THE UNIVERSITY OF MANITOBA

THE DISTRIBUTION AND ABUNDANCE OF SUB-ICE MACROFAUNA

IN THE BARROW STRAIT AREA, N.W.T.

BY

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ABSTRACT

The distribution of sub-ice macrofauna was investigated in the Barrow Strait area near Resolute, N.W.T. from April-June, 1985 and 1986, and in January 1986. Sampling was carried out using remotely deployed netting and video camera systems. Ten species of amphipods and two of mysids were found, but over 90% of the biomass was made up of three species of amphipods in both spring seasons: _Weyprechtia pinguis_, _Onisimus_ spp. juveniles and _Gammarus setosus_ in 1985, and _Onisimus littoralis_, _W. pinguis_ and _G. setosus_ in 1986. Only _O. littoralis_ was present under the ice in January 1986. Species composition exhibited considerable annual variation, with _W. pinguis_ dominating in spring 1985 and _O. littoralis_ dominating in spring 1986. There were also areal differences in species composition over distances of 10-100 km.

Total macrofaunal biomass decreased with increasing underlying water depth, and little biomass was present over water more than 50 m deep. Species composition was also related to underlying water depth, and it is hypothesized that spring sub-ice distribution is a reflection of summertime benthic distribution. Biomass decreased with increasing snow depth early in the spring, probably because the attenuation of incident light by snow reduces the concentration of sub-ice algae. In 1986, total biomass was lower within 1 km of the ice edge than in areas further from the ice edge.

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Arctic research demands teamwork: little can be achieved by one person working alone. I was extremely fortunate in being part of the most experienced and capable arctic research team in the world.

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I needed help, but allowed me enough freedom to make my own mistakes and
discoveries.

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THE DISTRIBUTION AND ABUNDANCE OF SUB-ICE MACROFAUNA IN THE BARROW STRAIT AREA, N.W.T

INTRODUCTION:

Arctic sea ice supports a large and diverse community of plant and animal life during the spring season. The soft undersurface of the ice may contain high concentrations of microalgae, composed principally of diatoms (Dunbar and Acreman 1980; Hsiao 1980). This flora is linked trophically to a community of invertebrates living on, within, or just below the sub-ice surface, including both a meiofaunal component, composed of protozoans, nematodes, polychaetes, rotifers and copepods, and a macrofaunal component composed of gammarid amphipods and mysids (Bradstreet and Cross 1982; Grainger et al. 1985). The sub-ice macrofauna is in turn utilized seasonally as a source of food by larger animals, including seabirds (Bradstreet 1980), immature ringed seals (Phoca hispida) (Bradstreet and Cross 1980), Arctic cod (Boreogadus saida) (Craig et al. 1982; Lowry and Frost 1981) and Arctic char (Salvelinus alpinus) (Grainger 1953; Moore and Moore 1974).

The direct trophic link between the sub-ice macrofauna and economically valuable fish and marine mammals makes knowledge of the distribution of the sub-ice macrofauna important in the management of marine resources. Continuing industrial development of the north makes the delineation of marine areas which might be particularly sensitive to

disturbance of great importance. Cross and Martin (1983) demonstrated that oil pollution had a pronounced deleterious effect on sub-ice communities. A sub-ice oil spill could therefore seriously disrupt the arctic marine food web. Damage to the sub-ice habitat could also result from other pollutants or the breaking up of the ice by shipping.

The species composition of the sub-ice macrofauna differs between nearshore and offshore areas. In general, species of benthic origin dominate in shallow areas, while pelagic species are more common in deeper waters. For example, Cross and Martin (1983) found that in shallow bays at Cape Hatt, north Baffin Island, the sub-ice macrofauna was dominated by the amphipods Weyprechtia pinguis, Gammarus setosus, Onisimus littoralis and Ischyrocerus anguipes, all listed as benthic species by Stephensen (1942). In contrast, the sub-ice communities over the deep waters of Pond Inlet (Cross 1982) and the Barents Sea (Gulliksen 1984) were dominated by the pelagic Apherusa glacialis. Carey (1985) also lists pelagic species as being dominant beneath multi-year ice, but does not say whether this is dependent on underlying water depth.

Food availability might also influence macrofaunal distribution. Cross (1982) showed that sub-ice algae was the major food source of sub-ice amphipods. The distribution of sub-ice algae is patchy on a scale of 10 to 50 metres, and this heterogeneity is primarily dependent on snow depth and ice thickness (Gosselin et al. 1986). Snow depth in particular controls the amount of light reaching the algae (Welch and Kalff 1974), and thus its photosynthetic rate. A negative correlation between sub-ice chlorophyll concentration and snow depth was suggested by Welch and Kalff (1975), observed at some fast ice stations by Cross

(1982) and quantified throughout the spring season by Welch et al. (in prep.). If food availability is a factor limiting macrofaunal abundance, a similar relationship might also be expected between snow depth and macrofaunal biomass.

The importance of ice edge areas and polynyas to marine mammals and birds has received a great deal of attention in recent years (Brown and Nettleship 1981; Dunbar 1981; Prach et al. 1981; Stirling et al. 1981; Bradstreet 1982). The apparent concentrations of marine life in such areas suggest that primary and secondary production must be higher there than in adjacent fast ice areas. Cross (1982) examined the distribution of sub-ice chlorophyll $\underline{a}$ and macrofauna in relation to the Pond Inlet ice edge, but found no consistent ice edge effects. In contrast, Barents Sea macrofauna surveyed by Gulliksen (1984) was more numerous and had higher biomass near the pack-ice edge. This survey was carried out in August, when little ice algae was present, so the increased densities at the ice edge could not have been due to higher sub-ice primary production. Because of the contradictory findings of these studies, the existence of an "ice edge effect" on sub-ice macrofaunal distribution remains in doubt.

The temporal distribution of the sub-ice community remains largely unknown. Only Cross and Martin (1983) sampled two consecutive seasons in the same area, and found considerable annual variation in macrofaunal community structure. Onisimus spp. juveniles were rare in 1981, but dominated in terms of numbers in 1982, while densities of another dominant species, $\underline{W}$. pinguis, declined over the same period. Total numbers and biomass did not change. The reasons for these changes in community composition, and the extent of their occurrence in other

areas, are not known.

The seasonal extent of the sub-ice community has been somewhat better documented. Sub-ice amphipods may be present during the winter: Greene and Steele (1975) found that O. littoralis, G. setosus and Gammaracanthus loricatus were present under the ice in December at Resolute, while Grainger et al. (1985) reported Onisimus spp. under the ice in mid-February at Iqualuit (formerly Frobisher Bay). Cross and Martin (1983) reported an increase in most species from early to late May, while Carey (1982) observed a striking order of magnitude increase in densities of O. littoralis from April to June under the ice in the Beaufort Sea. Sub-ice amphipods are also present under permanent ice pack in the Barents Sea during August (Gulliksen 1984), but in areas with a seasonal ice cover, they must return to a benthic or pelagic existence during the ice free season.

Amphipods and mysids are very mobile and they may migrate to and from the sub-ice surface in response to daily changes in light levels or current speeds. Only Gulliksen (1984) has examined this possibility. He found significant changes in density over 24 hour period at one station, with densities being highest near midnight. However, the high densities were caused by increased numbers of Parathemisto libellula, a holoplanktonic amphipod (Tencati and Geiger 1968), whose presence at the sub-ice interface was possibly an incidental result of diurnal vertical migration. At another station closer to shore where P. libellula was not present, no such changes in density occurred. If accurate estimates of macrofaunal densities are to be made, the extent of short term temporal variations in numbers must be assessed.

This study is an investigation of the spatial and temporal

distribution of the sub-ice macrofaunal community in the Barrow Strait area near Resolute Bay, N.W.T. The effects of such environmental factors as water depth, snow depth, ice thickness, distance from shore and distance from the ice edge on species composition, species biomass and total macrofaunal biomass are assessed. Annual, seasonal and short-term changes in the community, and their relation to environmental changes, are also described.

MATERIALS AND METHODS

1. SITE DESCRIPTION:

Fieldwork was carried out from the Department of Fisheries and Oceans South Camp Field Station at Resolute Bay, N.W.T (74° 42' N, 94° 50' W. See Figure 1) from March to July, 1985 and 1986, and in January 1986. The Barrow Strait area is covered by landfast first-year ice from freezeup in October until breakup in late July. Multiyear ice is relatively rare and occurs only in small, isolated patches. In some years, as in 1986, the North Water polynya extends as far west as Griffiths Island, within 10 km of Resolute (Smith and Rigby 1981). Ice thickness at the cessation of ice formation in early May ranges from 1.7 to 2.4 m. The ice varies in roughness: Typically, pans of smooth ice ranging in size from a few ha to many km^2 are surrounded by pressure ridges and areas of rough, jumbled ice. Smooth ice is areally predominant, and in some years, rough ice may be present only in nearshore areas. Snow cover is wind-packed and drifted, ranging from 0 to 50 cm in depth.

Growth of sub-ice algae begins once sufficient light begins to penetrate the ice. Maximum algal biomass is reached in early June, after which the algal layer begins to slough off (Welch et al. in prep.). Polar Bears (Ursus maritimus), Ringed seals and Arctic cod are abundant in the area during all seasons, while seabirds, bearded seals

