

Under-ice Biota at the Pond Inlet Ice Edge and in Adjacent Fast Ice Areas during Spring

WILLIAM E. CROSS¹

ABSTRACT. Distributions of nutrients, flora and fauna on the bottom of the ice in Pond Inlet during May-July 1979 were examined with respect to distance from the landfast ice edge, but temporal variability and local spatial variability confounded interpretation. Timing of the ice algal bloom was most delayed under fast ice where snow depth was thickest and was negatively correlated with chlorophyll *a* content in bottom ice. The bloom occurred first at the ice edge where snow and ice thickness were least and were positively correlated with ice chlorophyll. Standing stocks of ice microalgae at each station were dominated by pennate diatoms, especially *Nitzschia grunowii* and *N. frigida*, and were not closely related to distance from the ice edge.

High densities of nematodes and harpacticoid and cyclopoid copepodites in the bottom layer of ice were associated with high densities of microalgae, and maximum meiofaunal densities (~50 000 individuals · m⁻²) occurred in masses of algae sloughing off the ice. Macrofaunal communities on the under-ice surface included 9 amphipod and 1 mysid species, and were dominated by *Apherusa glacialis*, *Ischyrocerus anguipes* and *Onisimus* spp. Individuals of these species grew significantly from May to July. Macrofaunal densities were highly variable among both samples and stations, and were not obviously related to distance from the ice edge after allowing for local habitat effects, including influences of ice type (increased densities in rough ice), meltwater (decreased densities) and pan ice (increased densities).

Key words: under-ice, ice edge, fast ice, Pond Inlet, ice microalgae, ice fauna, amphipods, chlorophyll, nutrients

RÉSUMÉ. De mai à juillet 1979, nous avons examiné les distributions de nutriments, de la flore et de la faune sur la partie inférieure de la glace de Pond Inlet. Ces organismes ont été étudiés en relation avec la distance aux bords de la banquise continue. Les variations temporelles et spatiales observées ont bouleversé les interprétations. La croissance des algues de la glace a été surtout retardée sous la banquise continue où la profondeur de la neige était à son maximum, et était de plus corrélée négativement avec la chlorophylle *a* contenue au bas de la glace. La croissance a débuté premièrement au bord de la glace où l'épaisseur de celle-ci et de la neige était minimale et était corrélée positivement avec la chlorophylle de la glace. A chaque station, le nombre total des micro-algues de la glace immobile était composé principalement de diatomées pennées, surtout *Nitzschia grunowii* et *N. frigida*, et n'était pas étroitement relié à la distance du bord de la glace.

De fortes densités de nématodes et de copépodites harpacticoides et cyclopoïdes dans la couche inférieure de la glace étaient associées à de grandes densités de micro-algues. Les densités maximales de la meiofaune (~ 50 000 individus/m²) se trouvaient dans des masses d'algues se détachant de la glace. Les communautés de la macro-faune trouvées en surface du dessous de la glace comprenaient neuf (9) espèces d'amphipodes et une espèce de mysid et étaient dominées par *Apherusa glacialis*, *Ischyrocerus anguipes* et *Onisimus* spp. Les individus de ces espèces se sont développés significativement de mai à juillet. Les densités de macro-faune étaient très variables parmi les échantillons et les stations, et n'étaient pas reliées de façon évidente à la distance du bord de la glace après avoir considéré les effets de l'habitat local. Ceux-ci incluent le type de glace (augmentation de densités dans la glace rugueuse), l'eau provenant du dégel (densités décroissantes) et la banquise flottante à surface unie (densités croissantes).

Traduit par Pierre Bibeau, Arkéos Inc., Montréal.

INTRODUCTION

The observed high numbers and feeding activity of birds and mammals at solid ice edges and the edges of offshore pack ice fields (e.g. Uspenski, 1956; Watson and Divoky, 1972; Bradstreet, 1979, 1980) has led to speculation about increased primary productivity in these interface areas, particularly in the Bering Sea where most such studies have been carried out. McRoy (1968) suggested that the ice margin was a zone of intense ice algal production, and Fay (1974) further speculated that the southward transport of ice algal production from areas to the north accounted for the 'rich trophic system' in and near the ice front. Goering and McRoy (1974) suggested that nutrient cycling by marine birds and mammals increased nutrient concentrations in the waters around the ice edge. More recent studies in the Bering Sea have shown that the ice margin zone is indeed an area of increased phytoplankton production relative to open water to the south and ice-covered water to the north (McRoy and Goering, 1974, 1976; Alexander, 1981). This was attributed to increased light penetration and a shallow mixed layer of water resulting from ice melt (McRoy and Goering, 1974, 1976). A further rea-

son for increased productivity at ice edges, the upwelling of deep, nutrient-rich water under certain wind conditions, was predicted by Clarke (1978) and observed by Buckley *et al.* (1979).

Fewer speculations or data exist on secondary production at ice/water interfaces. Uspenski (1956) reported (without substantiation) that in the Barents Sea adult zooplankton congregated to reproduce near the ice edge during April and May, and that fish then concentrated to feed on the developing zooplankton from June to August. Cooney (1981), however, reported that zooplankton distribution in the Bering Sea was controlled by water mass properties independent of ice cover. Niebauer *et al.* (1981) estimated that phytoplankton in the ice margin zone were consumed by zooplankton or were available as a source of food for benthos, depending on the position of the ice edge relative to oceanic and shelf water masses. Fay (1974) cited Russian reports that the ice front region supported abundant benthos and important winter fisheries.

Another source of secondary production that may attract birds and mammals to ice/water interfaces is under-ice

¹LGL Limited, environmental research associates, 44 Eglinton Avenue West, Toronto, Ontario, Canada M4R 1A1

biota. In Barrow Strait, N.W.T., Bradstreet (1979, 1980) observed alcids diving under the ice edge to feed, and found that their diets included taxa known to be ice-associated, including the arctic cod *Boreogadus saida* and the amphipod *Onisimus glacialis*. Under-ice amphipods can be abundant (e.g. $36 \text{ g} \cdot \text{m}^{-2}$ — Golikov and Scarlato, 1973) and local swarms of amphipods whose stomachs contained ice algae have been observed in abundances as high as 105 000 individuals ($400 \text{ g} \cdot \text{m}^{-2}$ (W.E. Cross, pers. obs.)). Given a trophic link between ice flora and amphipods, and limited evidence of phototropism in ice amphipods (Lewis and Milne, 1977), under-ice amphipods may concentrate along ice edges in response to increased light or increased ice algal production. Arctic cod, birds and mammals may in turn congregate along ice edges to feed.

The present study examines the distribution and abundance of ice biota with respect to distance from the Pond Inlet ice edge during spring 1979. It is a companion paper to studies dealing with vertebrate distribution and habitat use (Bradstreet, 1982) and vertebrate and invertebrate diets (Bradstreet and Cross, 1982). Collectively, their purpose is to identify biological phenomena responsible for

the concentrations of vertebrates at the Pond Inlet ice edge in spring.

MATERIALS AND METHODS

Study Location

Studies were carried out in Pond Inlet during two sampling periods: 2-20 May and 18 June-2 July 1979 (Fig. 1). During May, three fast ice stations (1-3) and two ice edge stations (4, 5) were sampled by divers. During late June, five ice edge stations (6, 7, 9, 11, and 12) and two stations near the edge (8, 10) were sampled by divers, and on 1 and 2 July sampling was repeated at fast ice stations 2 and 3. Samples of ice and water for chlorophyll and nutrient determinations were collected from the surface along the ice edge and at two fast ice stations (1, 2) in each sampling period. Along the ice edge, 16 locations at roughly 400 m (June) or 1-1.5 km (May) intervals were sampled at 5, 25 and 75 m distances from the edge. At each fast ice station, 25 sampling locations within approximately 4 km of the dive hole were randomly selected in May and relocated as closely as possible during June.

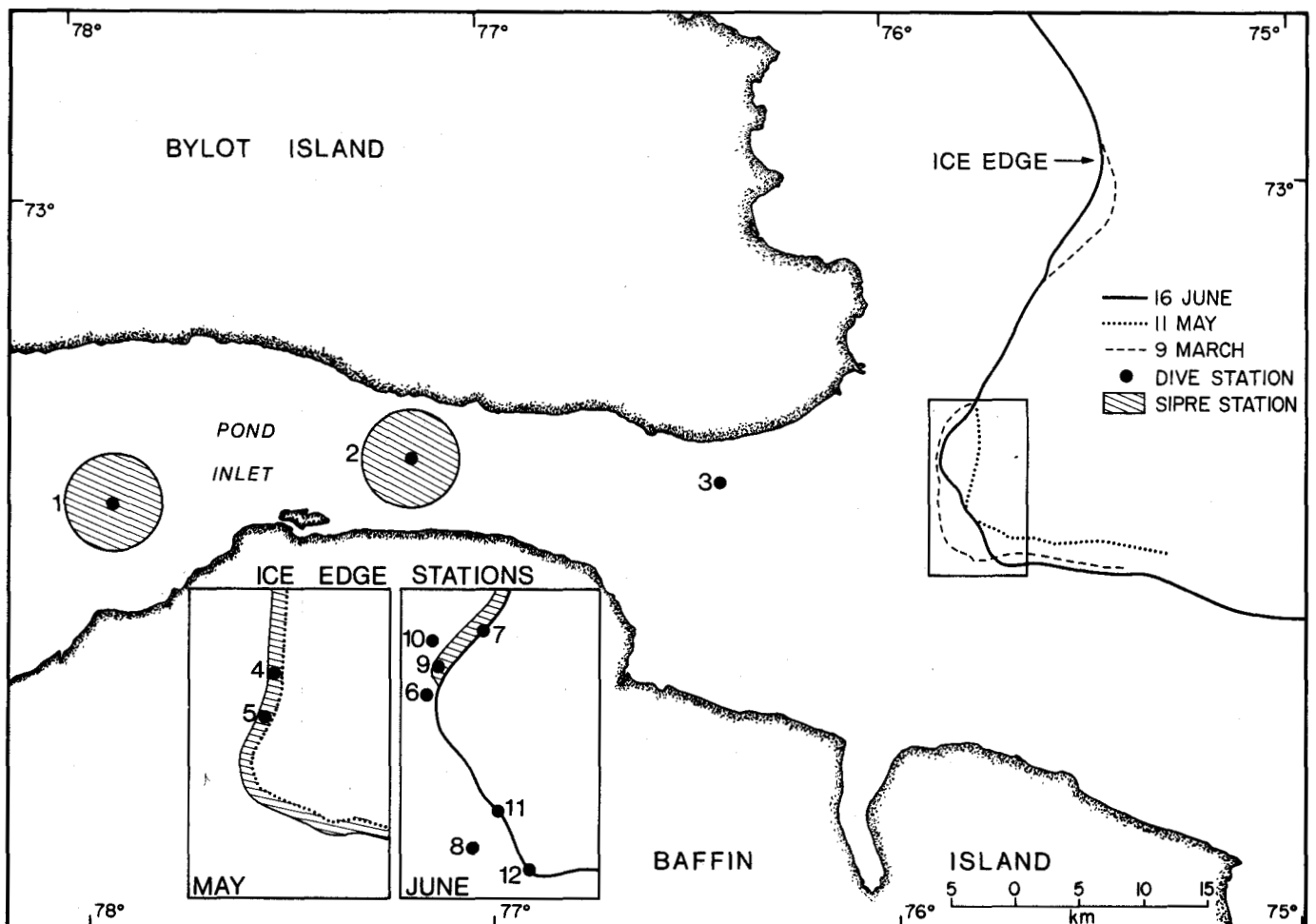


FIG. 1. Positions of the Pond Inlet ice edge during March-June 1979 (based on LANDSAT photographs) and sampling locations during May-June 1979.

