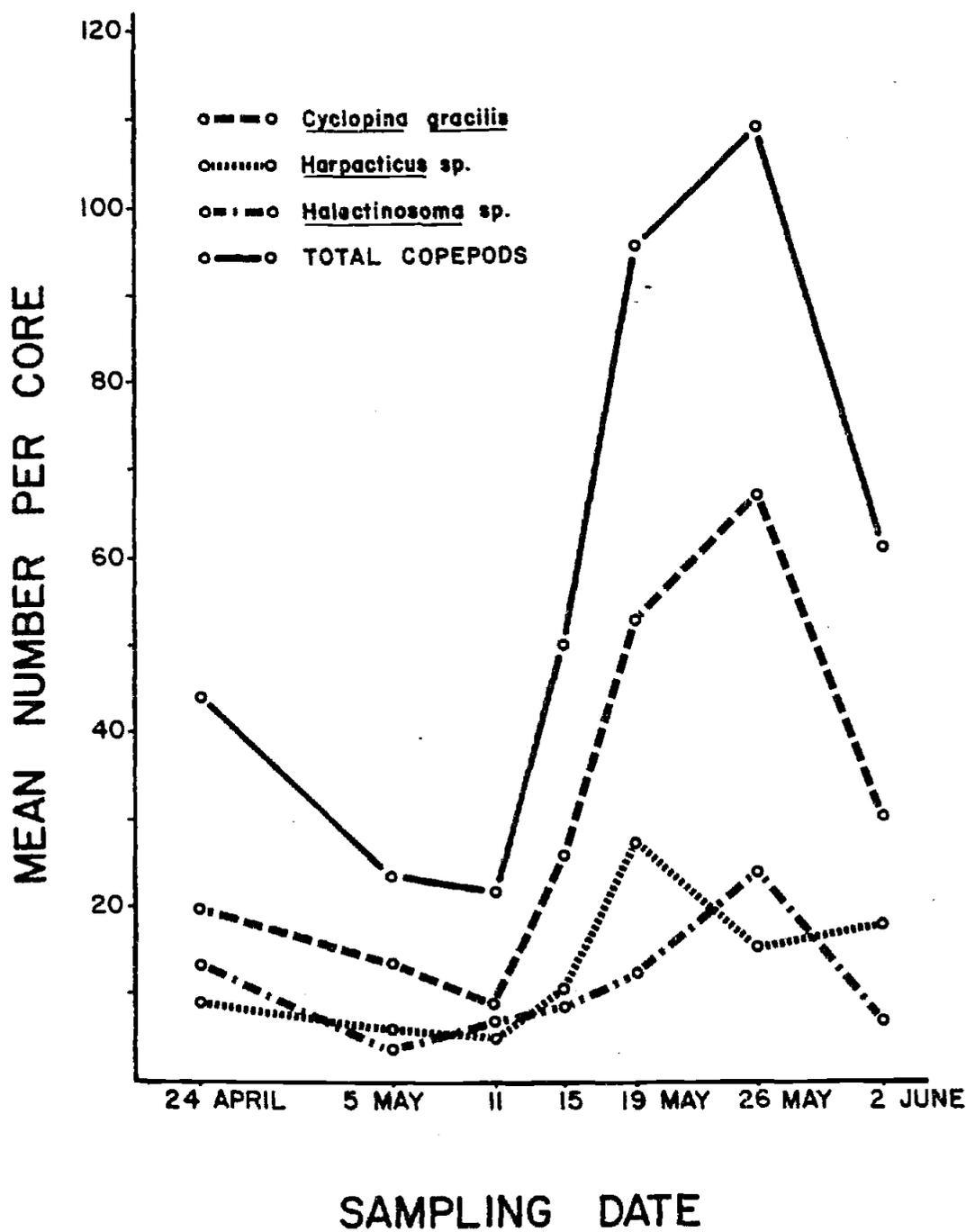Figure 2. Abundance trends for major taxa.

Figure 3. Abundance trends for total copepods, and each of the three dominant species.