FIGURE 1

Location of study area.
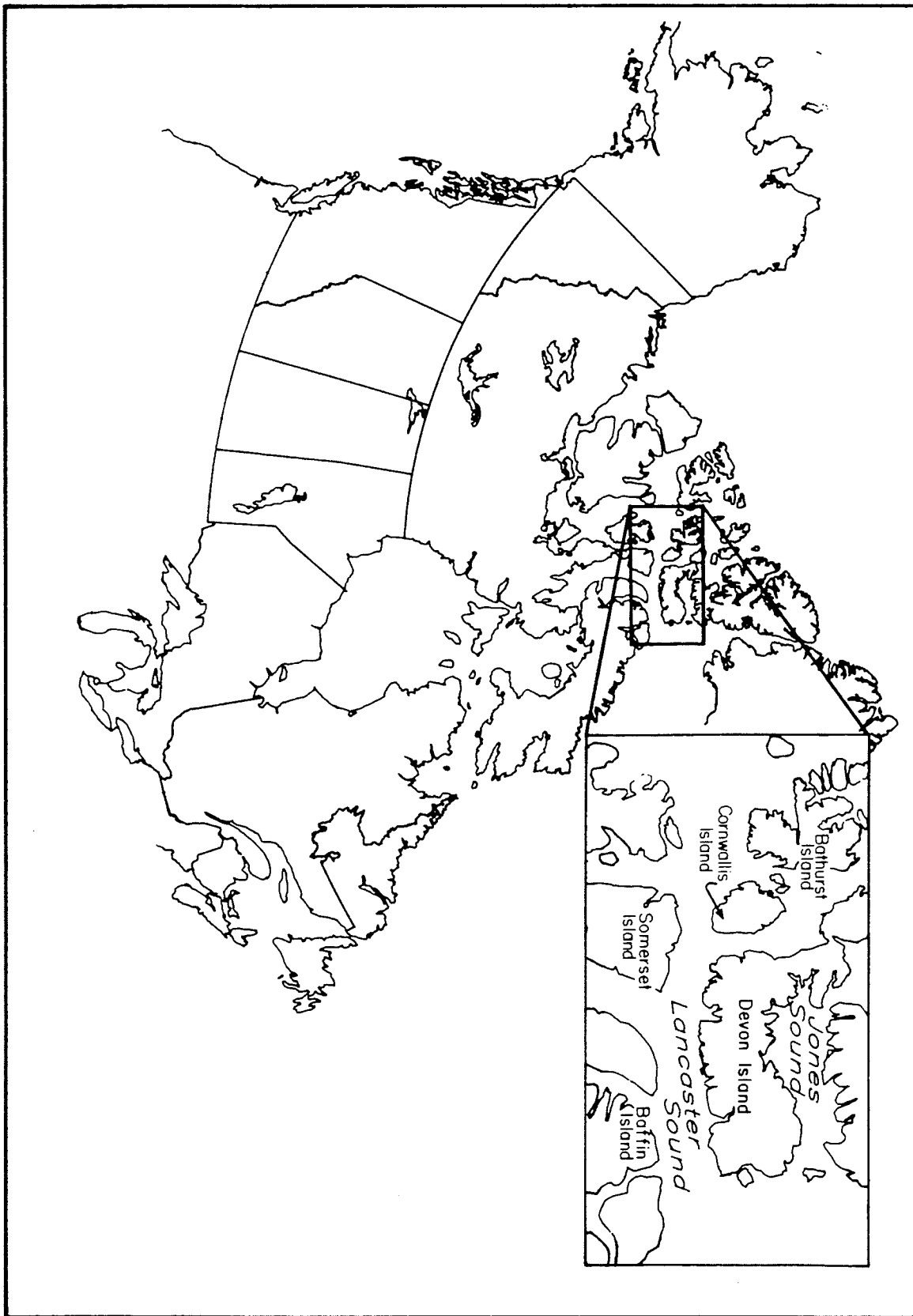
FIGURE 1

(<u>Erignathus</u> <u>barbatus</u>), walrus (<u>Odobenus</u> <u>rosmarus</u> <u>rosmarus</u>), beluga whale (<u>Delphinapterus</u> <u>leucas</u>) and narwhal (<u>Monodon</u> <u>monocerus</u>) are present seasonally.

2. SAMPLING APPARATUS:

i. Sweep Net:

The sweep net (Figure 2) was deployed through a 20-25 cm hole in the ice and sampled a doughnut-shaped area around the hole, scraping macrofauna off the undersurface of the ice. Diver observations showed that the area sampled was not disturbed by the drilling of the hole. Since an identical area was swept by the net for each sample (5.9 m^2), I assumed that catch was proportional to density. Slightly different sweep nets were used in 1985 and 1986, so catches are not strictly comparable between years.

ii. Video Camera System:

The video camera (Figure 3, Table 1) was deployed through a 46 cm hole drilled with a gasoline powered auger. Diver observations showed that the camera was out of range of the disturbance caused by the

Figure 2

The sweep net is pushed through the sampling hole (A) with the horizontal arm (B) extended to a position parallel to that of the vertical arm (C). Once the horizontal arm is through the ice, flotation on the net frame (D) causes it to float up against the sub-ice surface. The base (E) and insert (F) are placed over the vertical arm and set into the sampling hole, and a pin (G) placed through a hole in the vertical shaft prevents it from falling through the sampling hole. The T-handle (H) is attached to the vertical shaft, and the net is rotated one complete circle around the sampling hole (I-looking up at the sub-ice surface). The net is retrieved by removing the T-handle, base and insert, pushing down on the vertical arm while pulling up on the retrieval rope (J) until the horizontal arm is parallel to the vertical arm, then pulling it out of the hole.

SEA ICE
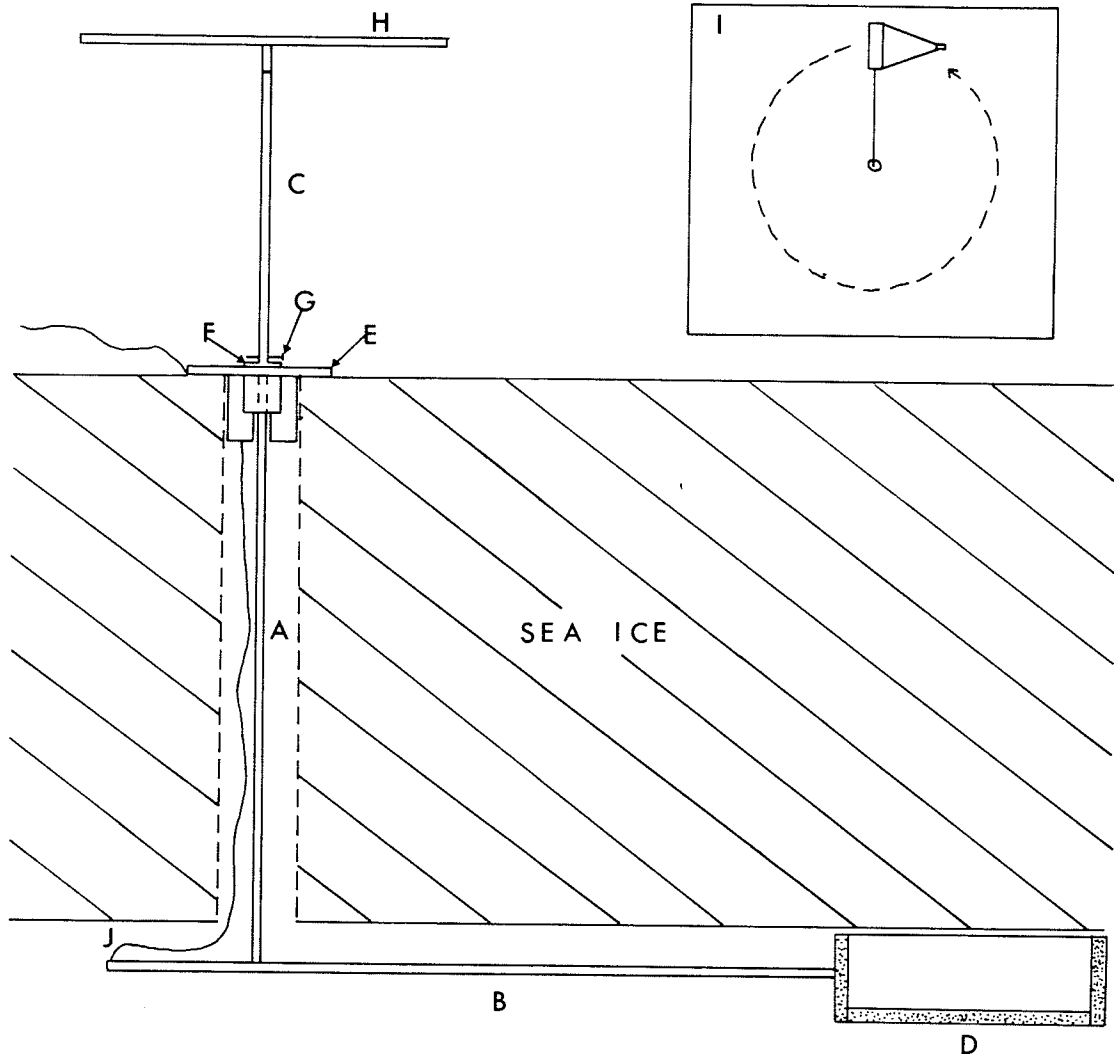
FIGURE 3

The video camera system was deployed through the sampling hole (A) with the horizontal arm (B) folded against the vertical arm (C) and the camera (D) pointing parallel to the horizontal arm. The cylindrical base (E), which was constructed from a 45 gallon drum split lengthwise and hinged together, was then placed into position beneath the tripod (F). The vertical shaft was lowered into the hole using the crank and toothed rod mechanism (G) until the camera was clear of the bottom of the sampling hole. The horizontal arm was then lowered into the 90° position (as shown) using the crank and chain drive mechanism (H). The camera was articulated using the pan-tilt unit (I) so that it pointed straight up at the ice (as shown), and the vertical arm was raised until the camera was the required distance from the ice. Finally, the system was levelled by placing a bubble level on the tripod and adjusting the clamps (J).
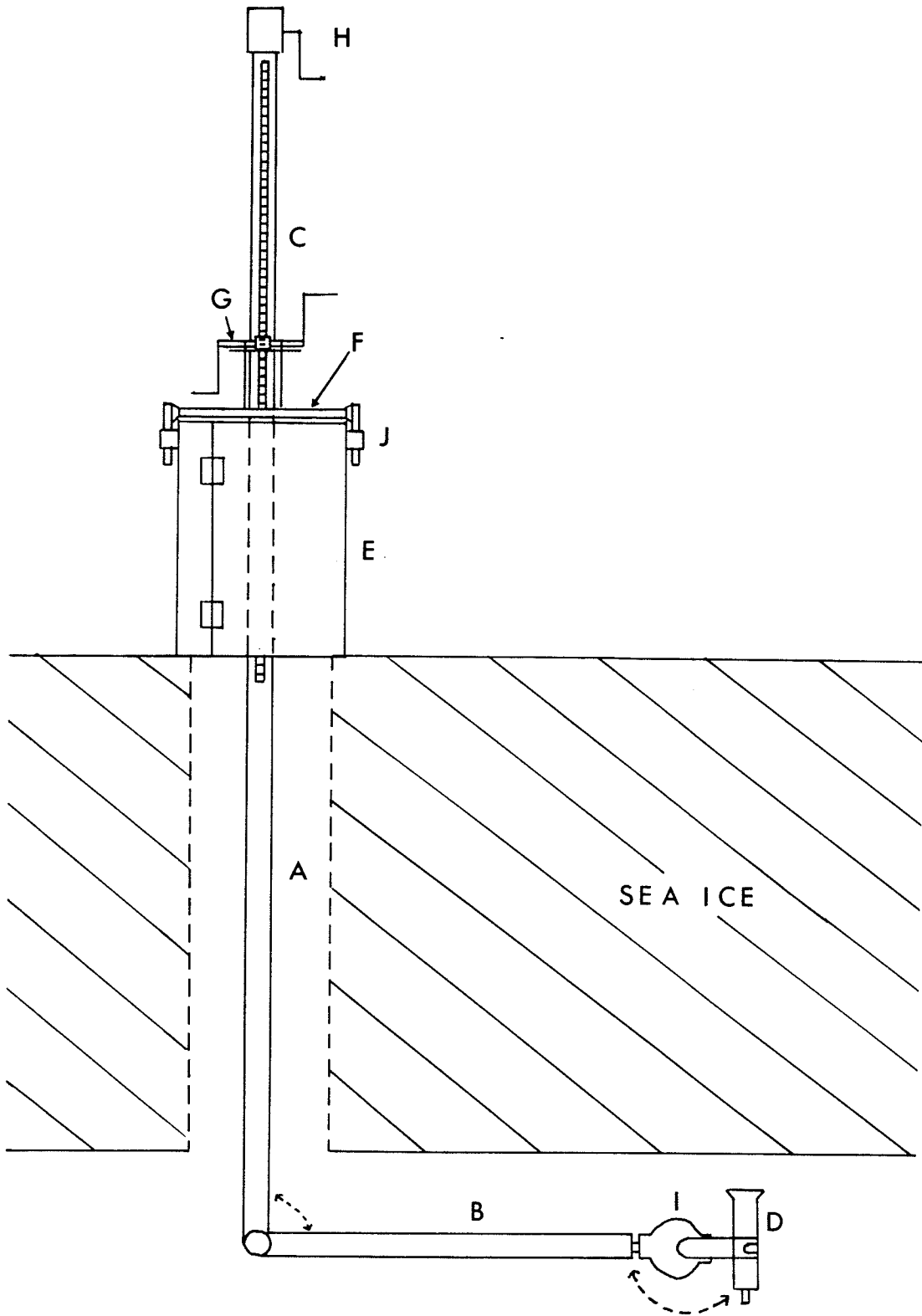
Table 1: Components of video camera system.