Sampling Procedures

Diver sampling. Two SCUBA divers worked through holes in the ice or over the ice edge (stations 11 and 12). For all stations, qualitative observations of surface and underwater ice features and the habitat use, behaviour and distribution of under-ice biota were recorded during debriefing sessions. At some stations macroinvertebrates were collected qualitatively from the under-ice surface. Fish were counted and as many as possible were captured with 'slurp guns' and dip nets.

All systematic sampling was at least 5 m from the entry hole to avoid disturbance artifacts. At stations with apparently homogeneous ice conditions, sampling locations were selected randomly, whereas at stations with heterogeneous habitat we tried to sample each habitat type. (A) Macrofauna (mainly amphipods) on the under-ice surface were sampled first to avoid sampling in areas previously disturbed by respired SCUBA air. At each station, 7-11 samples were collected by scraping fine mesh (1 mm) dip nets with a 40 cm flat top for 10 m distances along the under-ice surface. (B) Fauna occurring within the bottom layer of ice (and hence not sampled in nets) were collected in May with 10 cm diameter corers with 76 μm mesh netting (5-10 samples per station), and enumerated during both sampling periods by taking 7-35 color slides of known area (0.03 m^2) on the ice undersurface at each station using a Nikonos 35 mm camera and electronic flash. (C) Ice microalgae were sampled (3-5 samples per station) with 2.5 cm diameter stainless steel corers driven 10 cm into the ice from below, and subsequently removed and capped at both ends.

Estimates of macrofaunal densities based on photographs and on cores indicated that the nets used for systematic sampling were not entirely effective in collecting under-ice fauna. Nets were least effective in sampling under rough, irregular ice and in collecting *Onisimus* spp. and *Apherusa* juveniles; these amphipods occurred within the bottom layer of ice.

Remote sampling. Samples of the bottom layer of ice were collected by drilling through the upper layers of ice with a gasoline-powered ice auger, and then using a SIPRE ice corer to obtain a 7.5 cm diameter core of the lower 0.5 m of ice. The bottom 20 cm section was severed with a hacksaw and the percentage of the soft, discolored layer that was missing from the core bottom was estimated. Correction factors based on these estimates were applied to chlorophyll data; diver observations of SIPRE coring under bloom conditions in May indicated that these estimates were good indicators of the amount of ice and algae lost during coring. At each location, a plastic pump with a weighted length of flexible tubing was used to collect a 1000 mL water sample from about 15 cm below the ice. Immediately after collection, all samples were placed in darkened polyethylene containers and stored in insulated boxes to prevent freezing. Ice and water samples were

transported to the field laboratory and processed within 12 h of collection.

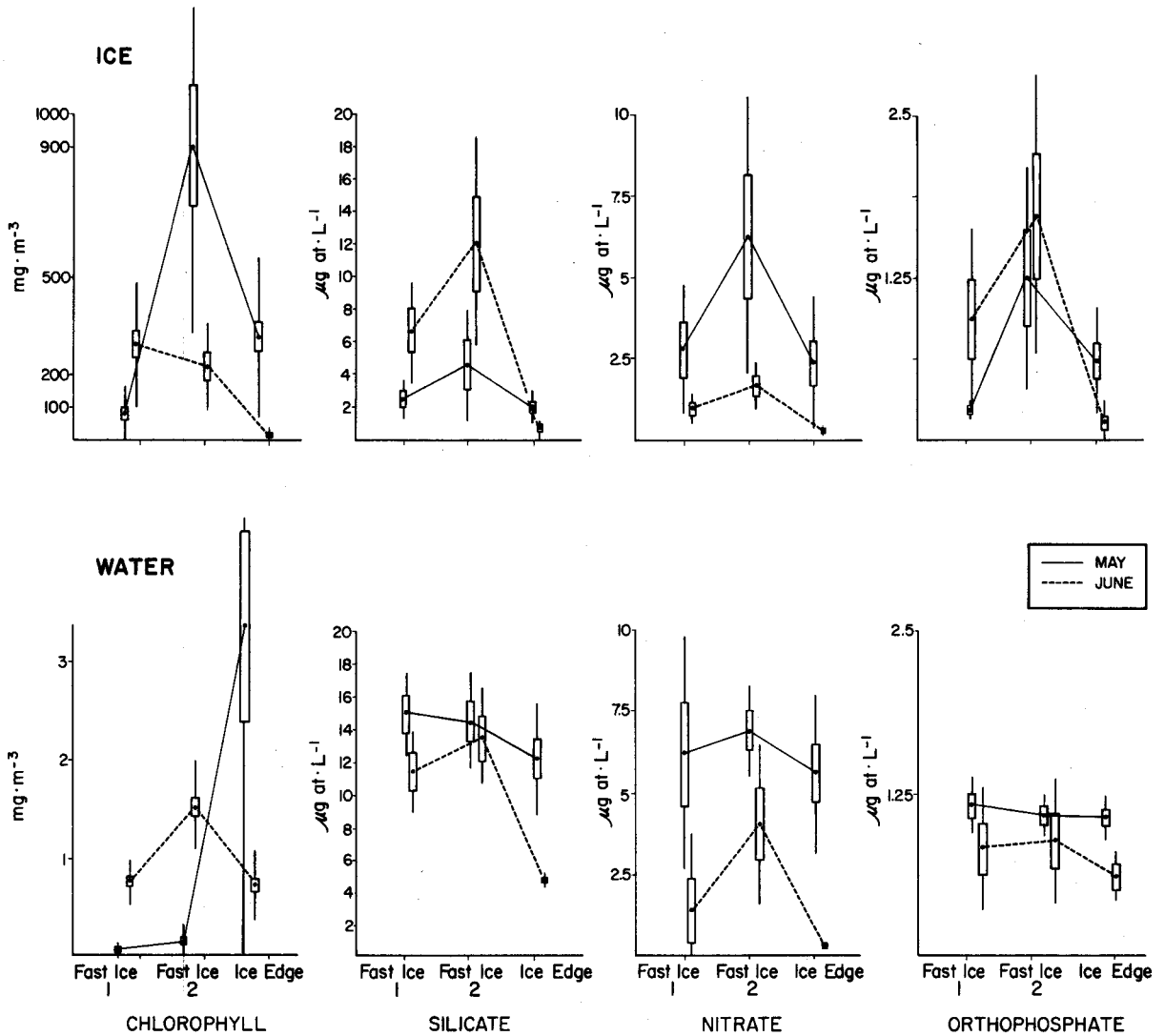
Laboratory Analysis

Diver-collected ice cores were transferred to glass jars, allowed to melt, and fixed in 3% formalin. Subsamples of 5 mL were identified and enumerated using a modification of the inverted microscope method of Utermöhl (1958) and magnifications to 625X. Invertebrates from net and core samples were preserved in 10% formalin. Amphipods, copepods and mysids were identified to species (when-ever possible), counted and weighed, and amphipod lengths were measured to the nearest mm. Amphipods of the genera *Apherusa* and *Onisimus* and mysids of the genus *Mysis* were not identified to species if <6 mm long. Wet weights were obtained by gently blotting dry and weighing on a Mettler PT200 balance to the nearest milligram.

Within 12 h of collection, SIPRE ice cores were thawed in a warm water bath (approx. 50°C) and removed as soon as all ice had melted. Subsamples (80-750 mL) of well-mixed melted ice, and entire water samples (1000 mL), were vacuum filtered through Millipore HA (0.45 μm) filters. Samples for chlorophyll determination were treated with MgCO_3 near the end of filtration, and the filters were placed in individual glassine envelopes and frozen in plastic bags containing silica gel. The filtrate from one of every five samples was also kept for nutrient analysis. For these samples, all glassware and polyethylene containers were acid-washed, and filters were pre-rinsed with 300 mL of distilled water. Three 50 mL samples of filtrate were taken before the addition of MgCO_3 , and preserved with either one or two drops of chloroform (for phosphate and silicate analyses) or two drops of conc. sulphuric acid (for nitrate-nitrite analysis), and frozen.

Chlorophyll *a* was extracted in 90% acetone according to the SCOR/UNESCO procedure (Strickland and Parsons, 1972:195) with the exception that the homogenized sample was stored for approximately 20 h (refrigerated and in the dark) before centrifugation and fluorescence determination. Relative fluorescence was determined using a Turner Model 430 spectrofluorometer at excitation and emission wavelengths of 440 and 670 nm, respectively (Yentsch and Menzel, 1963; Turner, 1973). A solution of unused Millipore filters extracted in 90% acetone was used as a blank. Chlorophyll extracts were diluted so that relative fluorescence readings were ≤ 1.0 to eliminate fluorescence quenching. Relative fluorescence readings were applied to a calibration curve determined for known concentrations (1.0-1000.0 $\text{mg}\cdot\text{m}^{-3}$) of purified chlorophyll *a* (Sigma Chemical Co., 99% pure) in 90% acetone.

Orthophosphate (PO_4^{3-}), nitrite (NO_2^-), nitrate + nitrite ($\text{NO}_3^- + \text{NO}_2^-$) and reactive silicate (SiO_3^{4-}) concentrations were determined on thawed samples using a Technicon Auto-Analyzer II continuous flow system and standard Technicon analysis procedures.