Figure 4. Size-frequency distributions of <u>Harpacticus</u>
sp. over time. Dates marked with an asterisk
indicate that the size-frequency distribution
is significantly different from the date
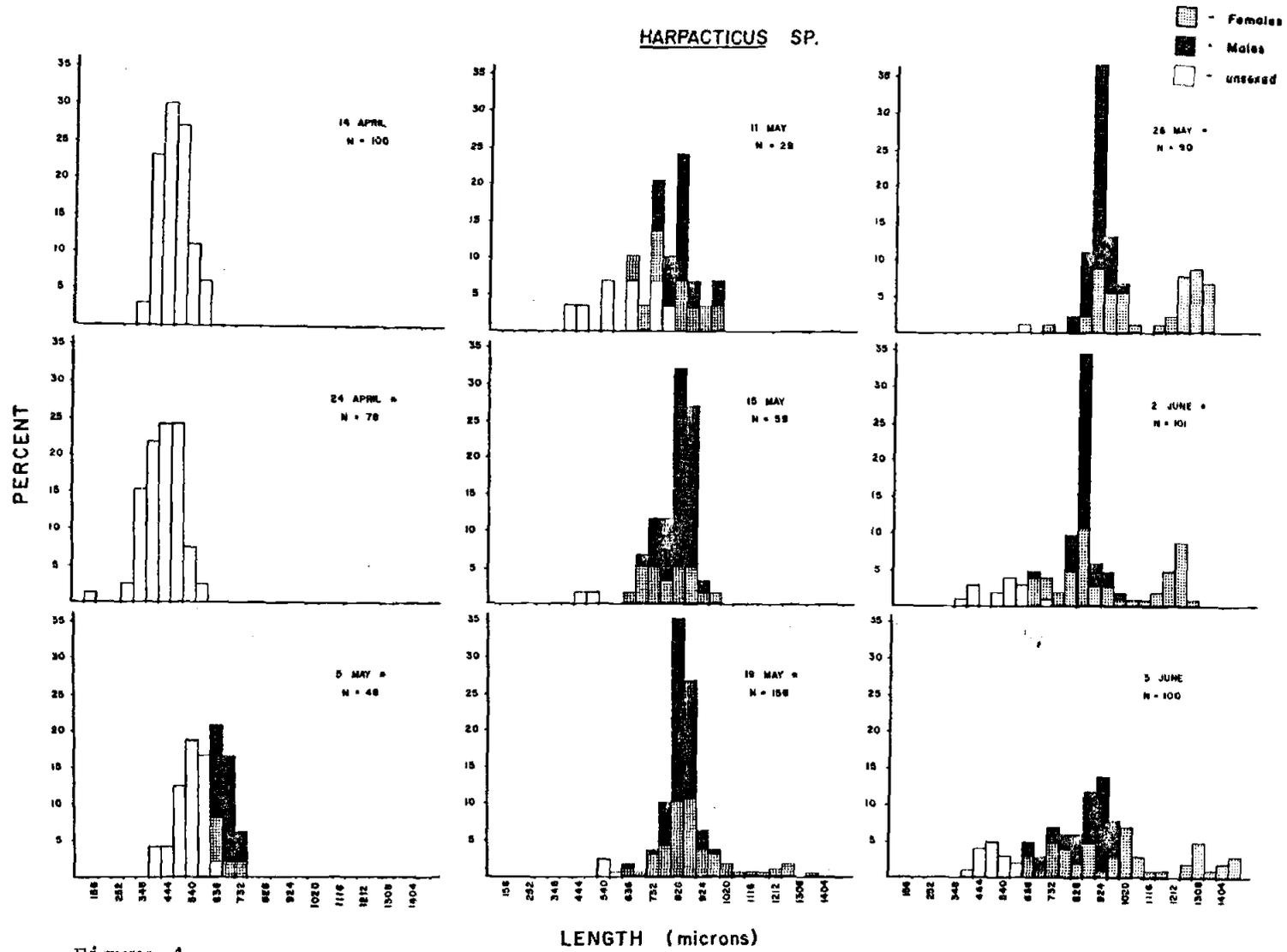immediately following it (Kolmogorov-Smirnov
test).

HARPACTICUS SP.

Figure 4.