Component	Description
Osprey OE 1321 Camera	- Silicon Intensifier Target - operates at very low light levels - Fixed Focus - 150 mm to infinity
Osprey OE 1141A Pan-tilt	- Articulates camera
Osprey OE 1321A Control Unit	- Power supply - control for camera, pan-tilt
Osprey OE 1342 A Information Inserter	- Generates station information, etc. as onscreen text
Panasonic NV-9240 XO Video Cassette Recorder	
Panasonic WV-5350 Video Monitor	

drilling of the hole, and that the camera itself caused no apparent disturbance except for a small release of bubbles when first deployed. The area affected by this disturbance was not used in macrofaunal density estimates. Distance between the camera and the subice surface was adjusted to 27 cm ($\pm$5%). The arm was rotated slowly, stopping briefly at 20 intervals spaced equally along the circumference traversed by the camera. One video "sample" therefore consisted of 20 video images, all subtending areas of equal size. This area was calculated by measuring the distance between grid lines on a flat target placed on the sub-ice surface.

3. SURVEY DESIGN:

i. Resolute Area Surveys:

The purpose of the Resolute area surveys was to ascertain the major environmental correlates of sub-ice macrofaunal distribution in areas within 25 km of Resolute, and to describe the changes in distribution patterns over time. The surveys consisted of multiple transects run perpendicular to the shoreline (Figure 4). The distance interval between stations increased with distance from shore, but the exact interval was dependent on the depth gradient of the transect. The sampling site was chosen by pacing a randomly chosen number of steps (2-10) ahead of the snowmobile. Since the sweep net could not be used

FIGURE 4

Locations of transects sampled in spring Resolute area surveys, 1985 and 1986. Ice edge was present in 1986 only, and its location is approximate.

a. Sampled 1985 and 1986.

b. Sampled 1986 only.

c. Sampled May 9-17, 1985 only.

d. Sampled June 4-13, 1985 only.

e. Small scale variance plot, sampled May 9 and 29, 1986.

Ice Edge (1986)

Open Water (1986)

Griffiths Island

Intrepid Bay

Allen Bay

Cape Martyr

Sight Point

Resolute Bay

Prospect Hills

Cornwallis Island

Wellington Channel

Barrow Strait

Ice Edge (1986)

Open Water (1986)

Somerset I.

Devon Island
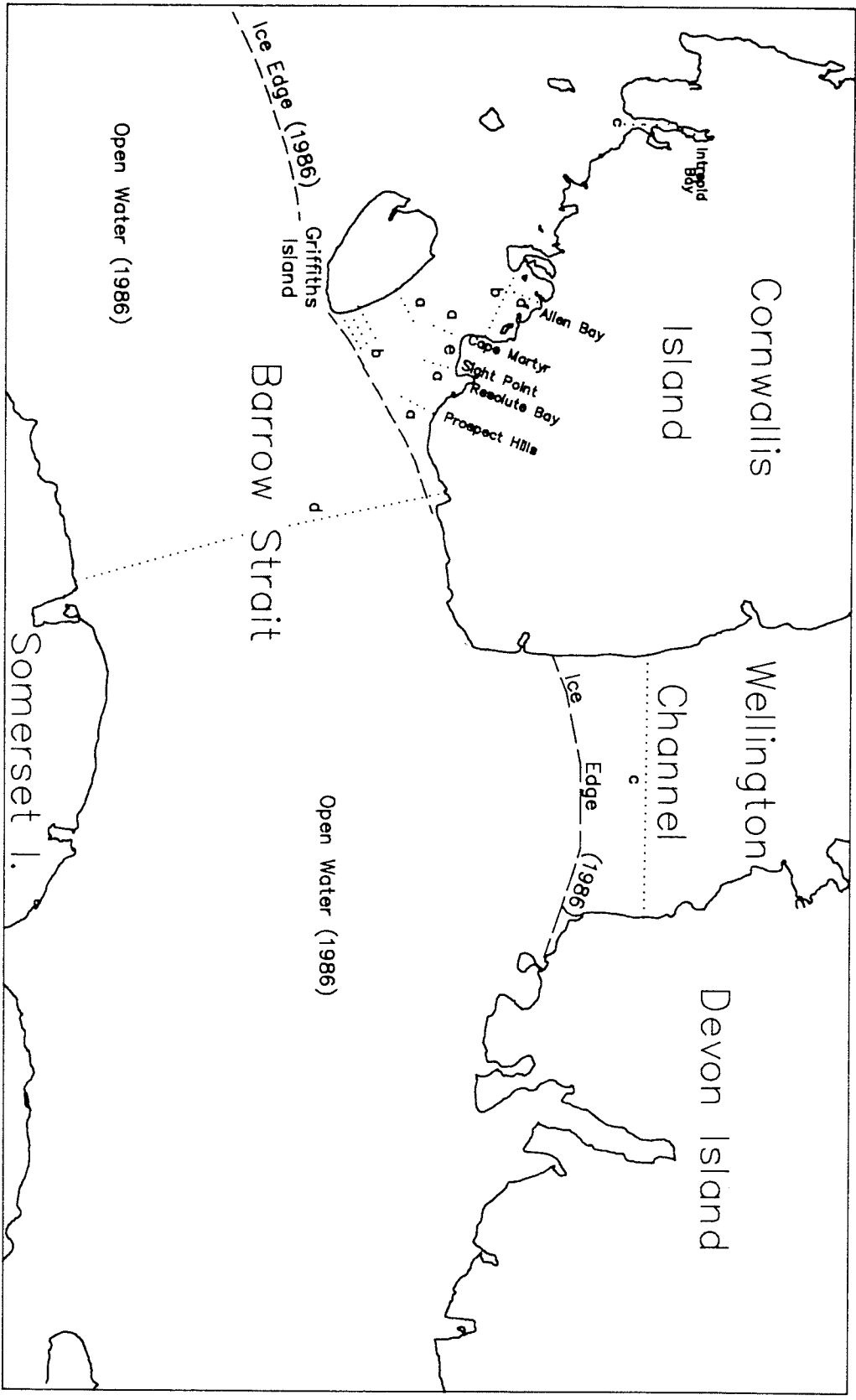
in rough ice, only smooth ice patches in rough ice areas could be sampled.

At each sampling site, four environmental factors were assessed. Snow depth was measured ($\pm$ 1 cm) at one pace intervals in a circle directly over the circumference traversed by the sweep net. Ice thickness was measured ($\pm$ 1 cm) in the sampling hole. Water depth was measured ($\pm$ 1 m) using either a sounding line or an echo sounder. Distance from shore was estimated visually and by monitoring the snowmobile odometer.

In 1985, sweep net surveys were done twice, in early May and in early June, each taking eight to ten days to complete. An extra transect was done in Intrepid Bay in May. Additional long distance transects crossed Wellington Channel in May and Barrow Strait in June.

Transect locations were similar in 1986; however, the presence of open water near Resolute presented an opportunity to assess the influence of an ice edge on sub-ice macrofaunal distribution. Hence, three additional transects were done from Griffiths Island parallel to and at increasing distances from the ice edge. Also, an additional transect was done in Allen Bay since this area had in 1985 proven to have a distinctive sub-ice community. Long distance transects were not done in 1986. The surveys were carried out four times at three week intervals beginning April 19, with about five days needed to complete each.

A limited survey, consisting of one transect plus four additional stations, was carried out in January of 1986 (Figure 5).

FIGURE 5

Location of transect and other stations sampled during January
13-17, 1986 Resolute area survey.

LEGEND

..... – Transect location
x – Other stations

Resolute Bay

Ice Edge

Open Water
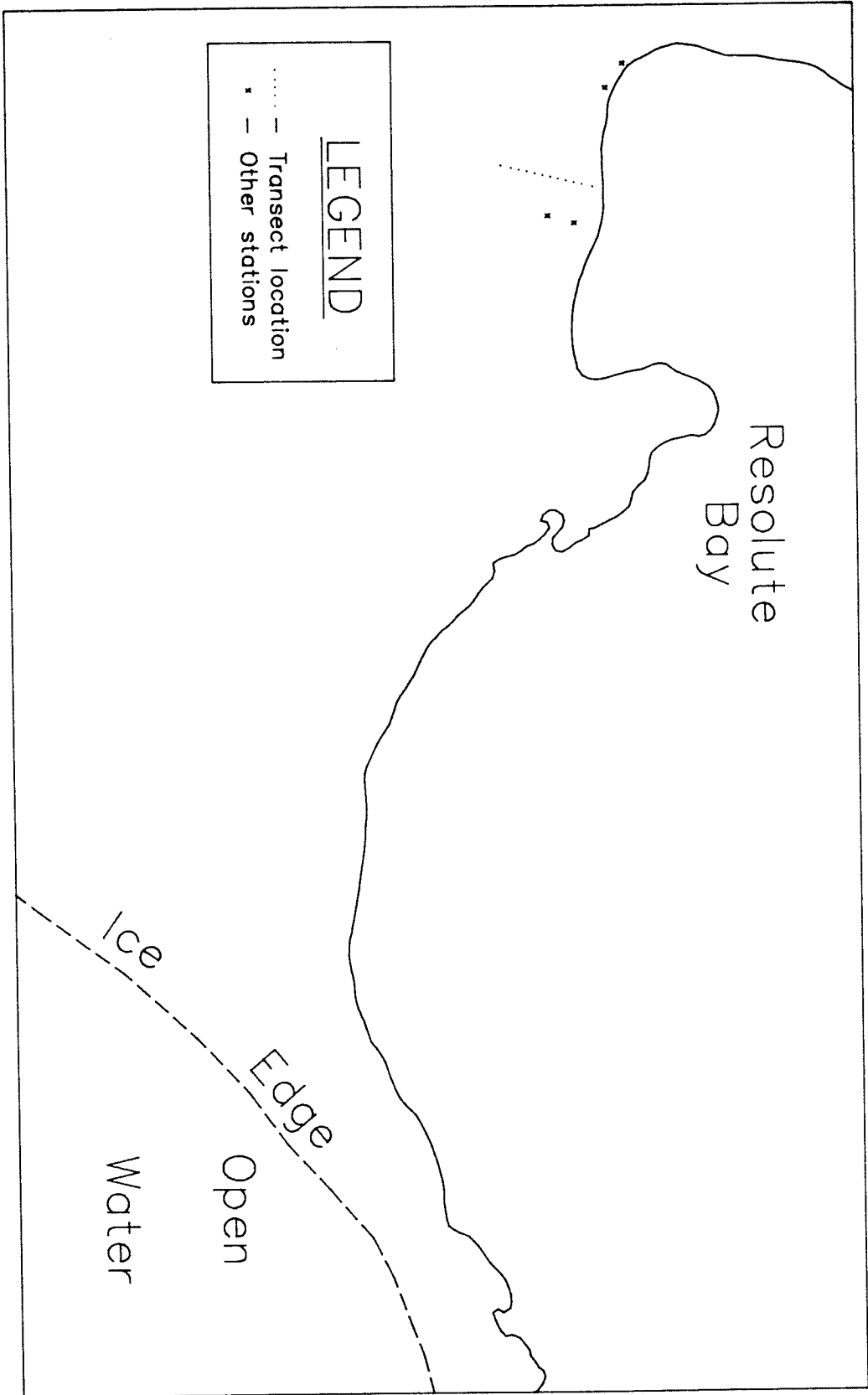
ii. Remote Surveys:

Additional sweep net surveys were carried out in spring 1986 in areas farther from Resolute (Figure 6) to determine if species composition and total biomass were comparable to that found in the Resolute area surveys.

iii. Small Scale Surveys:

To assess small-scale distributional patterns of macrofaunal abundance due to local variations in snow and ice conditions, on two occasions in spring 1986 (May 9 and May 29) 16-20 samples were taken from randomly located sites within a 100 x 100 m area (location shown in Figure 4). Water depth within the area varied between 35 and 40 m.

iv. Video Camera Surveys:

The video camera system provided a method of directly comparing sweep net catch with total macrofaunal density. The sweep net sampled a circumference identical to that traversed by the camera, and could be

FIGURE 6

Locations of stations sampled in remote surveys, spring 1986. As
many as 3 samples were taken at each station. Transects were similar in
design to those of the Resolute area surveys.
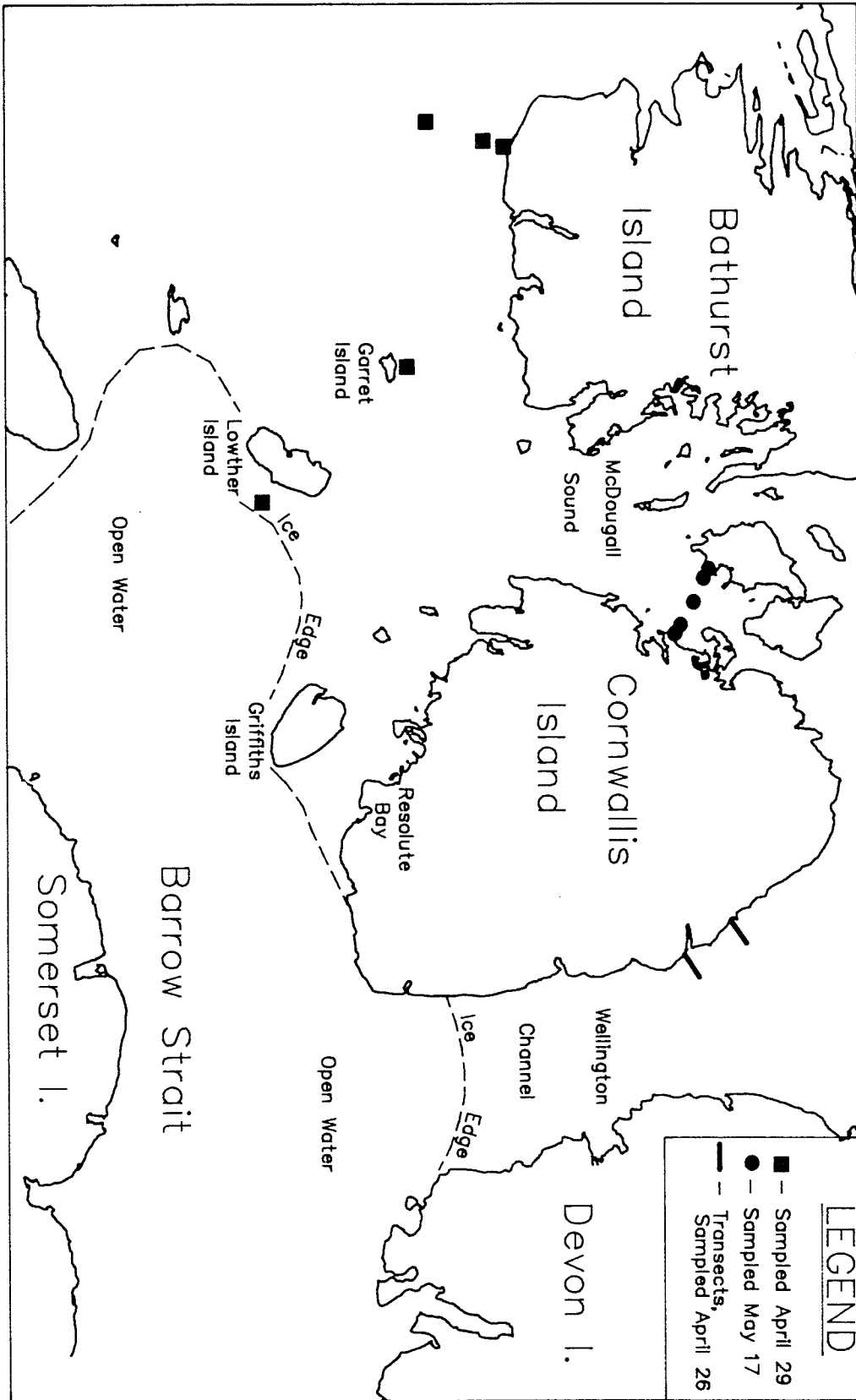
deployed in the same hole after camera sampling was completed. The major purpose of the video camera surveys, therefore, was to calibrate the sweep net.

Video sampling was carried out in the three time intervals between Resolute area surveys in 1986. Stations were concentrated in nearshore areas where macrofaunal densities were highest (Figure 7). Environmental variables were measured at each station as previously described. After camera sampling was completed, a sweep net sample was taken from the same sampling hole.

v. Short Term Variation Experiments:

Since the video camera did not remove or disturb macrofauna, it was used to determine if macrofaunal density varied over short periods of time at the same location, and if any variation found could be related to tidal cycle or current speed. On two occasions (June 9 and 14, 1986), the camera was left deployed at one station (location shown in Figure 7) for a period of about 10 hours. Sampling was carried out at four times over this period: at high and low tide, when current speeds should have been at a minimum, and midway between high and low tides, when current speeds should have been at a maximum. On June 14, a current meter was used to determine current speeds at each sampling time.

Dates and environmental attributes of all surveys are shown in Table 2.

FIGURE 7

Locations of video camera survey stations, spring 1986.

LEGEND

. — sampled all surveys

• — sampled May 20–27, June 11–16

+ — sampled May 1–8, May 20–27

✳ — diurnal station, June 8 and 14

Resolute Bay

Ice Edge

Open Water
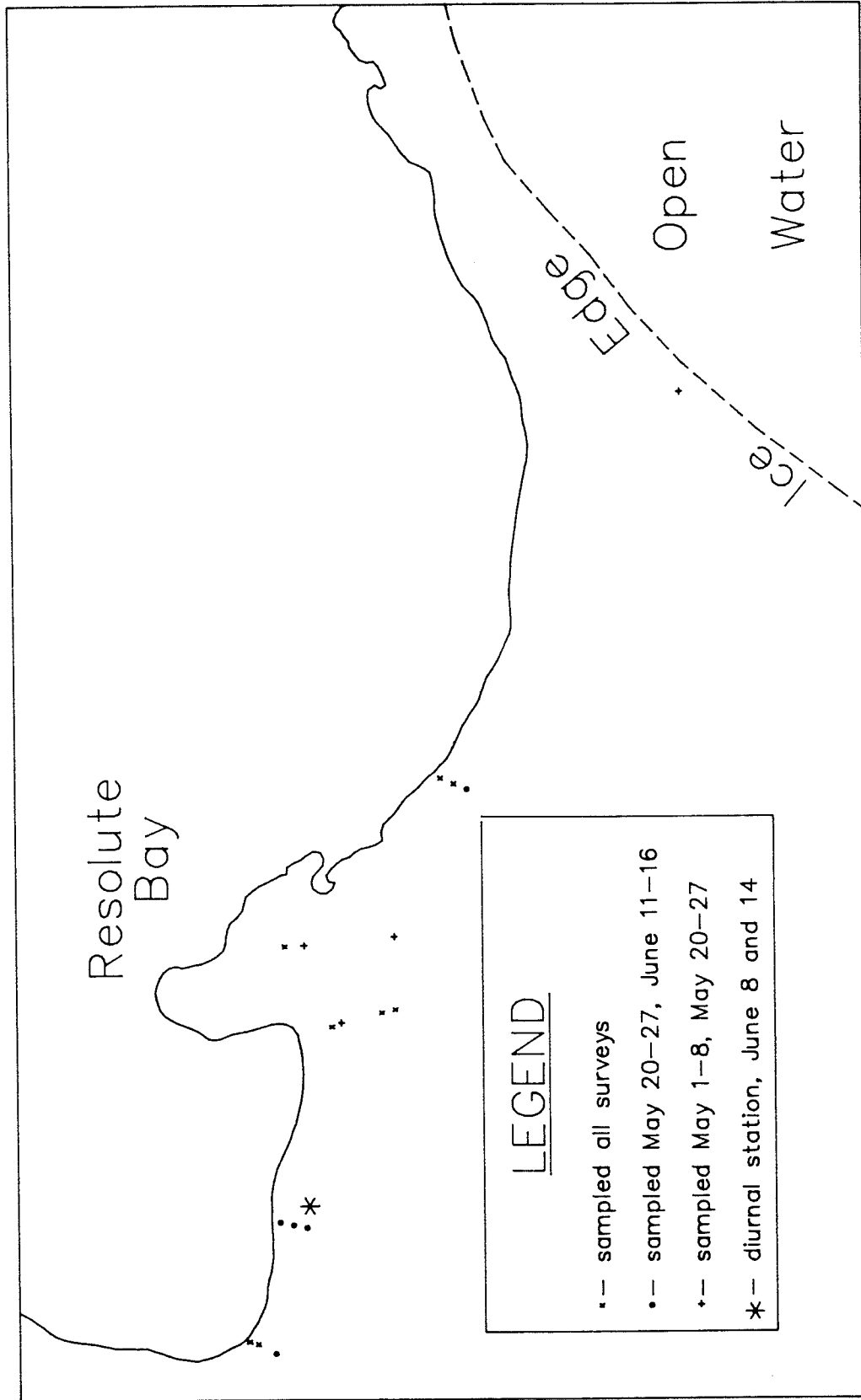
Table 2: Dates and environmental attributes of sub-ice macrofauna surveys, 1985-86.