2-way ANOVA

Ice	Station	***	***	***	**
	Month	***	<i>ns</i>	***	<i>ns</i>
	Interaction	***	***	<i>ns</i>	*
Water	Station	***	***	***	<i>ns</i>
	Month	***	***	***	*
	Interaction	***	***	*	<i>ns</i>

1-way ANOVA (LSD)

Ice	May	*** (1<23; 2>3)	<i>ns</i>	<i>ns</i>	<i>ns</i>
	June	*** (12>3)	*** (12>3)	*** (12>3)	*** (2>3)
Water	May	*** (12<3)	<i>ns</i>	<i>ns</i>	<i>ns</i>
	June	*** (2>13)	*** (12>3)	*** (2>13)	<i>ns</i>

ns = P > 0.05 * P ≤ 0.05 ** P ≤ 0.01 *** P ≤ 0.001

FIG. 2. Concentrations of chlorophyll *a* and nutrients in bottom ice and near-ice water from Pond Inlet during 2-9 May and 18-24 June 1979, and results of ANOVA and multiple comparisons (Least Significant Difference, $P < 0.01$). Vertical lines are \pm SD and boxes are \pm SE. Sample sizes in each month were 19-25 for chlorophyll *a* and 5 for nutrients at each fast ice station, and 46-48 for chlorophyll *a* and 8-18 for nutrients at the ice edge.

RESULTS

Chlorophyll a and Nutrients

Data on chlorophyll *a* and three nutrients were obtained from bottom ice and near-ice water samples collected during 2-9 May and 18-24 June at two fast ice stations (1, 2) and at three distances (5, 25, and 75 m) from the ice edge. No variable differed significantly among the three 'distance from ice edge' categories in either month (ANOVA, lowest $P = 0.130$), so data from the three distances (5-75 m from ice edge) were pooled for subsequent analyses. All analyses were based on log-transformed data.

Chlorophyll a. Chlorophyll *a* content in bottom ice varied significantly among locations and between the months of May and June (2-way ANOVA, $P < 0.001$). However, the significant interaction term, one-way analyses for each month, and inspection of the data all showed that the pattern of among-station variation differed from month to month (Fig. 2). Chlorophyll *a* content in the ice increased from May to June at fast ice station 1, but decreased at fast ice station 2 and at the ice edge (Fig. 2).

Chlorophyll *a* content in the water about 15 cm below the ice also varied significantly among locations and between months, and again the pattern of among-station variation differed between months (Fig. 2). Chlorophyll *a* content in the water increased from May to June at both fast ice stations, but decreased at the ice edge. The increase under fast ice may have resulted from increased light penetration and the progress of the phytoplankton bloom, but was more likely due to the increased amounts of detritus (small, evenly dispersed strands of microalgae) that divers observed in the water column during June. This detritus was probably ice algae that had sloughed off the ice and fragmented. In May, the only concentrations of algae or detritus observed by divers at the ice edge were masses and strands of pennate diatoms on the under-ice surface. Contamination of water samples by this algal material displaced from the under-ice surface during sampling was likely responsible for the high and variable chlorophyll *a* content of water samples from under the ice edge in May.

Nutrients. Nitrate content in ice and water decreased markedly ($P < 0.001$) from May to June, as did silicate content in the water. There were no major differences between months in silicate content in the ice or in orthophosphate concentrations in water or ice (Fig. 2). Significant interaction effects ($P < 0.001$) confound interpretation of silicate concentrations in both ice and water; however, there was some evidence of a seasonal decrease in silicate concentration in both ice and water near the ice edge.

In May, among-station variation in nutrient concentrations was not significant for any nutrient in either ice or water, whereas in June among-station variation was highly significant for all ice nutrients and for all water nutrients but orthophosphate ($P < 0.001$; Fig. 2). Nutrients were generally less abundant at the ice edge than under fast ice; this

trend was present but non-significant in May, and was present and generally significant (LSD, $P < 0.01$) in June. Differences between fast ice stations were significant only in the case of nitrate content in the water.

Concentrations in ice and water. Chlorophyll *a* concentrations were always much higher in ice than in corresponding water samples (Fig. 2); the difference was greatest at fast ice stations in May (differed by $> 10^3$ x) and smallest at the ice edge in June (but still > 10 x). Nutrient concentrations were generally of the same order of magnitude in ice and water (Fig. 2), although nitrate and silicate concentrations were often somewhat higher (up to 6x) in water than in ice. Ice algae and nutrients are, however, concentrated in the bottom few centimetres of ice (Meguro *et al.*, 1967; Grainger, 1977) whereas our results are average concentrations in the bottom 20 cm. The above values thus underestimate actual concentrations of chlorophyll *a* and nutrients in the soft bottommost layer of ice, perhaps by an order of magnitude.

Chlorophyll a vs. snow depth. The correlation between snow depth and ice chlorophyll was negative but non-significant at fast ice station 1, negative at fast ice station 2 ($P < 0.001$), and positive at the ice edge ($P < 0.01$; Fig. 3). Results were similar in May and June. A positive correlation between snow depth and ice chlorophyll has been suggested previously, and attributed to the adaption of ice algae to low light intensities (Apollonio, 1965). This effect may have occurred at the ice edge, where light intensities below the ice were probably quite high because of the moderate snow depths (< 20 cm) and thin ice (mean of 76 cm); ice thickness and ice chlorophyll were also positively correlated at the ice edge ($r = +0.63$ and $+0.46$ in May and June, respectively). At fast ice station 2, however, ice thicknesses of 186-233 cm and snow depths up to 39 cm may have reduced transmitted light below the level required for maximal ice algal growth. This situation could account for the negative correlation between ice chlorophyll and snow depth at station 2; Welch and Kalff (1975) also reported a negative correlation.

Ice Microalgae

Microalgae on the under-ice surface were observed by divers at both fast ice and ice edge stations in both May and June. During May, a well-developed dense brown layer of algae was present in some areas at fast ice stations 2 and 3, but in other areas the algae had apparently already begun to separate from the under-ice surface. At station 1 on 12 May, for example, areas of clear ice alternated with sharply delineated dark brown patches of unattached granular matter that was stirred up into the upper water column by divers' bubbles. Core samples (length 10 cm) from the clear and brown areas had correspondingly low and high microalgal cell densities (min. and max. values in Table 1). In a large area at station 3 on 20 May, the algae had the appearance of an irregularly perforated, fragile, dark brown sheet, floating against and adhering in places to the

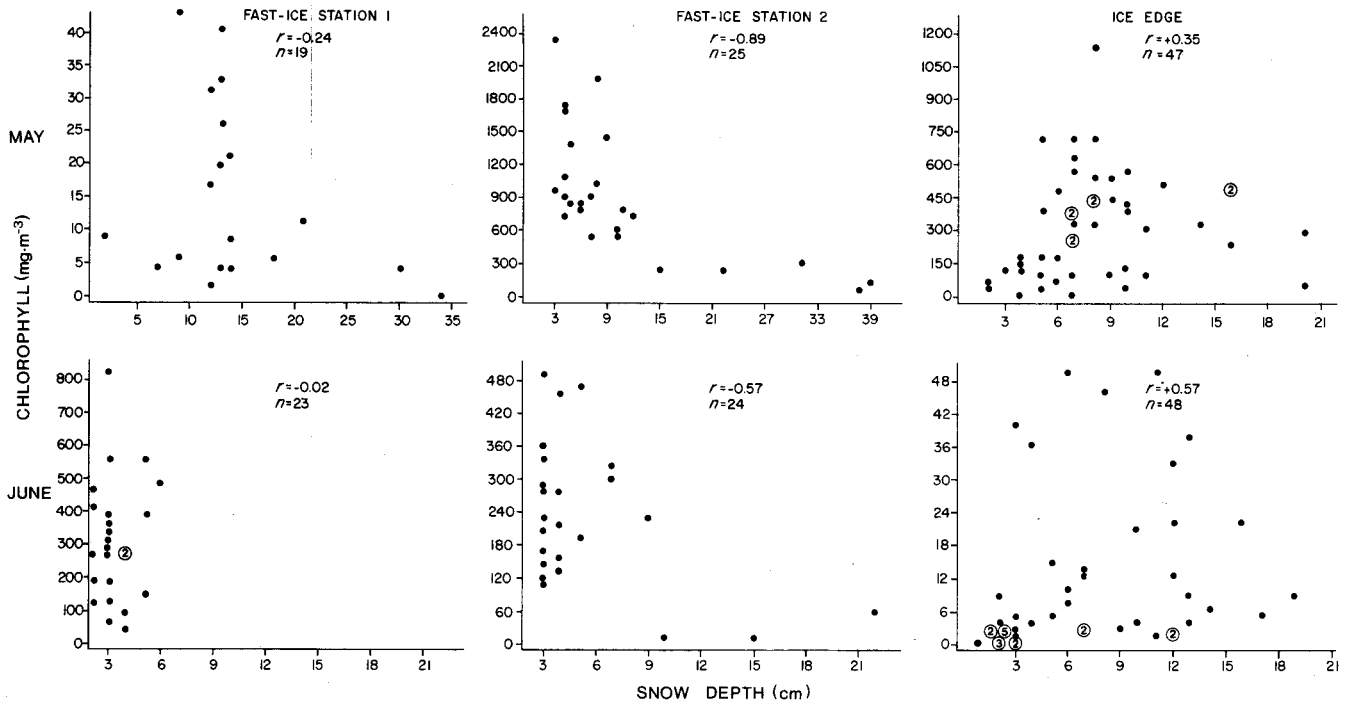


FIG. 3. Chlorophyll *a* concentrations in bottom ice vs. snow depth at fast ice and ice edge stations in Pond Inlet during 2-9 May and 18-24 June 1979. Untransformed data are plotted; *r* values are based on log₁₀ transformed data. Numbers within open circles are numbers of coincident data points.

under-ice surface. In early July, divers noted a marked decrease in apparent microalgal density. A patchy, low density layer and clear ice were observed at stations 2 and 3, respectively. The corresponding May to July decrease in standing stock at these stations (Table 1) was significant (pooled data; Mann-Whitney *U*-test, $P = 0.002$).

Algal densities in the ice varied markedly among samples and stations, but there was no clear evidence that densities were related to distance from the ice edge in the 22 June-2 July period (no samples were obtained at the ice edge in May). To test for any effect of increasing distance from the ice edge, hierarchical ANOVA was applied to log-transformed algal densities at stations 16-41 km, 1-2 km and 10-200 m from the ice edge; stations were nested within the three distance categories (Table 1). Variation among stations within distance categories was highly significant ($P < 0.0001$). After allowing for among-station variability, variation among distance categories was not significant ($P = 0.24$).