LENGTH (microns)

PERCENT

Figure 5. Size-frequency distributions of <u>Cyclopina</u>
<u>gracilis</u> over time. Dates marked with
an asterisk indicate that the size-frequency
distribution is significantly different from
the date immediately following it (Kolmogorov-
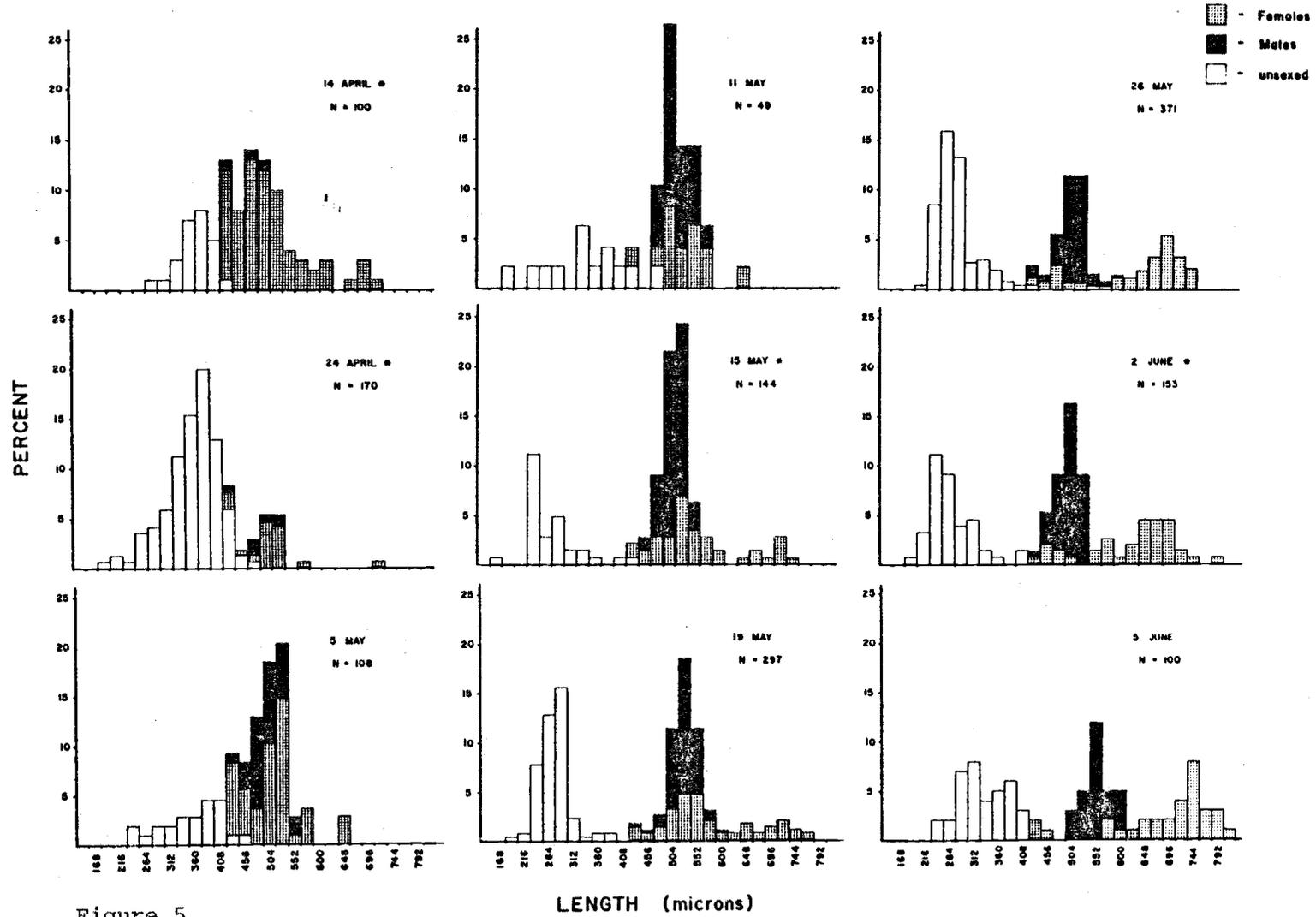Smirnov test).