Survey Type	Dates	Sampler	N	Water Depth (m) X	Range	Snow Depth (cm) X	Range	Ice Thickness (m) X	Range	Distance from Shore (km) X	Range
Resolute Area Surveys	May 9-17/85	Sweep Net[a]	58	59	7-200	11	1-26	1.94	1.22-2.32	2.4	0.05-18.5
	Jun 4-13/85		50	65	5-173	2	0-10	1.77	0.89-2.28	3.8	0.05-26.5
	Jan 13-17/86		13	26	8-86	0	0-0	0.88	0.80-1.40	0.8	0.05-2.0
	Apr 19-24/86		50	46	7-115	7	1-27	1.49	0.54-2.05	1.1	0.02-7.2
	May 10-16/86		67	49	8-128	10	0-30	1.52	0.55-2.19	1.1	0.02-7.4
	May 31-Jun 4/86		67	47	8-125	12	0-32	1.48	0.45-2.19	1.0	0.02-4.5
	Jun 21-26/86		65	48	6-138	9	0-32	1.64	1.00-2.20	1.0	0.02-4.0
Remote Surveys	Apr 26/86	Sweep Net	14	33	14-86	21	4-54	1.65	1.45-1.90	1.1	0.5 - 2.7
	Apr 29/86		18	31	16-40	7	2-16	1.52	1.15-1.90	6.1	0.5 -17.0
	May 17/86		15	34	12-58	15	5-30	1.94	1.74-2.10	0.4	0.1 - 1.0
Small Scale Surveys	May 9/86	Sweep Net	16	38	35-40	12	4-25	1.65	1.57-1.73	1.0	1.0 - 1.0
	May 29/86		20	34	33-37	12	2-23	1.54	1.47-1.60	0.6	0.6 - 0.6
Video Camera Surveys	May 1-8/86	Video Camera and Sweep Net	13	30	9-75	9	0-26	1.74	1.44-2.13	1.1	0.05-2.7
	May 20-27/86		17	27	8-73	7	1-41	1.71	1.49-2.09	1.0	0.05-2.7
	Jun 11-16/86		14	28	8-51	8	0-33	1.61	1.34-2.05	0.6	0.02-1.7
Short Term Variation Experiments	Jun 9/86	Video Camera	4	39	-	-	-	1.55	-	0.6	-
	Jun 14/86		4	34	-	-	-	1.48	-	0.6	-

[a] Two versions of the sweep net were used: one up to and including January 1986, the other in spring 1986. Only the later version was calibrated.

4. LABORATORY METHODS:

i. Sample Enumeration and Biomass Estimation:

Sweep net samples were returned from the field packed in slush to prevent interspecific predation and preserved in 5% freshwater formaldehyde solution within 8 hrs of capture. Samples were sorted to species and cohort, except for Onisimus spp. and Parathemisto spp. juveniles which were sorted to genera. Species such as G. setosus, for which cohorts were not identifiable, were sorted into predetermined size classes.

Species biomass was estimated using dry weight-length relationships, either from this study or the literature (Table 3). Animals used in weight-length relationships were frozen within two hours of capture. Head length was measured ($\pm$0.01 mm) using a Wild MMS 235 length measuring unit. The animals were dried at 60° C for at least 12 hours, equilibrated in a desiccator for at least two hours, then weighed ($\pm$0.01 mg).

Mean weights for species-cohorts or size classes were calculated for the sweep net survey samples only. Biomass was estimated for samples from remote, small scale and video camera surveys using the mean weights for each species cohort or size class from the most temporally proximal Resolute area survey. A subsample from each species-cohort or

Table 3: Dry weight-length relationships. Equations are of the form:

$$Ln(dry\ wt.\ (mg)) = a(ln(head\ length\ (mm))) + b$$

Sources: 1. This study.
2. Percy and Fife 1983.
3. Bradstreet 1980.

Species	N	R^2	a	b	Source
Onisimus littoralis[a]	50	0.93	3.410	2.617	1
Weyprechtia pinguis	85	0.98	3.397	0.394	1
Gammarus setosus	52	0.99	3.515	0.809	1
Apherusa glacialis	40	0.72	3.292	1.252	1
Ischyrocerus anguipes	39	0.87	3.636	0.565	1
Gammarus wilkitzkii	16	0.96	3.419	0.845	1
Gammaracanthus loricatus	9	0.95	2.586	0.167	1
Parathemisto spp. juveniles[b]	150	0.98	2.793	5.348	2
Mysis oculata[b,c]	?	0.94	2.35	0.011	3

[a] Also used for Onisimus glacialis, Onisimus nanseni and Onisimus spp. juveniles.

[b] Equation of the form:
$$Log_{10}(dry\ wt.\ (mg)) = a(Log_{10}(total\ length\ (mm))) + b$$

[c] Also used for Mysis polaris

size class was chosen randomly, the number of animals taken from each sample proportional to its contribution to the total for the species. The total number of each species cohort or size class measured from each survey was 10-20 for smaller amphipods such as W. pinguis juveniles and 30-40 for larger amphipods such as O. littoralis. All representatives of very rare species were measured.

Species biomass in a sample was estimated by multiplying the number of a particular species cohort or size class in the sample by its mean weight. Cohorts or size classes were then summed for each species.

ii. Video Enumeration:

It was not possible to speciate animals on video images; thus only total numbers per image were counted. The four images closest to the point where the camera was initially deployed were not used because of possible disturbance effects. Each image covered 0.2 m^2 and 16 images were counted for every station, for a total areal coverage of 3.2 m^2.

5. STATISTICAL METHODS:

i. Data Transformations:

Species-abundance data must usually be transformed in order to comply with the assumptions of parametric statistical techniques (Green 1979). Assumptions common to analysis of variance (ANOVA) and linear regression include: (i) that the data are normally distributed; (ii) that treatment effects are additive, and (iii) that variances are equal across treatments in ANOVA and independent of the regressor in linear regression (Green 1979). Glass et al (1972) found that ANOVA was very robust to violations of the normality and additivity assumptions, but that heteroscedasticity could lead to a higher probability of type 1 error, particulary if sample sizes were unequal across treatments. Taylor's power law (Downing 1979; Green 1979) provides a method to eliminate dependence of treatment variances on treatment means, and thus reduce heteroscedasticity. Taylors power regressions were therefore used to derive variance stabilizing transformations for each dataset (see Appendix 1). The log(X+1) transform was found to be the best overall for the sweep net data, and was applied for all statistical analyses.

ii. Species Composition:

One-way analyses of variance were used to determine if the abundance of each species changed over time. Each Resolute area survey was considered as a separate treatment, giving two in spring 1985 and four in spring 1986.

iii. Total Biomass Analysis:

Log-transformed total biomass was assumed to respond linearly to environmental gradients. This assumption was verified whenever possible by examining bivariate scatterplots of log-transformed total biomass against environmental variables. Stepwise multiple regression analysis (SAS Institute 1982) was applied to the Resolute area survey data to determine which environmental variables were related to total macrofaunal biomass. Environmental variables included underlying water depth, distance from shore, snow depth and ice thickness. Also, each transect location was coded as a dummy variable to see if locational differences in biomass not accounted for by the environmental variables measured were present.

Water depth and distance from shore were highly correlated with one another, while the other environmental variables were intercorrelated to a much lesser extent. When intercorrelated independent variables are included in a stepwise regression, the one most closely correlated with the dependent variable enters the equation, and the other is usually dropped. However, it is possible that both will be included in the equation if both contribute explanatory power to the model. Water depth and distance from shore were both used in the analyses because the inclusion of both factors in a regression model would indicate that shore slope might be a determinant of total sub-ice biomass.

Analysis of variance (ANOVA) and covariance (ANCOVA) (SAS Institute

1982; Steele and Torrie 1980) were used to test for temporal and spatial differences in total macrofaunal biomass. ANCOVA was used in cases where total biomass was significantly related to an environmental variable, usually underlying water depth. Assumptions made in using ANCOVA include: (i) that the relationship between the independent and dependent variable is linear, and (ii) that the slope of this relationship does not vary across treatments (Steel and Torrie 1980). The assumption of slope equality was tested in every case where ANCOVA was used, and comparisons of treatment means proceded only if the slopes were found to be homogenous across treatments.

iv. Species Distribution:

Individual species' abundances are generally assumed to respond to underlying environmental gradients in a nonlinear fashion (Gauch 1982; Green 1979). Ordination techniques are widely used by ecologists to determine which environmental factors are important in defining species distribution (Gauch 1982; Legendre and Legendre 1983; Pielou 1984). Reciprocal averaging (RA) (Hill 1973) is a technique closely related to principal components analysis, but contains implicit standardizations for species and site: ie. the effects of species dominance and site richness are removed from the analysis. Since in this case, the major aim of the analysis was to define the environmental gradient determining species distribution, regardless of how rare or common the species, such a standardization was desirable. This method produces simultaneous

ordinations of species and samples, and has been found to be the most
successful of the metric ordination methods in retrieving at least the
rank order of sites on environmental gradients in real and simulated
ecological data (Fasham 1977; Hill 1973; Kenkel and Orloci 1986).

Ordinations were performed on the log-transformed species-biomass
data from the Resolute area surveys and remote surveys using the
ORDIFLEX computer package (Gauch 1977). Species occurring in less than
10% of the samples were deleted from the analyses. RA tends to be
rather sensitive to outliers, and these may dominate the first few axes,
obscuring real trends in the data (Kenkel and Orloci 1986). In some
cases, therefore, species having distributions obviously disjunct from
the others after an initial ordination were also deleted.

Bivariate scatterplots of the RA axis scores against environmental
variables were examined visually, and if linear trends were apparent,
sample scores on the RA axes were related to environmental variables
using stepwise linear regression. Significant correlations between
environmental variables and axis scores were considered indicative of an
environmental gradient controlling species distribution, and the
gradient was analyzed further by direct graphical methods.

RESULTS

1. SWEEP NET CALIBRATION:

In spring 1986, all video camera stations (Table 2, Figure 7) were sampled with the sweep net immediately after video sampling, making possible the derivation of a relationship between sweep net catch and total macrofaunal density. Juveniles were not included in the sweep net catch data, as they were too small to be counted effectively with the video system. Analysis of scatterplots revealed that the relationship between mean total macrofaunal density and sweep net catch was linear up to a density of about 70 organisms m^{-2}, above which the relationship broke down. Therefore, only stations with densities of less than 70 m^{-2} were included in the regression. The regression of sweep net catch against macrofaunal density was significant ($p<.01$). Since the intercept term was not significantly different from 0 ($p>.05$), regression through the origin (Steele and Torrie 1980) was used to derive an equation to transform the 1986 sweep net catches into true macrofaunal densities (see Figure 8). The capture efficiency of the sweep net was 65%

FIGURE 8

Relationship between sweep net catch and sub-ice macrofaunal density as determined with the video camera system. Juveniles are not included in the counts. The regression is forced through the origin. This relationship was used to estimate actual densities from spring 1986 sweep net catches.