Among-station variation in apparent algal density was also reported by divers. At all ice edge stations in May and June, and at fast ice station 2 on 2 July, most of the algae observed was in two forms — long (up to 0.5 m) brown or green mucous-like strands hanging from or floating up against the ice, and rounded brown masses several cm in diameter occurring on the ice or, more commonly, in brine channels. These strands and masses varied in abundance from station to station, and were too patchy to be adequately sampled by coring. Rather, the algae sampled was that occurring in, or attached to, the ice superstrate. At most ice edge stations the bottom layer of the ice was

clear, but sparsely distributed areas of light-colored attached algae were observed at stations 2, 8 and 11. The latter were the stations with high standing stock values in cores during June and July (Table 1).

A total of 50 microalgal species was identified in the 41 core samples from Pond Inlet in May-July 1979 (Table 2), and at least 27 additional distinct but unidentified species were found. Pennate and centric diatoms comprised 56 and 12 of these 77 species, respectively, and the balance included green and golden brown algae, euglenoids, dinoflagellates and microflagellates.

The pennate diatoms *Nitzschia frigida* and *N. grunowii* were co-dominant in terms of abundance (35.3 and 33.1% of total numbers); each occurred in all but one of 41 samples, and one of these two species was dominant in all but two of 41 samples. Ten species of pennate diatoms accounted for more than 95% of the total numbers of microalgae collected, and eight of these were also among the 10 species occurring in more than 50% of the samples (Table 3). The other two species, *Achnanthes taeniata* and *Navicula vanhoefennii* (ranked 5th and 7th in abundance), occurred not only in fewer samples, but at relatively few stations when compared with other abundant species (Table 3). Many of the 50 identified species were rare, in terms of both abundance and occurrence: 20 species (together forming 0.19% of total numbers) each occurred in three or fewer of the 41 samples. The 27 unidentified species accounted for only 1.57% of the total number of cells.

Species composition varied among stations, but at all stations pennate diatoms dominated total cell numbers (70.6% to 99.7%) and contributed the highest number (10

TABLE 1. Standing stock (cell·L⁻¹) and group composition of microalgae in diver-collected ice cores from Pond Inlet during 12 May-2 July 1979

	Fast ice stations					Near edge stations		Ice edge stations				
	May		July			June		June				
Station	1	2	3	2	3	8	10	6	7	9	11	12
km from ice edge	66	41	16	41	16	2	1	0.025	0.025	0.2	0.010	0.010
Sampling date	12 Ma	14 Ma	20 Ma	2 JI	1 JI	25 Jn	27 Jn	22 Jn	23 Jn	26 Jn	28 Jn	30 Jn
Standing Stock (cells × 10 ⁶ ·L ⁻¹)												
Mean	16.98	24.50	25.79	9.97	0.20	11.95	0.14	2.87	0.82	0.25	2.78	0.23
SD	19.13	11.33	16.13	6.46	0.16	3.56	0.03	1.19	0.15	0.16	3.41	0.04
<i>n</i>	4	5	3	5	3	3	3	3	3	3	3	3
Minimum	1.33	14.66	13.84	1.09	0.08	8.43	0.11	1.51	0.66	0.08	0.53	0.21
Maximum	41.70	37.41	44.14	16.15	0.39	15.54	0.17	3.75	0.97	0.40	6.71	0.28
Percent Composition												
Pennate diatoms	99.5	99.7	98.4	99.6	70.6	99.6	85.4	95.1	70.9	84.8	97.4	81.7
Centric diatoms	<0.1	<0.1	0.5	0.2	19.6	0.2	2.0	1.5	21.9	0	0.7	2.3
Microflagellates	0.4	0.2	0.8	0.1	7.5	0.2	10.1	3.2	6.2	11.4	1.6	14.3
Other ^a	<0.1	<0.1	0.3	<0.1	2.3	0	2.5	0.2	0.9	3.8	0.3	1.7
Number of Species												
Pennate diatoms	33	36	46	36	10	25	15	34	23	19	23	12
Centric diatoms	2	1	2	2	8	2	3	4	9	0	2	2
Other	2	3	5	5	2	1	3	2	3	3	2	5

^a Includes Chlorophyceae, Dinophyceae and Euglenophyceae.

to 46) of species (Table 1). Significant correlations ($P < 0.001$) existed between number of pennate diatom species and total standing stock in a sample (Spearman $r_s = 0.92$), and between percent contribution of pennate diatoms to total numbers and total standing stock ($r_s = 0.81$). No major differences in species composition were apparent among 'fast ice', 'near ice' and 'ice edge' stations (Table 1).

Ice Macrofauna

The under-ice macrofauna found in Pond Inlet included the arctic cod *Boreogadus saida* (Bradstreet, 1982) and crustaceans, mostly gammarid amphipods. These amphipods occurred both on the undersurface of the ice and in shallow burrows, small pockets, and larger brine channels in the bottom layer of the ice. Our results and analyses are based on net samples, which collected most of the amphipods on the ice but were relatively ineffective in sampling those occurring in the ice. The values presented below, therefore, underestimate total abundance of under-ice fauna.

Species composition. Ten species of macroinvertebrates were collected, including eight gammarid amphipod species, one hyperiid amphipod, and one mysid (Table 4). The highest numbers of species (5 to 7) occurred at fast ice stations 2 and 3 in May and July, and at the two ice edge stations (9, 10) with rough, irregular ice. Only two to four species were collected at other ice edge stations and at fast ice station 1 in May.

Two species, *Apherusa glacialis* and *Ischyrocercus anguipes*, together accounted for more than 95% of the total numbers and nearly 90% of the total biomass in systematic net col-

lections (Table 4). *Apherusa glacialis* was present at all stations, and dominant at all but station 3 (Fig. 4). *Ischyrocercus anguipes* was found at only five stations and abundant at only one (fast ice station 3), where it was dominant both in mid-May and in early July. *Onisimus glacialis* and unidentified *Onisimus* juveniles (probably *O. glacialis*, given the observed low abundance of *O. litoralis* and *O. nanseni*) occurred at most stations and together contributed 3.8 and 9.2% to total abundance and biomass, respectively. These values underestimate the importance of *Onisimus* in the under-ice faunal community, probably quite considerably, because of their location within the ice, and hence their inaccessibility to our sampling nets at some stations.

Gammarus wilkitzkii, *Parathemisto libellula* and mysids were relatively widespread, but contributed little toward total abundance or biomass. Mysids included some large *Mysis polaris* but consisted primarily of small (<6 mm) *Mysis* juveniles. All of the *P. libellula* in systematic collections were small, <6 mm long; two larger individuals (13, 22 mm) were collected at station 2 in May and one (19 mm) was found on the surface of the water at the ice edge on 30 June. *Gammarus wilkitzkii* were relatively large (9 to 45 mm long), and hence conspicuous to divers, but were not included in systematic net collections due to their sparse distribution, and probably also to their tendency to occupy brine channels.

Spatial distribution. Mean densities and biomass of under-ice fauna at each station, based on systematic net samples, are shown in Fig. 5. Mean densities ranged from 0.3 to 163.0 individuals·m⁻² (overall mean 32.0·m⁻²) and mean biomasses were 0.8 to 619.8 mg·m⁻² (overall mean 127 mg·m⁻²). Among-sample variability in total abundan-

TABLE 2. Genera and species of microalgae found in diver-collected ice cores from Pond Inlet during 12 May-2 July 1979

Bacillariophyceae	<i>N. gelida</i> Grunow
Centrales ^a	<i>N. kariana</i> Grunow
<i>Chaetoceros</i> ^a	<i>N. pelagica</i> Cleve
<i>C. compressus</i> Lauder	<i>N. quadripedis</i> Cleve-Euler
<i>C. decipiens</i> Cleve	<i>N. rhynchocephala</i> Kützing
<i>C. septentrionalis</i> Östrup	<i>N. salinarum</i> Grunow
<i>C. wighamii</i> Brightwell	<i>N. spicula</i> (Hickie) Cleve
<i>Melosira</i>	<i>N. valida</i> Cleve et Grunow
<i>M. arctica</i> (Ehrenberg) Dickie	<i>N. vanhoeffennii</i> Gran
<i>Rhizosolenia</i> ^a	<i>Nitzschia</i> ^a
<i>Thalassiosira</i> ^a	<i>N. angularis</i> Wm. Smith
<i>T. gravis</i> Cleve	<i>N. asteroides</i> Otto Müller
<i>T. nordenskiöldii</i> Cleve	<i>N. cylindrus</i> (Grunow) Hasle
Pennales ^a	<i>N. delicatissima</i> Cleve
<i>Achnanthes</i>	<i>N. dissipata</i> (Kützing) Grunow
<i>A. taeniata</i> Grunow	<i>N. distans</i> Gregory
<i>Amphiprora</i>	<i>N. frigida</i> Grunow
<i>A. alata</i> (Ehrenberg) Kützing	<i>N. grunowii</i> Hasle
<i>A. angustata</i> Hendey	<i>N. longissima</i> (Brébisson) Grunow
<i>A. gigantea</i> Grunow	<i>N. seriata</i> Cleve
<i>A. kjellmanii</i> Cleve	<i>N. sigma</i> (Kützing) Wm. Smith
<i>A. paludosa</i> Wm. Smith	<i>Pinnularia</i> ^a
<i>Amphora</i> ^a	<i>P. quadratera</i> (Schmidt) Cleve
<i>A. laevis</i> Gregory	<i>Pleurosigma</i>
<i>Cocconeis</i> ^a	<i>P. angulatum</i> (Quekett) Wm. Smith
<i>Cylindrotheca</i>	<i>P. cuspidatum</i> (Cleve) H. Peragallo
<i>C. closterium</i> (Ehrenberg) Reimann et Lewin	<i>P. elongatum</i> Wm. Smith
<i>Diploneis</i> ^a	<i>P. marinum</i> Donkin
<i>D. litoralis</i> (Donkin) Cleve	<i>Rhoicosphenia</i>
<i>Gomphonema</i>	<i>R. curvata</i> (Kützing) Grunow
<i>G. exiguum</i> Kützing	Chlorophyceae ^a
<i>Gyrosigma</i>	Chrysophyceae
<i>G. tenuissimum</i> (Wm. Smith) Griffith et Henfrey	<i>Dinobryon</i>
<i>Hantzschia</i> ^a	<i>D. balticum</i> (Schutt) Lemmermann
<i>Licmophora</i> ^a	Dinophyceae ^a
<i>Navicula</i> ^a	<i>Goniaulax</i> ^a
<i>N. cancellata</i> Donkin	<i>Peridinium</i> ^a
<i>N. digitoradiata</i> (Gregory) Ralfs	<i>Prorocentrum</i> ^a
<i>N. directa</i> (Wm. Smith) Ralfs	Euglenophyceae ^a
<i>N. forcipata</i> Greville	<i>Euglena</i> ^a
<i>N. gastrum</i> (Ehrenberg) Kützing	Microflagellates

^aTaxa for which unidentified cells or colonies were found.