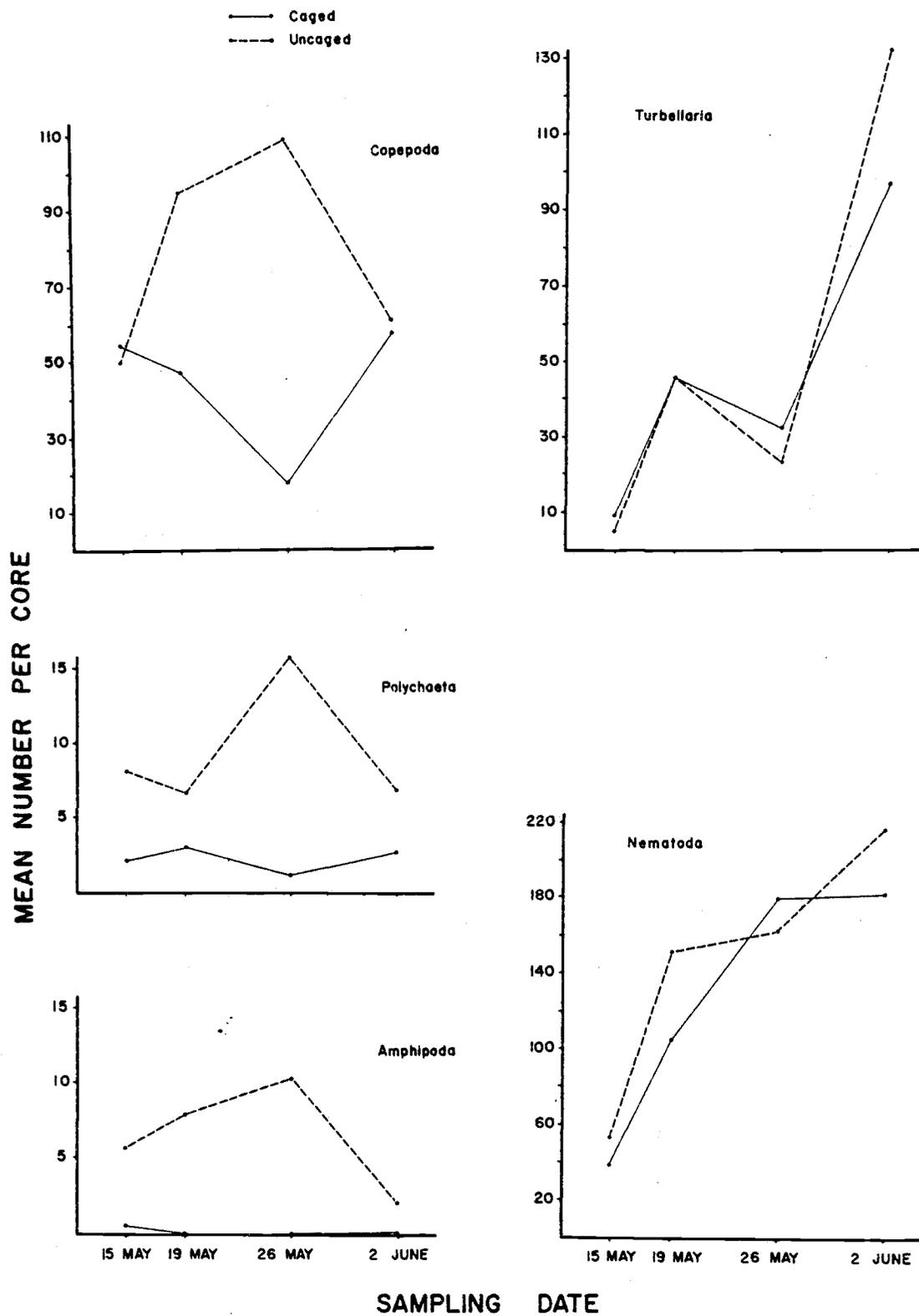CYCLOPINA GRACILIS

Figure 5.

LENGTH (microns)

PERCENT

Figure 6. Plot of major taxa densities in caged and uncaged areas of the ice over time.