Y=0.65(X)
R=0.89, N=30
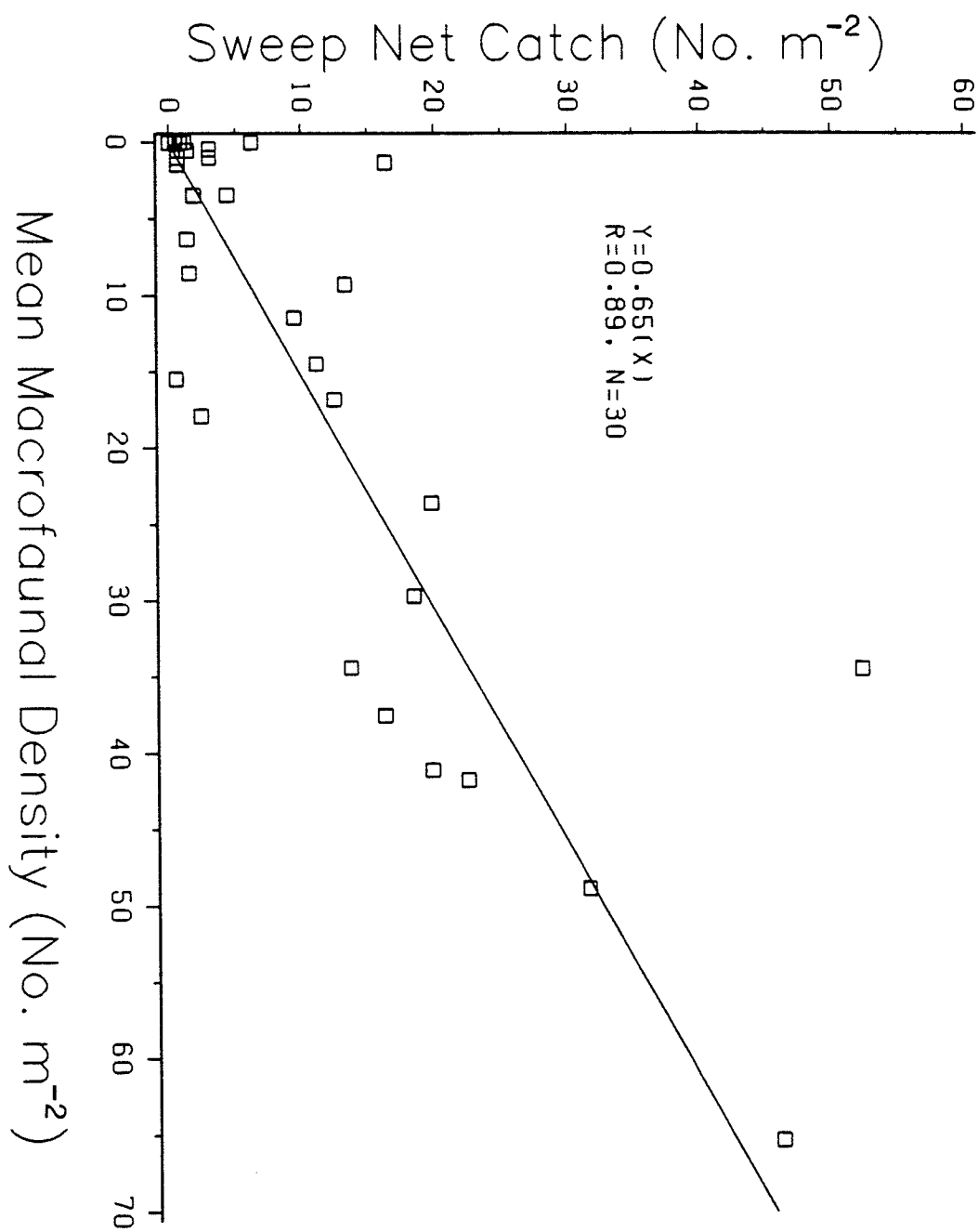
2. SPECIES COMPOSITION:

i. Annual Changes:

The species composition of the sub-ice community varied considerably over the two years sampled (Figure 9). Over two thirds of the sub-ice biomass was made up of W. pinguis alone in spring 1985. W. pinguis, G. setosus and Onisimus spp. juveniles together made up over 95% of the total macrofaunal biomass. In January 1986, O. littoralis was virtually the only amphipod present under the ice. Similarly, O. littoralis, which was a very minor constituent of the community in 1985, dominated the sub-ice fauna in spring 1986. Weyprechtia pinguis was vastly reduced in number, and Onisimus spp. juveniles were extremely rare. O. littoralis, G. setosus and W. pinguis together comprised over 98% of the sub-ice biomass. Thus, W. pinguis and O. littorallis alternated in abundance between 1985 and 1986, while the abundance of G. setosus remained relatively constant over the period.

ii. Seasonal Changes:

Three species in 1985 and five in 1986 showed significant changes

FIGURE 9

Sub-ice macrofaunal species composition in the Resolute area as determined from all Resolute area surveys, spring 1985 and 1986.
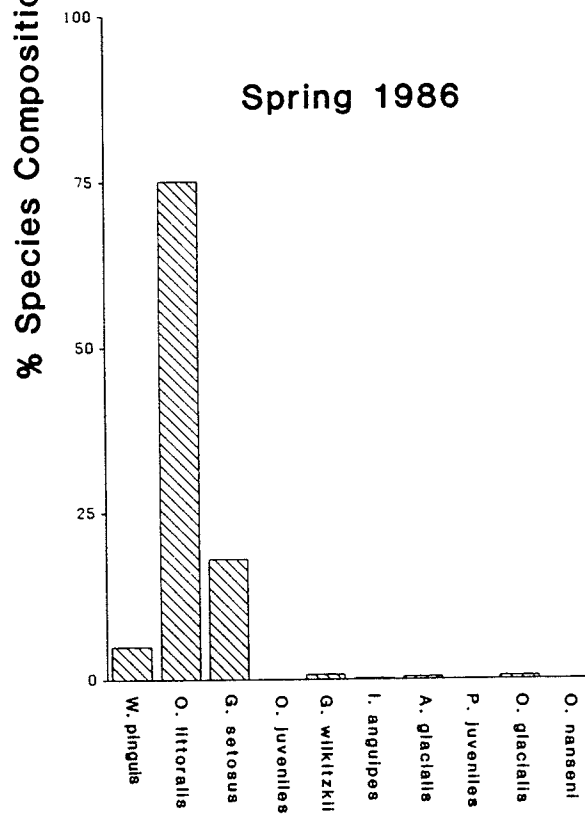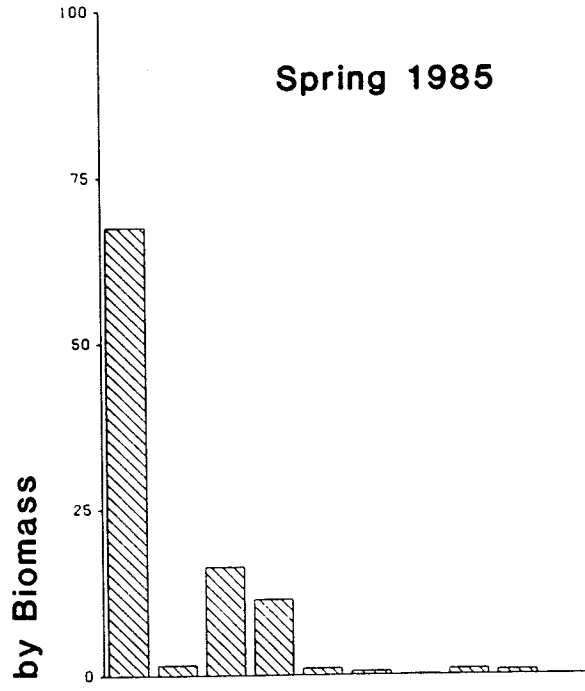
in abundance over the spring (ANOVA's, p<.05) (Figure 10). In 1985, the abundances of O. glacialis, Onisimus spp. juveniles and Gammarus setosus increased from early May to early June. Similarly, the abundances of O. glacialis, Onisimus spp. juveniles, G. setosus and A. glacialis generally increased over the course of the spring in 1986. The abundance of Parathemisto spp. juveniles decreased from early to late spring in 1986.

iii. Spatial Variation:

In 1986, sampling in areas remote from Resolute demonstrated the existence of large scale geographical differences in species composition (Figure 11). Wellington Channel and McDougall Sound had communities similar to each other in which Mysis oculata, which was very rare in the Resolute area, and O. littoralis co-dominated to make up almost all the sub-ice biomass. There also appeared to be a general east-west trend in species composition. At the westernmost stations near Bathurst Island on Viscount Melville Sound, 98% of the biomass was made up of W. pinguis, a situation more similar to that of the Resolute area in 1985 than in 1986. Garret Island had a species composition similar to that found at Western Bathurst Island, but at Garret Island, A. glacialis made up a significant proportion of the biomass, a situation seen nowhere else. Further east at Lowther Shoal, species composition was midway between those observed at Bathurst Island and Resolute, with W. pinguis and O. littoralis making up roughly equal parts of the sub-ice

FIGURE 10

Change in species biomass over the 1985 and 1986 spring seasons as determined from all Resolute area surveys. Only species that showed significant variations over time are shown.

1986

1985

MEAN BIOMASS (mg. m⁻²)

MEAN CATCH (mg)

SURVEY DATE

SURVEY DATE
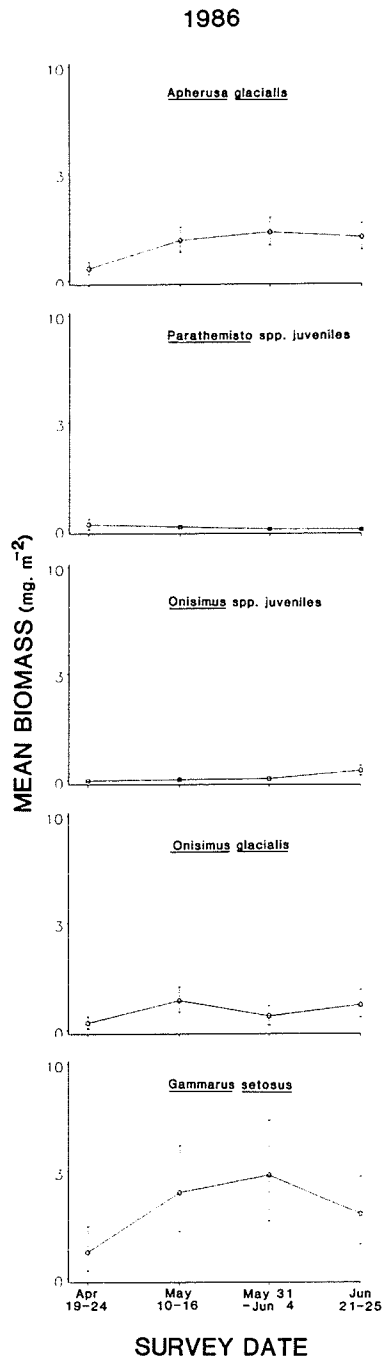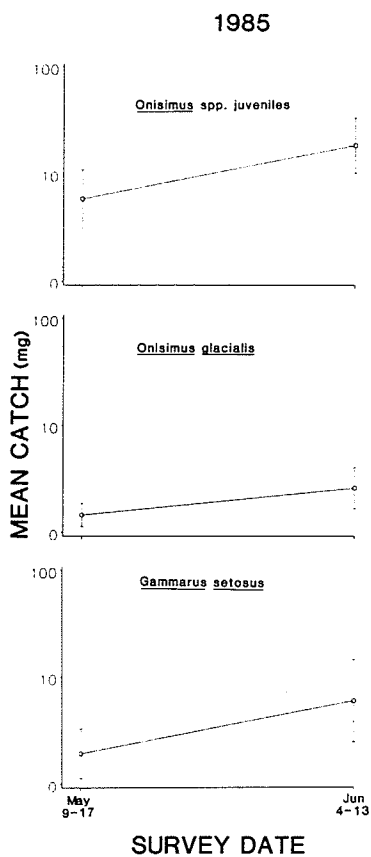
FIGURE 11