TABLE 3. Occurrence and relative abundance of the ten most abundant species of microalgae in diver-collected ice cores from Pond Inlet during 12 May-2 July 1979. Based on 41 samples from 12 stations.

Species	Relative abundance (% of total numbers)	Occurrence		
		% of samples	Rank	Number of stations
<i>Nitzschia frigida</i>	35.3	97.6	1	12
<i>N. grunowii</i>	33.1	97.6	1	12
<i>N. cylindrus</i>	8.3	87.8	4	12
<i>Navicula pelagica</i>	7.6	65.9	5	10
<i>Achnanthes taeniata</i>	5.0	46.3	11	7
<i>Nitzschia delicatissima</i>	2.3	90.2	3	12
<i>Navicula vanhoeffennii</i>	1.5	36.6	14	5
<i>Nitzschia longissima</i>	0.8	92.7	2	12
<i>Nitzschia seriata</i>	0.7	51.2	9	9
<i>Amphiprora kjellmanii</i>	0.5	58.5	6	8

ce and biomass of under-ice fauna was high at all stations except fast ice station 3 on 20 May (Fig. 5). Coefficients of variation (C.V.) in this special case were 16.6% and 25.4% for abundance and biomass, respectively. At all other stations, the C.V. was 62.5%-151.2% for abundance and 61.7%-195.7% for biomass. At some stations the variability was attributable to the presence of different types of ice or large and sparsely distributed aggregations of amphipods associated with brine channels or masses of detritus. At other stations with patchy under-ice fauna, no corresponding habitat patchiness was evident.

Among-station variability in abundance and biomass was high, and at least in the second sampling period, no clear trends were evident in the distribution of under-ice fauna with respect to distance from the ice edge (Fig. 5).

TABLE 4. Species and relative abundances of under-ice macrofauna in systematic net samples from Pond Inlet during 12-20 May and 22 June-2 July 1979. Based on 16 516 individuals of total biomass 65.5 g collected in 130 net samples from 14 stations.

Species	Percent composition		No. of stations ^d
	Numbers	Biomass	
<i>Apherusa glacialis</i> ^a	74.07	65.73	14
<i>Ischyrocerus anguipes</i>	21.77	23.90	5
<i>Onisimus glacialis</i>	1.49	8.29	10
<i>O. litoralis</i>	0.02	0.27	2
<i>O. nanseni</i>	0.05	0.73	6
<i>Onisimus juveniles</i>	2.29	0.86	11
<i>Gammarus wilkitzkii</i>	0	0	6
<i>Gammarus juveniles</i>	0.01	<0.01	1
<i>Gammaracanthus juveniles</i>	0.01	0.01	1
<i>Eusirus holmi</i>	0	0	1
<i>Parathemisto libellula</i>	0.05	0.06	5
Unidentified amphipods ^b	0.05	0.01	3
<i>Mysis polaris</i> ^c	0.26	0.08	9
Fish (young of year)	0.01	<0.01	2

^a Includes *Apherusa* juveniles and damaged *Apherusa* sp.

^b Damaged.

^c Includes *Mysis* juveniles

^d No. of stations includes those where species were found only in non-systematic net collections.

To test for any effect of distance, hierarchical ANOVA was applied to log-transformed data for each month, with stations nested within three categories of distance from the edge (Fig. 5). During both periods, abundance and biomass of under-ice fauna differed significantly ($P < 0.001$) both among distance categories and among stations within distance categories. In May mean abundance and biomass were higher in fast ice than at the ice edge. In June-July, abundance and biomass were highest in fast ice, intermediate at the ice edge, and lowest 1-2 km from the edge (Fig. 5).

Habitat associations. The most abundant species, *Apherusa glacialis*, *Onisimus glacialis* and *Ischyrocerus anguipes*, were associated with the undersurface of the ice in different ways. Most *Apherusa glacialis* were on the under-ice surface, although some were within brine channels, with or without other amphipod species. At stations where *A. glacialis* was abundant, its distribution was patchy; these patches included aggregations of juveniles clinging to clumps and strands of ice algae, and of juveniles and adults on pan ice floes that were in contact with the ice edge. *Ischyrocerus anguipes* was abundant at only one station, where it had a relatively even distribution. Some *I. anguipes* were on the under-ice surface; others had imbedded the posterior parts of their bodies in the ice. *Onisimus glacialis*, on the other hand, was rarely observed on the under-ice surface. Individuals or groups inhabited shallow burrows, small pockets, or larger brine channels in the bottom of the ice. *Gammarus wilkitzkii* was larger (9 to 45 mm) and more sparsely distributed than the preceding species; it was also observed most commonly within cavities and brine channels in areas with a rough, irregular under-ice surface.

Mysids occurred immediately beneath rough ice and in the interstices of pressure ridges that were present at some stations.

Many more crustaceans were observed on rough ice than on smoother ice or on loose platey ice crystals. At three stations where two ice types occurred (stations 3, 9, 10) systematic net sampling was stratified. Abundance and biomass were higher in samples taken on rough ice than in those taken on flat ice (stations 9, 10) or in loose platey ice (station 3), and the difference was significant at two of the three stations ($P = 0.01$; Table 5). Allowance for amphipods buried in the ice would magnify the differences, as systematic net sampling underestimated amphipod densities more seriously in rough than in smooth ice. The high abundance at stations 9 and 10, where rough ice occurred, and the low abundance at stations 6 and 8, where soft 'new' ice occurred (see Fig. 5), are likely attributable to the condition of the under-ice surface.

At stations where pan ice occurred under the ice edge (stations 7 and 11), divers saw many *Apherusa glacialis* on the pan ice and on the under-surface of the ice edge. Densities of *A. glacialis* at these stations (11.8 and 87.1 ind·m⁻², respectively) were higher than the density at the single station (12) at the immediate ice edge where no pan ice was observed (4.7 ind·m⁻²). At these 3 stations the percentage contribution by *Apherusa* to total numbers was similar (98.4 to 98.7%) and higher than at other stations separated from the edge by distance (0.2-2 km) or a pressure ridge (45.5 to 95.5%). The mean length of the smaller *Apherusa* cohort was not significantly different at the two groups of ice edge and near-edge stations, probably due to

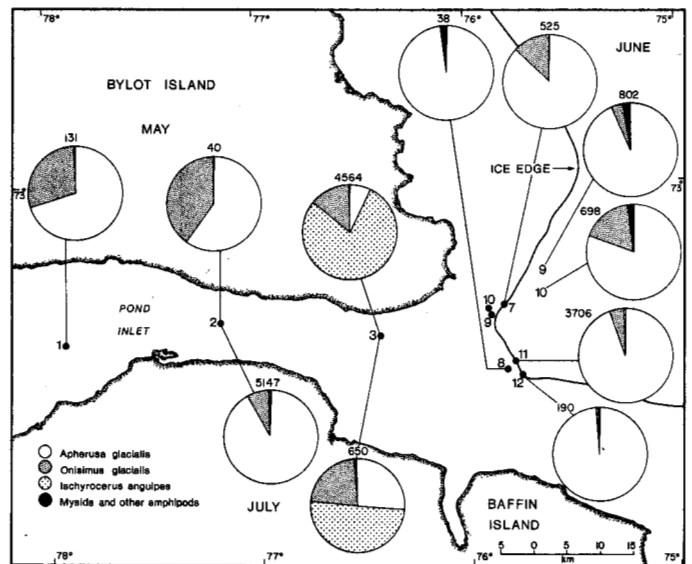


FIG. 4. Percent composition of biomass of under-ice macrofauna in systematic net samples from fast ice stations in Pond Inlet during 12-22 May and 1-2 July 1979 and from ice edge stations during 22-30 June 1979. Number above each circle is total number of crustaceans collected at the station ($n = 7-11$ samples per station and date). 'Other' category also includes *I. anguipes* when densities low.

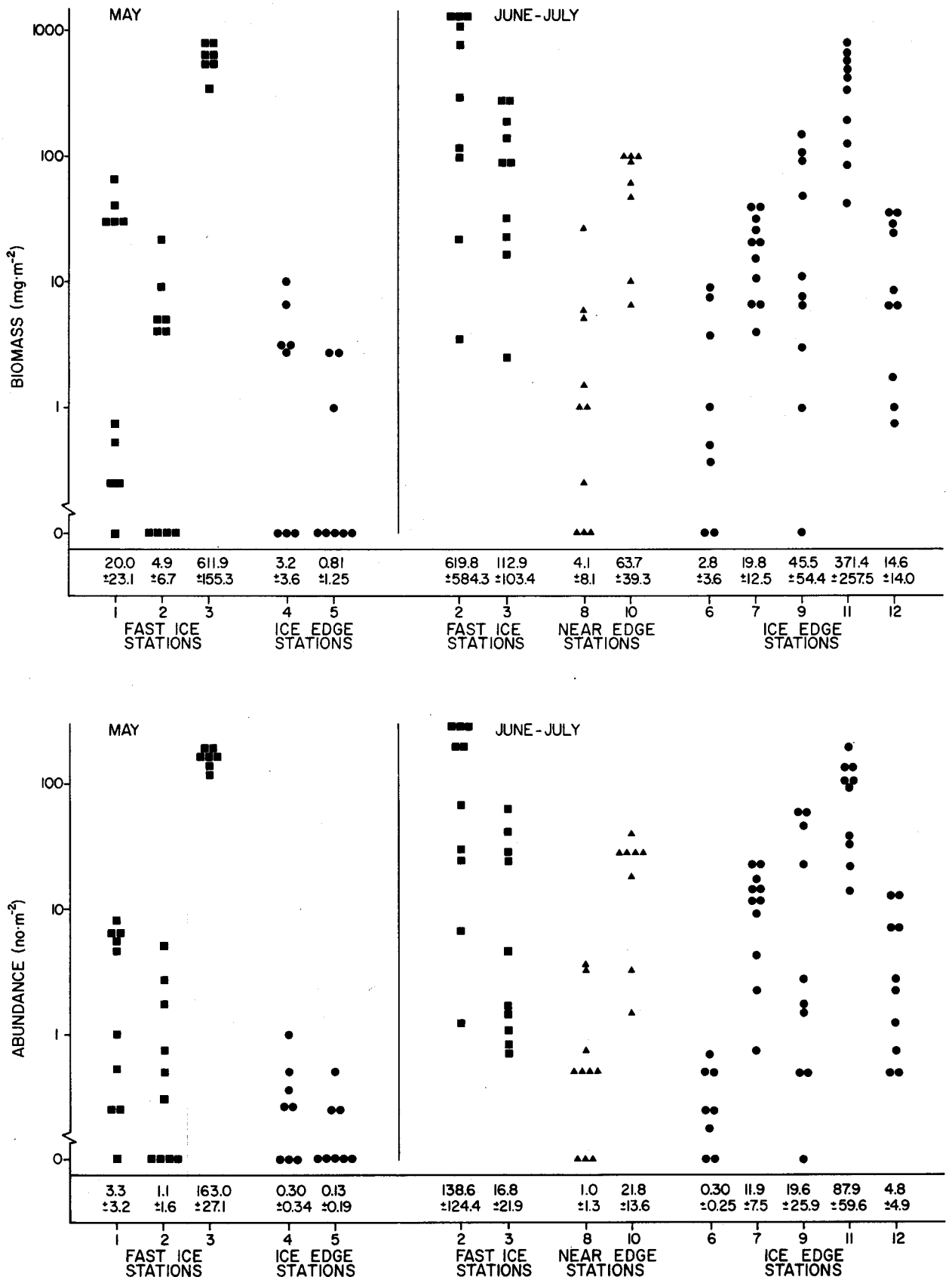


FIG. 5. Abundance and biomass of under-ice macrofauna in systematic net collections from fast ice and ice edge stations in Pond Inlet during 12-20 May and 22 June-2 July 1979. Each point represents one sample; data plotted are log₁₀ transformed and number shown for each station are mean ± SD of untransformed data. Squares, triangles and circles indicate fast ice, near edge and ice edge stations, respectively.

TABLE 5. Comparison of abundance and biomass of under-ice fauna on smooth and rough ice at three stations in Pond Inlet

Station	Abundance (no. m ⁻²)			Biomass (mg. m ⁻²)		
	Rough ice	Smooth ice	Statistics ^a	Rough ice	Smooth ice	Statistics ^a
3	39.4 ± 17.5	1.7 ± 1.4	<i>P</i> = 0.01	219.3 ± 67.1	41.9 ± 37.9	<i>P</i> = 0.01
9	47.3 ± 17.7	1.2 ± 1.0	<i>P</i> = 0.01	99.1 ± 41.7	4.8 ± 4.2	<i>P</i> = 0.01
10	28.7 ± 9.8	14.9 ± 14.5	ns	73.7 ± 24.4	53.6 ± 52.3	ns
Pooled	38.4 ± 16.1	4.8 ± 8.9	<i>P</i> < 0.002	130.7 ± 79.2	30.9 ± 38.6	<i>P</i> < 0.002

Data shown are mean ± SD; *n* = 4 net samples per ice type at a station except for smooth ice stations 3 and 9 where *n* = 6.

^a Mann-Whitney *U*-test (two-tailed).

significant among-station variability in lengths at the immediate ice edge (Kruskal-Wallis test; *P* < 0.001). Sizes were not significantly different at stations farther back from the edge. This among-station variability at the ice edge may indicate that *Apherusa* at the immediate ice edge were recruited from pan ice floes carrying different populations of *Apherusa glacialis*.

Temporal aspects. Seasonal development of under-ice fauna can be examined at fast ice stations 2 and 3, the only stations sampled in both mid-May and early July. Abundance and biomass increased by more than two orders of magnitude at station 2, but decreased less than one order of magnitude at station 3 (Mann-Whitney *U*-tests, *P* < 0.002; Fig. 5). The increase at station 2 included all of the species occurring there in May except *Onisimus nanseni* (one collected in May and none in July), but too few specimens were collected in May (40) to warrant any discussion of quantitative change in species composition. At station 3 (where larger numbers were collected), *Ischyrocerus anguipes* was dominant in May but declined in importance by July whereas *Apherusa glacialis* increased in importance (Fig. 4). The relative contribution by *Onisimus* spp. to total numbers was similar at station 3 in both time periods, but their contribution to biomass increased, partly due to the occurrence of relatively large *Onisimus nanseni* in July, but also due to growth.

Size-frequency distributions of the three dominant species in May and July samples from fast ice stations are shown in Fig. 6. During both time periods, two cohorts of *O. glacialis* and *A. glacialis* and a single cohort of *I. anguipes* were present. The cohort of larger *Apherusa* (probably one-year-olds) formed a much smaller proportion of total *Apherusa* numbers in July (0.8%) than in May (11.0%), whereas the two *Onisimus* cohorts were collected in similar numbers in both time periods (Fig. 6). The apparent May to July increase in length was significant for each cohort of each species (*P* < 0.01; Mann-Whitney *U*-tests for pooled stations; unit of observation was mean amphipod length in a sample). The increase in mean size was greatest in both *Apherusa* cohorts (2.5 mm), intermediate in *I. anguipes* (1.5 mm) and least in *Onisimus glacialis* (1.2 mm) and *Onisimus* juveniles (0.5 mm). The low apparent growth rate and the similar relative abundances of the two *Onisimus* cohorts in May and July are consistent with the hypothesis

that this species has a two-year life cycle (e.g. Steele, 1961). The higher apparent growth rate in *Apherusa glacialis*, the lower relative abundance of the larger cohort and its decrease with time suggest that this species has a one-year life cycle.

Ice Meiofauna

Small invertebrates (<1 mm long) in the soft bottom layer of ice were sampled in May with 10 cm diameter corers. The total number of animals collected (1797) was dominated by nematodes and copepods (58.8 and 39.7%, respectively) and also included small unidentified polychaetes (1.5%). Harpacticoid and cyclopoid copepods accounted for the majority of the 625 copepods identified (89.8 and 9.4%, respectively) and the only calanoid copepods present were *Calanus* sp. nauplii (0.8%). Dominant species were *Harpacticus superflexus* (74.7% of copepods), *Ectinosoma finmarchicum* (12.3%) and *Cyclopina schneideri* (8.2%); common species were *Tisbe furcata* (2.4%) and *Oithona similis* (1.1%); and rare species (only one individual found) were *Harpacticus uniremis* and *Oncaea borealis*. Both adults and copepodites of each common species were present; adults dominated samples of *H. superflexus* (56.3%) and *C. schneideri* (76.5%) whereas *E. finmarchicum* copepodites (77.3%) outnumbered adults.

Meiofaunal abundance during May was very low at the ice edge stations (0-25 individuals·m⁻²), but much higher at fast ice stations (~300 - 53 000 ind·m⁻²; Table 6). The latter values were similar to densities of meiofauna (~16 800 ind·m⁻²; *n* = 16) found in 10 cm core samples from the under-ice surface in Brentford Bay, N.W.T., during 22-27 May 1977 (W.E. Cross, unpubl. data).

At stations 1 and 3 during May, core sampling was stratified according to ice type: both clear ice and brown ice were sampled at station 1, and both brown ice and a loose algal layer (apparently in the process of sloughing off from the under-ice surface) were sampled at station 3 (Table 6). At station 1, copepod abundance was greater in brown ice than in clear ice (Mann-Whitney *U*-test; *P* = 0.016), but numbers of nematodes were not significantly different (*P* = 0.015). At station 3, samples from the loose algal layer contained significantly more copepods and nematodes than did those from brown ice (*P* = 0.008 in each case). High densities of ice algae (see above) as well as

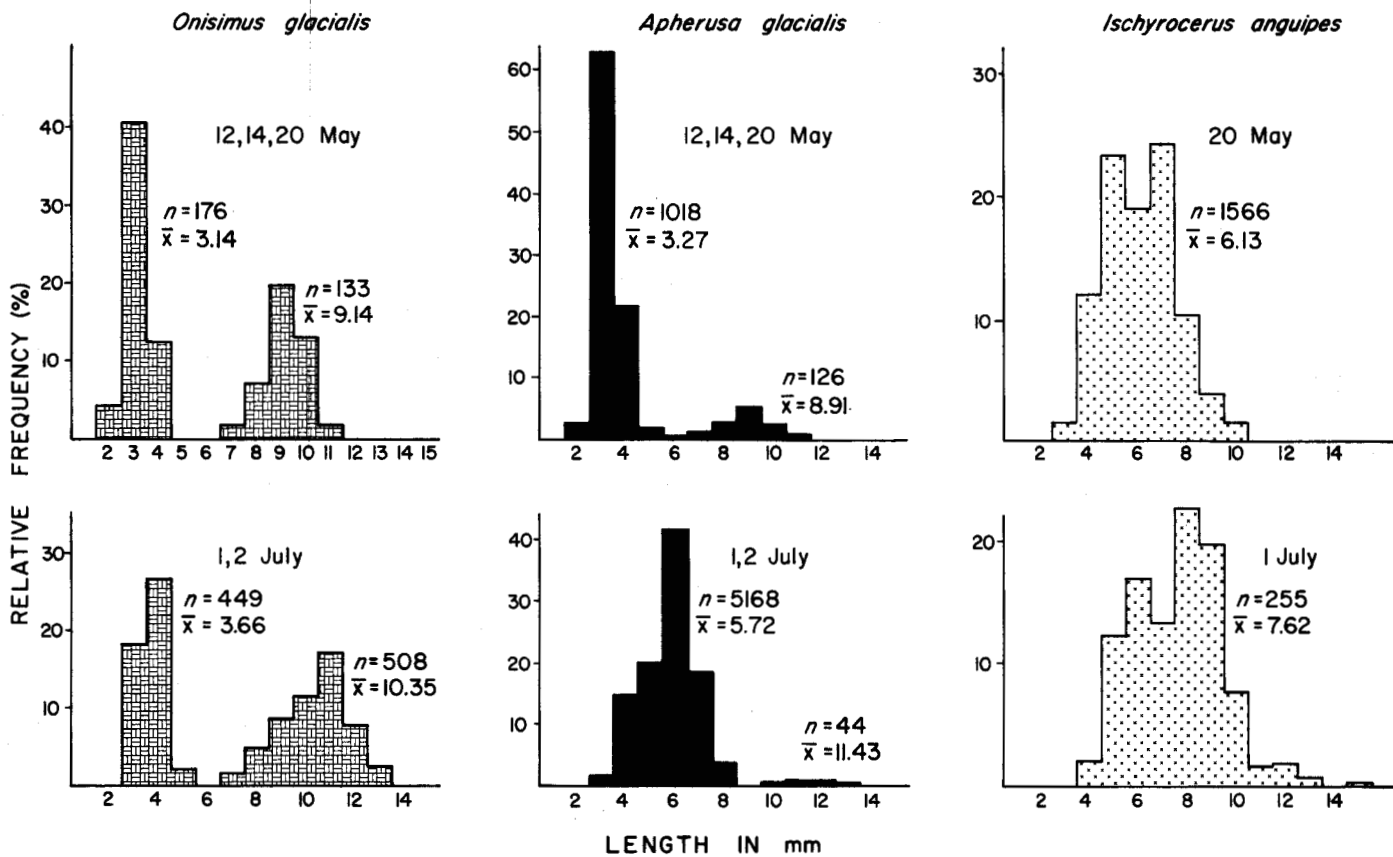


FIG. 6. Length-frequency histograms for *Onisimus glacialis*, *Apherusa glacialis* and *Ischyrocerus anguipes* at fast ice stations in Pond Inlet during 12-20 May and 1-2 July 1979. Individuals of *O. glacialis* and *A. glacialis* <6 mm long are juveniles identified only to generic level.

copepods occurred in brown ice at station 1. These results are consistent with Horner's reports (1976, 1977) that ciliates, worms and copepods in the ice feed on ice algae (diatoms and flagellates).