Sub-ice macrofaunal species composition (% by biomass) outside the Resolute area as determined from remote surveys, spring 1986.
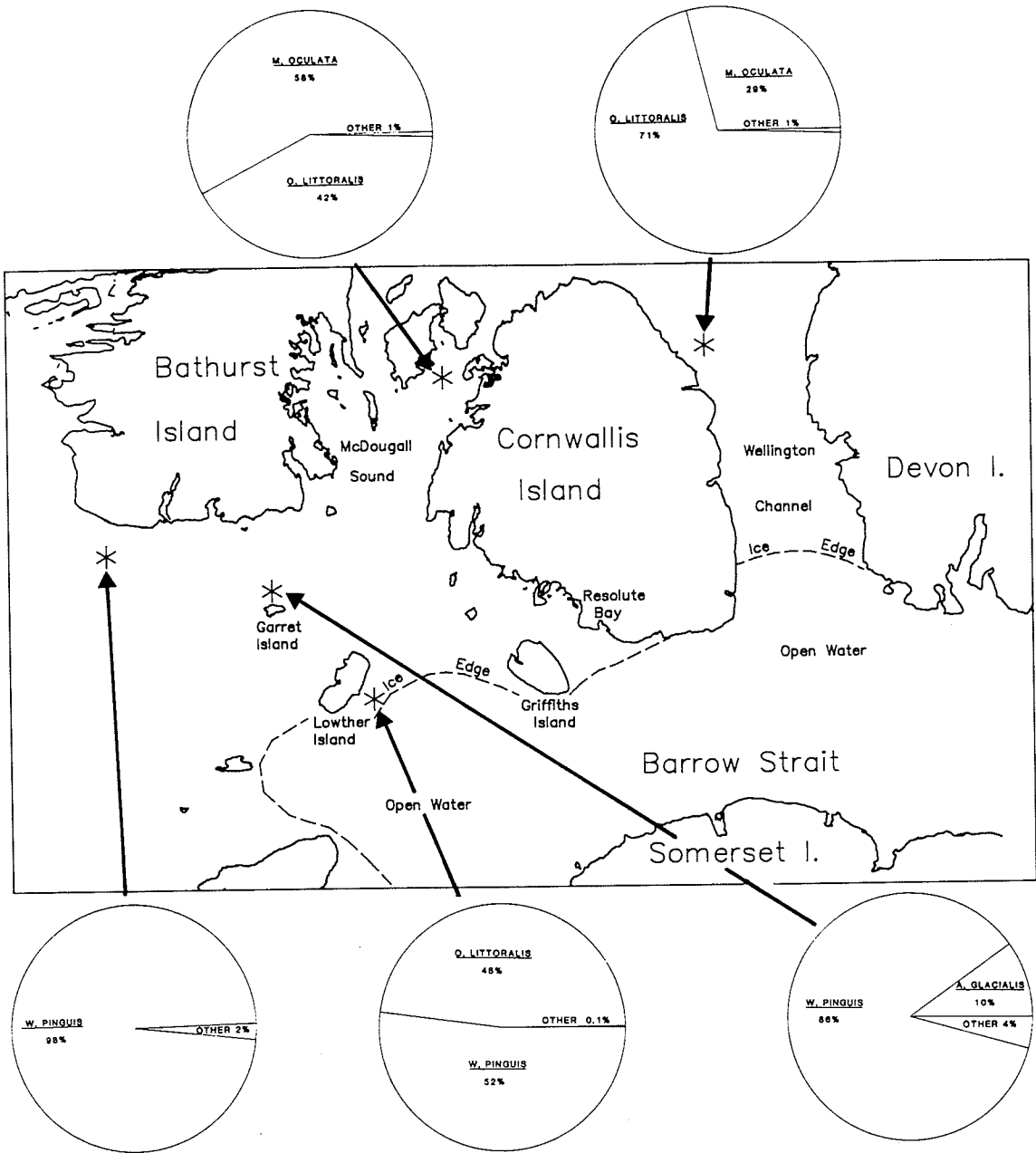
biomass.

3. TOTAL BIOMASS DISTRIBUTION:

i. Environmental Correlates:

Stepwise multiple regressions relating log-total macrofaunal biomass to environmental and locational variables (Table 4) were significant at at the $p<.05$ level except that for the Wellington Channel survey in 1986 which was significant at the $p=.07$ level. Regression accounted for 35-73% of the total variance. Underlying water depth was always the most important variable in explaining biomass distribution, again with the exception of the 1986 Wellington Channel survey, where snow depth was most important. Water depth alone accounted for over half the total variance absorbed by regression in most cases. Biomass always decreased with increasing underlying water depth. Other environmental and locational variables contributed significantly to the regressions, but only the effect of water depth was temporally consistent.

In 1985, snow depth had a negative influence on total macrofaunal biomass in early May but not in early June. Ice thickness had a positive effect in June. Biomass was atypically low in Intrepid Bay in May and Allen Bay in June (Intrepid Bay was not sampled in June). In general, it appears that bays had sub-ice biomasses lower than those in

Table 4: Stepwise multiple regression models relating Ln(Total Sub-ice Macrofaunal Biomass) to environmental and locational variables for all sweep net surveys.

* - Coefficient is significant at $p < .05$ level
** - Coefficient is significant at $p < .01$ level
NS - Not Significant ($p > .05$)

| | 1985 | | 1986 Resolute Area | | | | | Wellington | McDougall |
Independent Variable	May 9-17	June 4-13	Jan. 13-17	April 19-24	May 10-16	May 31-June 4	June 21-26	April 26	May 17
Water Depth	-**	-**	-*	-**	-**	-**	-**	-NS	-**
Distance from Shore	-*			-**			+**		-*
Snow Depth		+*		-**	-*		+***	-*	
Ice Thickness						-**			-*
Intrepid Bay	-*			-*	-*	+**			
Allen Bay		-**					+**		
Cape Martyr				-**	-*	-**			
Griffiths 1									
Griffiths 2							+***		
Griffiths 3									
Griffiths 4	+*								
Prospect Hills									
Sight Point									
Wellington									
Barrow									
N	58	50	13	50	67	67	65	14	15
R2	0.49**	0.73**	0.41*	0.59**	0.50**	0.52**	0.35**	0.38[a] NS	0.71**

[a] $p = .07$

other areas in 1985.

In January of 1986, water depth alone affected the distribution of sub-ice biomass. No snow was present on the ice at this time. During the spring season, snow depth and ice thickness were negatively correlated with biomass in the first survey in April, but not at any other time. In fact, by mid-June (fourth survey), snow depth had a positive correlation with biomass. Locational variables were also significant in the regressions, but none was consistent between surveys.

Total macrofaunal densities determined in the video camera surveys were poorly correlated with environmental variables. In contrast to the results of the Resolute area sweep net surveys, water depth had no significant effect. During the first camera survey (May 1-8), snow depth was negatively correlated with macrofaunal density. No other correlations were found. Similarly, no significant correlations between total macrofaunal densities determined from sweep net catch at the same stations and environmental variables were found. The lack of a significant depth effect is therefore probably due to the smaller range of station depths in these surveys, not to the type of sampler used.

Small scale variance surveys showed that snow depth had a significant effect on biomass distribution (Figure 12). Snow depth had a strong negative correlation with macrofaunal biomass on May 9. By May 29, snow depth had a positive correlation with biomass, although this correlation was weakened but still significant with the removal of one outlier.

FIGURE 12

Relationships between sub-ice macrofaunal biomass as estimated from sweep net catch and snow depth in a 100 x 100 m area on two dates. Circled point is considered an outlier.

MAY 29, 1986

R=0.59 N=20
R=0.44 With Circled Outlier Removed
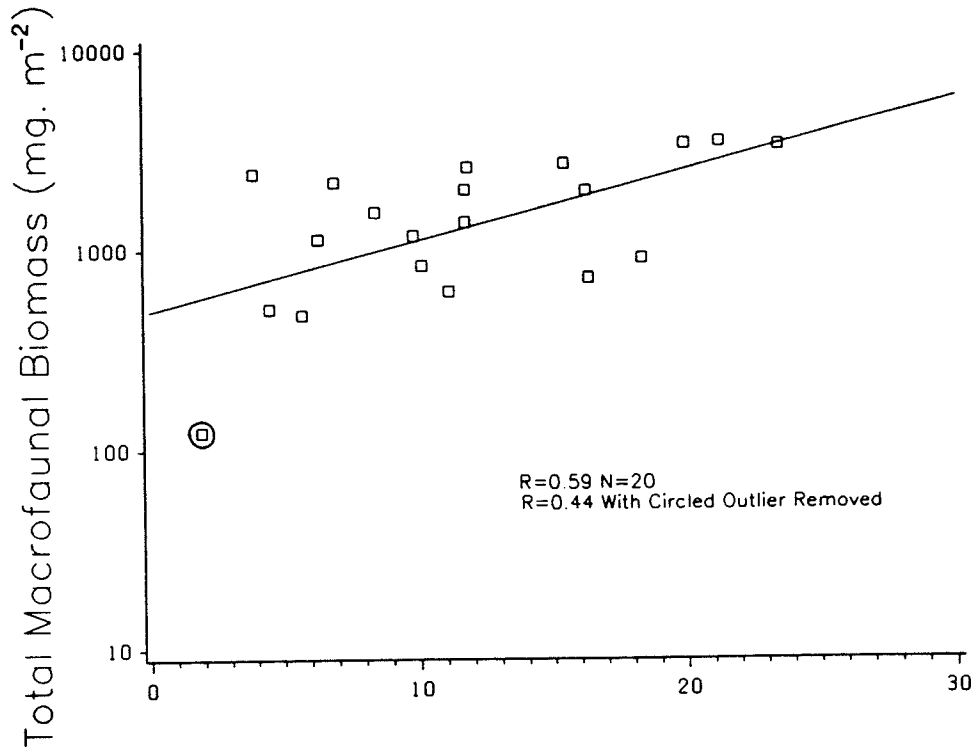
MAY 9, 1986