During June-July, estimated mean abundances at all stations in Pond Inlet were 0-1130 nematodes·m⁻² and 0-1410 copepods·m⁻². These estimates, however, are based on a total of only 17 individuals contained in 37 ice algae samples (2.5 cm diameter cores), and hence are not expected to be as accurate as the estimates for May (based on larger cores). Meiofaunal estimates based on ice algae samples taken in May were neither consistently higher nor lower than those based on larger cores (estimates differed by 1.3 to 5.7x), so abundance estimates for June-July may be of at least order of magnitude accuracy despite the small sample sizes.

DISCUSSION

Habitat Effects

Spatial heterogeneity was particularly evident during the June-July period. At that time, several different types of bottom ice were observed, including (1) flat and relatively smooth ice, (2) rough irregular ice probably caused by the melting of pressure ridges, and (3) soft new ice apparently formed from a fresh-water layer under the ice.

This local variability probably accounts for most of the among-station variability documented in the present study. Increased habitat in areas of rough ice and increased food availability in large brine channels containing concentrations of algal detritus probably accounted for the higher densities of macroinvertebrates found in these areas than in surrounding areas of flat, relatively featureless ice. Low faunal densities in areas where a layer of low salinity

TABLE 6. Meiofaunal abundance in diver-collected cores of soft bottom ice from Pond Inlet during 12-20 May 1979. Based on randomly located 80.1 cm² cores of 0.5-1 cm depth; data expressed as no. × 10³·m⁻².

Station	1 ^a	1 ^b	2	3 ^b	3 ^c	4	5
No. of samples	5	5	10	4	5	6	5
Copepoda							
mean	0.27	1.88	0.05	3.58	20.47	0	0.02
(SD)	(0.34)	(1.01)	(0.09)	(3.07)	(2.50)		(0.06)
Nematoda							
mean	0	0.20	0.32	5.12	31.90	0	0
(SD)		(0.13)	(0.51)	(9.84)	(12.44)		
Polychaeta							
mean	0.02	0	0	0.25	0.40	0	0
(SD)	(0.06)			(0.10)	(0.42)		

^a Clear ice.

^b Brown ice.

^c Loose, thick algal layer.

meltwater and/or new ice occurred under the ice may indicate intolerance of fresh water, and salinity preferences may also have contributed to the concentration of fauna on patches of rough, irregular ice that extended below the meltwater layer.

Pack ice consisting of floes of various ages was common at the Pond Inlet ice edge in 1979, and rafted ice was observed at most stations along the immediate ice edge during both sampling periods. The dominant amphipod at the ice edge and at most fast ice stations was *Apherusa glacialis*, an amphipod whose habitat is otherwise pelagic (Dunbar, 1954) and whose affinity for pan ice in late summer is well known (e.g. MacGinitie, 1955; Divoky, 1978). *Apherusa* was observed on the sides and undersurfaces of pan ice near and in contact with the ice edge in June, and populations of *Apherusa glacialis* at the immediate ice edge may have been transported there on pan ice floes. Populations with different size-frequency distributions, possibly originating from different floes, were found at three stations along the ice edge. The importance of this source of recruitment to the under-ice surface at stations near the ice edge, where pan ice had frozen into a matrix of new ice during March, is not known. *Apherusa* was also common under ice that was landfast throughout the winter.

Temporal Effects

Events leading up to the peak of the spring bloom of ice microalgae have been described near Resolute Bay, N.W.T. (Welch and Kalff, 1975), and from detailed studies at Barrow, Alaska (Horner and Alexander, 1972; Clasby *et al.*, 1973; Alexander, 1974; Horner, 1976, 1977). In Pond Inlet, the ice algal bloom apparently peaked in early May at fast ice station 2, but later at fast ice station 1 where the snow depth was greater (Fig. 2). At the ice edge, where snow and ice cover were thin, the peak of the bloom may have been even earlier than at station 2; concentrations of chlorophyll in the ice in May were similar to June values at fast ice stations, and by late June ice edge values were very low (Fig. 2).

The fate of the ice algae following bloom conditions, however, has been uncertain (Horner, 1976, 1977). Amphipods graze on the ice algae (Apollonio, 1965) but apparently much ice algae is sloughed off the ice and enters planktonic and benthic systems (Meguro *et al.*, 1966, 1967; Horner, 1976, 1977). Most of our diver observations of under-ice flora and fauna were obtained after the peak of the algal bloom, and they provide the first direct information about the fate of ice algae after it sloughs off the ice. Following peak bloom conditions in Pond Inlet, thin sheets of algae partially detached from the ice, but persisted for some time as strands and amorphous masses attached to the under-ice surface and in brine channels. Judging from the high densities of meio- and macrofauna associated with algal detritus, much of the spring's ice algal production was probably consumed and recycled at or near the under-ice surface.

Increases of chlorophyll *a* in the water column during ice melt have been reported (Clasby *et al.*, 1973; Grainger, 1977) but increased productivity was not apparent (Clasby *et al.*, 1973) and few living diatoms have been recovered at this time (Horner, 1977). In Pond Inlet during May, no algae were visible in the water column to the unaided eye, whereas at most stations in June, brown or white particles up to 3 mm long resembling sloughed-off ice algae were abundant in the water column. These observations probably account for the observed May-June increases in chlorophyll *a* in the water immediately under fast ice (Fig. 2).

Ice Edge Effects

Concentrations of nutrients and chlorophyll *a* in ice samples at and near the Pond Inlet ice edge indicated that the ice microalgal bloom was earlier at the ice edge than under fast ice. This was apparently attributable to thinner ice and snow cover at the ice edge, which had formed in March and April when pack ice was blown onto the fast ice edge and frozen into place (Fig. 1). This may in itself constitute an ice edge effect, but the frequency of this type of unstable ice edge, characterized by breakage and re-formation, is uncertain. No evidence of edge re-formation following breakage existed at ice edges in Barrow Strait and Wellington Channel during 1976 (Bradstreet, 1979) or in Pond Inlet during 1978 (K.J. Finley, pers. comm.). The 1979 Pond Inlet ice edge may be more comparable to offshore pack ice edges (including the ice margin zone in the Bering Sea) where pan ice floes are alternately compacted and dispersed by changing wind conditions.

No published reports on under-ice biota at offshore pack ice edges are available, but water column studies in the Bering Sea (McRoy and Goering, 1974, 1976; Alexander, 1981) showed increased phytoplankton production at the edge relative to open water to the south and ice-covered water to the north; this was attributed to increased light penetration and ice melt. At the Pond Inlet ice edge, water samples from immediately beneath the ice provided no evidence of such an increase in phytoplankton biomass, nor of the upwelling or wind-driven mixing at ice edges described by Clarke (1978) and Buckley *et al.* (1979).

Neither ice algae nor ice invertebrates were consistently more abundant or different in species composition at the ice edge versus under fast ice. Apparent differences in the abundance of macrofauna (highest under fast ice, least near the ice edge, and intermediate at the edge) probably were local habitat effects rather than a 'distance from ice edge' effect. Thus, the importance of this ice edge as a feeding area for seabirds and marine mammals probably arises from the accessibility of ice biota near the ice edge rather than from enhanced production at the ice edge. Possible differences between this type of unstable ice edge and persistent edges must be considered, however, when extrapolating these results to feeding studies at other ice edges.

Comparisons with Other Studies

There are few previous studies against which to compare these results concerning community composition and standing stock of under-ice biota. Concentrations of chlorophyll *a* in the bottom layer of ice at most of our stations and sampling times were similar to or somewhat higher than mean values previously reported from arctic and subarctic locations (Apollonio, 1965; Meguro *et al.*, 1966, 1967; Clasby *et al.*, 1973; Welch and Kalff, 1975; Grainger, 1977; Dunbar and Acreman, 1980). However, the highest mean values found here (900 mg·m⁻³ or 180 mg·m⁻² at station 2 in May) were considerably higher than any previously reported. Standing stocks of microalgae in Pond Inlet are similar to those previously reported by Horner (1976) at Barrow, Alaska, and by Hsiao (1979a,b,c) in three widely separated parts of the Northwest Territories. The dominant species in Pond Inlet (*Nitzschia frigida* and *N. grunowii*) were among the dominant or abundant species both nearby in Eclipse Sound (Hsiao, 1979a) and 2500 km to the west at Point Barrow, Alaska (Horner, 1977). Species dominance varied among samples in the aforementioned studies; these two species dominated our samples consistently.

The only previous quantitative data on under-ice macrofauna based on replicated samples, to my knowledge, are those of Cross (in prep.) who found under-ice communities dominated by the amphipods *Onisimus* spp. and *Gammarus* spp. at four stations in small central arctic bays during May and June 1977. Mean abundance and biomass of amphipods in those bays and in Pond Inlet were comparable, but Pond Inlet communities were dominated by either *Apherusa glacialis* or *Ischyrocerus anguipes*. Pond Inlet communities were more similar in this respect to the *Apherusa glacialis*-dominated communities reported by Golikov and Scarlato (1973) on the undersurface of pack ice in the Barents Sea, although their value of 24 g·m⁻² for *A. glacialis* was higher than the maximum for any single sample taken in the present study (1.24 g·m⁻²). Differences among studies may be related to ice type (e.g. pan ice vs. landfast ice), mode of formation of landfast ice (freezing in place in fall vs. freezing together of ice pans in winter), or other habitat, topographic or bathymetric factors. To date, however, there is little evidence of geographic variation in the community structure of under-ice fauna.

The importance of ice as a habitat for certain flora and fauna, and the importance of these under-ice biota in food chains leading to seabirds and marine mammals, are becoming well documented. Results of this study suggest that the ice biota at the Pond Inlet ice edge in 1979 were similar to those under nearby areas of fast ice, although peak under-ice productivity probably occurred earlier in the season at the ice edge. Ice biota accessible to seabirds and marine mammals along the ice edge during spring did provide a more concentrated food supply (directly or channeled through arctic cod) than was available in open water during spring.

ACKNOWLEDGEMENTS

Assistance was provided by many people without whose efforts and expertise this study would not have been possible. Special thanks are due to my diver associates, J.D. Barrie, T. Jackoosie and P.V. Mladenov. Invaluable field assistance was also provided by P. Aglak, I. Akpaliapik and I. Milton of Pond Inlet, and by M.S.W. Bradstreet, E.J. Gibb, W.G. Johnston, J. Kristensen, K. Loftus, C.J. Risley and R.E. Salter of LGL Ltd. Laboratory analyses were performed at the Water Analysis Facility, Memorial University of Newfoundland (nutrients), and by M.G. Foy, G.P. Vickers, H.E. Stallard, J.E. Poliacik and D.H. Thomson of LGL Ltd. The assistance of B. DeLong, C. Holdsworth, B.M. Griffen and I. Ramirez in preparing the report, and W.J. Richardson in study design, data interpretation and scientific editing, is gratefully acknowledged.

This study was a part of the Eastern Arctic Marine Environmental Studies program, funded by Petro-Canada and administered by the Department of Indian Affairs and Northern Development. Thanks are extended to R.A. Davis of LGL Ltd., and to G.T. Glazier, H. Hume, P. Idlout, G. Koenig, A. MacKenzie and R. Wallace of Petro-Canada, for administrative and logistical support throughout this study.

REFERENCES

- ALEXANDER, V. 1974. Primary productivity regimes of the nearshore Beaufort Sea, with reference to potential roles of ice biota. In: Reed, J.C. and Sater, J.E. [eds.]. *The Coast and Shelf of the Beaufort Sea*. Arlington: Arctic Institute of North America. 609-635.
- . 1981. Ice-biota interactions: an overview. In: Hood, D.W. and Calder, J.A. [eds.]. *The Eastern Bering Sea Shelf: Oceanography and Resources*. Office of Marine Pollution Assessment, NOAA and Department of the Interior (Bureau of Land Management). Seattle: University of Washington Press. 2:757-762.
- APOLLONIO, S. 1965. Chlorophyll in arctic sea-ice. *Arctic* 18:118-122.
- BRADSTREET, M.S.W. 1979. Thick-billed murres and black guillemots in the Barrow Strait area, N.W.T., during spring: distribution and habitat use. *Canadian Journal of Zoology* 57:1789-1802.
- . 1980. Thick-billed murres and black guillemots in the Barrow Strait area, N.W.T., during spring: diets and food availability along ice edges. *Canadian Journal of Zoology* 58:2120-2140.
- . 1982. Occurrence, habitat use, and behaviour of seabirds, marine mammals, and arctic cod at the Pond Inlet ice edge. *Arctic* 35 (this issue).
- and CROSS, W.E. 1982. Trophic relationships at high arctic ice edges. *Arctic* 35 (this issue).
- BUCKLEY, J.R., GAMELSRØD, T., JOHANNESSEN, J.A., JOHANNESSEN, O.M. and RØED, L.P. 1979. Upwelling: oceanic structure at the edge of the arctic ice pack in winter. *Science* 203:165-167.
- CLARKE, A.J. 1978. On wind-driven quasi-geostrophic water movements near fast ice edges. *Deep-Sea Research* 25:41-57.
- CLASBY, R.C., HORNER, R. and ALEXANDER V. 1973. An *in situ* method for measuring primary productivity of arctic sea ice algae. *Journal of the Fisheries Research Board of Canada* 30:835-838.
- COONEY, R.T. 1981. Bering Sea zooplankton and micronekton communities with emphasis on annual production. In: Hood, D.W. and Calder, J.A. [eds.]. *The Eastern Bering Sea Shelf: Oceanography and Resources*. Office of Marine Pollution Assessment, NOAA and Department of the Interior (Bureau of Land Management). Seattle: University of Washington Press. 2:947-974.
- CROSS, W.E. 1982 (in prep.) Quantitative studies on under-ice fauna in the central arctic archipelago.
- DIVOKY, G.J. 1978. The distribution, abundance and feeding ecology of birds associated with pack ice. In: *Environmental Assessment of the Alaskan Continental Shelf, Annual Report of the Principal Investigators, March 1978. Vol. II*. NOAA, Boulder, CO. 167-509.
- DUNBAR, M.J. 1954. The amphipod Crustacea of Ungava Bay. *Canadian Eastern Arctic. Journal of the Fisheries Research Board of Canada* 11:709-798.

- _____ and 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.
- FAY, R.H. 1974. The role of ice in the ecology of marine mammals of the Bering Sea. In: Hood, D.W. and Kelley, E.J. [eds.]. *Oceanography of the Bering Sea with Emphasis on Renewable Resources*. University of Alaska, Institute of Marine Science Occ. Publ. No. 2. 383-399.
- FINLEY, K.J., DAVIS, R.A. and SILVERMAN, H. 1980. Aspects of the narwhal hunt in the eastern Canadian High Arctic. Report of the International Whaling Commission 30:459-464.
- GOERING, J.J. and McROY, C.P. 1974. Sea ice and under-ice plankton. In: Odum, H.T., Copeland, B.J. and McMahan, E.A. [eds.]. *Coastal Ecological Systems of the United States, Vol. 3*. Washington, D.C.: The Conservation Foundation. 55-70.
- GOLIKOV, A.N. and SCARLATO, O.A. 1973. Comparative characteristics of some ecosystems of the upper regions of the shelf in tropical, temperate and arctic waters. *Helgolander wiss. Meeresunters* 24:219-234.
- GRAINGER, E.H. 1977. The annual nutrient cycle in sea ice. In: Dunbar, M.J. [ed.]. *Polar Oceans*. Calgary: Arctic Institute of North America. 285-300.
- HORNER, R.A. 1976. Sea ice organisms. *Oceanography and Marine Biology* 14:167-182.
- _____. 1977. History and recent advances in the study of ice biota. In: Dunbar, M.J. [ed.]. *Polar Oceans*. Calgary: Arctic Institute of North America. 269-283.
- _____ and ALEXANDER, V. 1972. Algal populations in arctic sea ice: an investigation of heterotrophy. *Limnology and Oceanography* 17:454-458.
- HSIAO, S.I.C. 1979a. Sea ice microalgal data from Eclipse Sound, 1976 and 1977. Canadian Fisheries and Marine Service Data Rep. No. 131. 34 p.
- _____. 1979b. Sea ice microalgal data from the Eskimo Lakes, 1972 to 1974. Canadian Fisheries and Marine Service Data Rep. No. 146. 43 p.
- _____. 1979c. Phytoplankton and sea ice microalgal data from Frobisher Bay, 1971 to 1978. Canadian Fisheries and Marine Service Data Rep. No. 155. 82 p.
- LEWIS, E.L., and MILNE, A.R. 1977. Underwater sea ice formations. In: Dunbar, M.J. [ed.]. *Polar Oceans*. Calgary: Arctic Institute of North America. 239-245.
- MacGINITIE, G.E. 1955. Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. *Smithsonian Miscellaneous Collections* 128(9). 201 p.
- McROY, C.P. 1968. Biological oceanographic observations in the ice-covered Bering Sea, 6 to 29 March, 1968. Progress report, R/V Alpha Helix Bering Sea Expedition, 1968 (A):83-105.
- _____ and 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 with Emphasis on Renewable Resources*. University of Alaska, Institute of Marine Science Occ. Publ. No. 2. 403-421.
- _____. 1976. Annual budget of primary production in the Bering Sea. *Marine Science Communications* 2:255-267.
- MEGURO, H., ITO, K. and FUKUSHIMA, H. 1966. Diatoms and the ecological conditions of their growth in sea-ice in the Arctic Ocean. *Science* 152:1089-1090.
- _____. 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.
- NIEBAUER, H.J., ALEXANDER, V. and COONEY, R.T. 1981. Primary production at the Eastern Bering Sea ice edge: the physical and biological regimes. In: Hood, D.W. and Calder, J.A. [eds.]. *The Eastern Bering Sea Shelf: Oceanography and Resources*. Office of Marine Pollution Assessment, NOAA and Department of the Interior (Bureau of Land Management). Seattle: University of Washington Press. 2:763-772.
- STEELE, D.H. 1961. Studies in the marine amphipods of eastern and north-eastern Canada. Ph.D. thesis, McGill University, Montreal, P.Q. 350 p.
- STRICKLAND, J.D.H. and PARSONS, T.R. 1972. A practical handbook of seawater analysis. 2nd ed. Fisheries Research Board of Canada Bulletin 167. 310 p.
- TURNER, G.K., Associates. 1973. Determination of algae in natural waters by fluorometry. *Fluorometry Reviews, Algae*. May 1973. 4 p.
- USPENSKI, S.M. 1956. The bird bazaars of Novaya Zemlya. U.S.S.R. Academy of Sciences, Moscow (English translation: Canadian Wildlife Service, Translations of Russian Game Reports, No. 41, 1958). 159 p.
- UTERMÖHL, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitteilung Internationale Vereinigung für theoretische und angewandte Limnologie* 9:1-38.
- WATSON, G.E. and DIVOKY, G.J. 1972. Pelagic bird and mammal observations in the eastern Chukchi Sea, early fall 1970. U.S. Coast Guard Oceanographic Rep. No. 50:111-172.
- WELCH, H.E. and KALFF, J. 1975. Marine metabolism at Resolute Bay, N.W.T. In: *Proceedings of the Circumpolar Conference on Northern Ecology*. National Research Council of Canada. Section II:69-75.
- YENTSCH, C.S. and MENZEL, D.W. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. *Deep-Sea Research* 10:221-231.