R=0.75 N=16
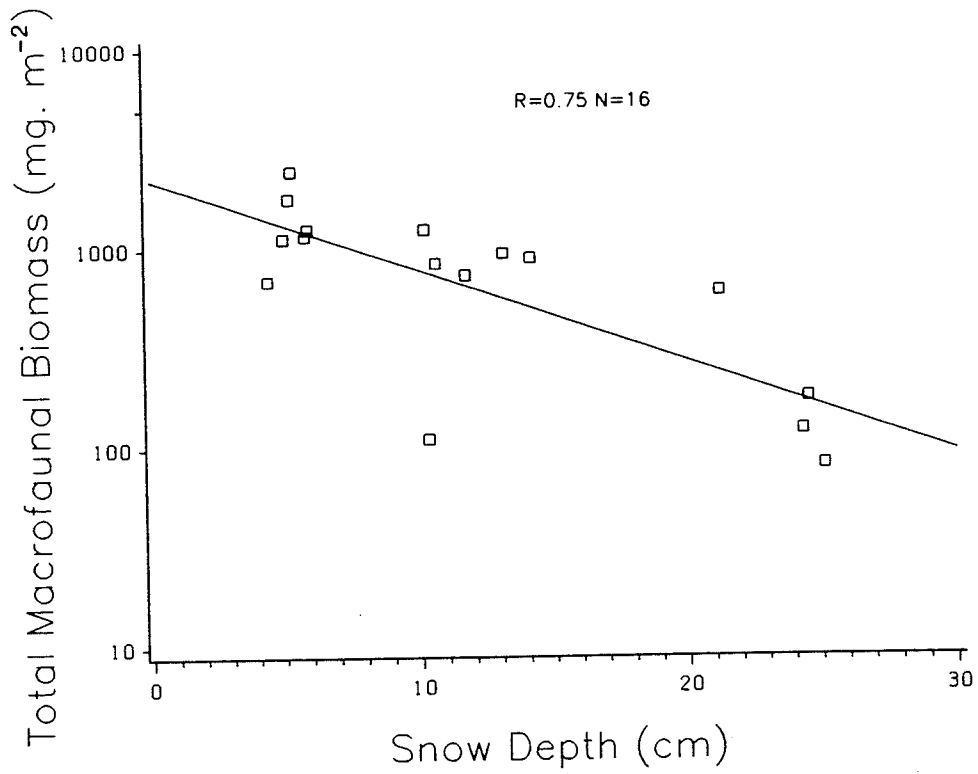
ii. Ice Edge Effects:

Griffiths Island stations in the 1986 Resolute area surveys were analyzed as a separate group to determine if the proximity of the ice edge in 1986 had any effect on total biomass distribution. In stepwise multiple regressions relating total biomass to environmental variables in each survey (Table 5), water depth was always the most important correlate of total biomass, and in no case did distance from the ice edge contribute significant explanatory power. Since the slopes of the water depth-total biomass relationships were homogenous across the last three survey dates (ANCOVA, p>.05), the data from these surveys were combined to allow a stronger test for ice edge effects. The data were classified into three groups by distance from the ice edge: <1 km, 1-2 km and 10 km. The slopes of the water depth-total biomass relationships were homogenous across distance classes (ANCOVA, P>.05), but proximity to the ice edge had a significant effect on mean total biomass levels (ANCOVA, P<.01). Biomass was much lower within 1 km of the ice edge than in areas farther from the ice edge (Figure 13).

iii. Temporal Patterns:

Since different sweep nets were used in the spring 1985 and spring

Table 5: Stepwise linear regression models relating Ln(Total Sub-ice Macrofaunal Biomass) to environmental variables. 1986 Griffiths Island transects only.
  * - Coefficient is significant at $p < .05$ level.
  ** - Coefficient is significant at $p < .01$ level.

Independent Variable	April 19-24	May 10-16	May 31-June 4	June 21-26
Water Depth	-**	-**	-**	-**
Distance from Shore				+*
Snow Depth				
Ice Thickness				
Dist. from Ice Edge				
N	12	24	24	24
R^2	0.72**	0.57**	0.44**	0.33**

FIGURE 13

Change in mean total sub-ice macrofaunal biomass with distance from the ice edge in the Griffiths Island area, spring 1986. Data from the last three Resolute area surveys (May 10-June 26) are combined, and mean macrofaunal biomass is adjusted to the overall mean underlying water depth of 51 m.

Mean Macrofaunal Biomass (mg. m^{-2}) versus Mean Distance From Ice Edge (km)
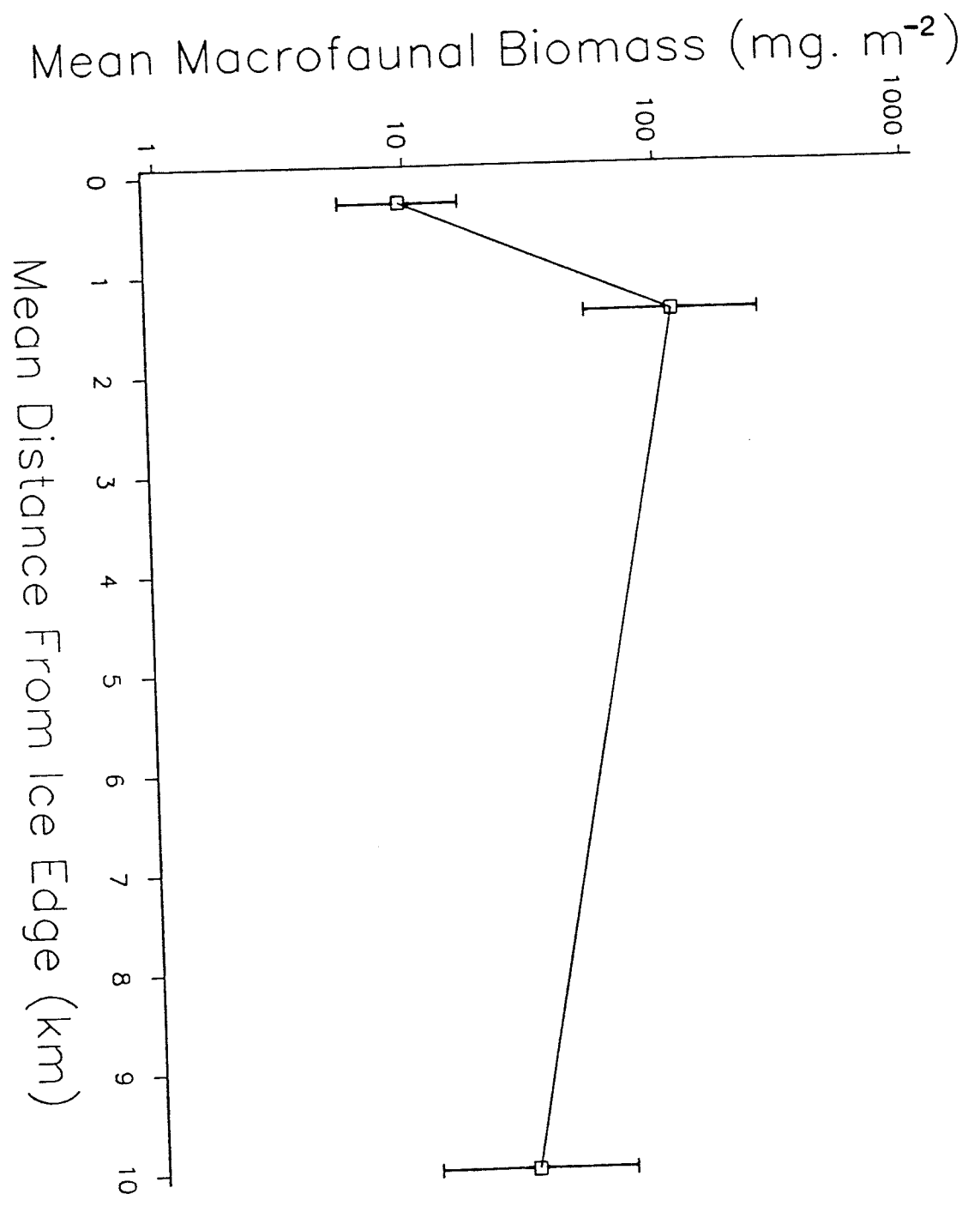
1986 Resolute area surveys, comparisons of absolute biomass levels between the two years were not appropriate. However, the pattern of biomass change with underlying water depth did change from 1985 to 1986 (see Figure 14). In 1985, sub-ice macrofauna was present over depths of up to 200 m, while in 1986, there was essentially no biomass over depths greater than 150 m, except for late in the spring when biomass extended out to greater depths.

Seasonal changes in biomass distribution were investigated using ANCOVA with depth as a covariate (Figure 14). Samples from Intrepid Bay (Figure 4) were omitted from May 9-17, 1985 Resolute area survey dataset since: (i) Intrepid Bay was not sampled in the second survey of 1985, precluding temporal comparisons, and (ii) stepwise regressions (Table 4) indicated that Intrepid Bay had atypically low biomass levels. In spring 1985, the slopes of the water depth - sub-ice biomass relationships were not significantly different over the two surveys (p>.05). Sub-ice biomass was significantly higher in June than in May (p<.05). The slope of the water depth - sub-ice biomass relationship in the January 1986 survey was significantly different from those of the two earlier surveys (p<.05). Biomass was generally lower and decreased more quickly with underlying water depth than at either time in the spring.

Neither the slopes of the water depth - sub-ice biomass relationships nor mean biomass levels changed significantly over the first three Resolute area surveys of 1986, encompassing a period from April 19 to June 4. The slope did change significantly in the final sampling survey in late June (p<.05), but sub-ice biomass was poorly correlated with underlying water depth at this time. Biomass was more evenly distributed over all water depths at this time than at any other

FIGURE 14

Regressions between sweep net catch (spring 1985 and January 1986) or total sub-ice biomass as estimated from sweep net catch (spring 1986), and water depth in the Resolute area. Data for the first three Resolute area surveys of 1986 are combined into one regression, as ANCOVA showed no significant differences in slope or mean biomass levels over this period. 95% confidence intervals for the mean predicted biomass are shown for the mean, minimum and maximum water depths of each survey.

SPRING 1985 AND WINTER 1986

May 9–17, 1985. R=−0.66, N=46
June 4–13, 1985. R=−0.82, N=50
Jan. 13–17, 1986. R=−0.64, N=13

SPRING 1986

Apr. 19–June 4, 1986. R=−0.62, N=184
June 21–26, 1986. R=−0.25, N=65
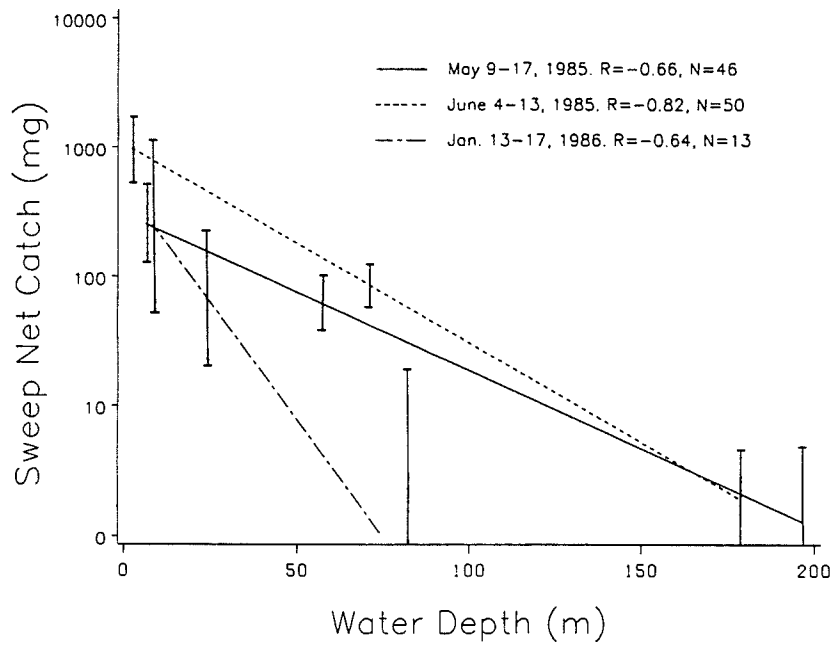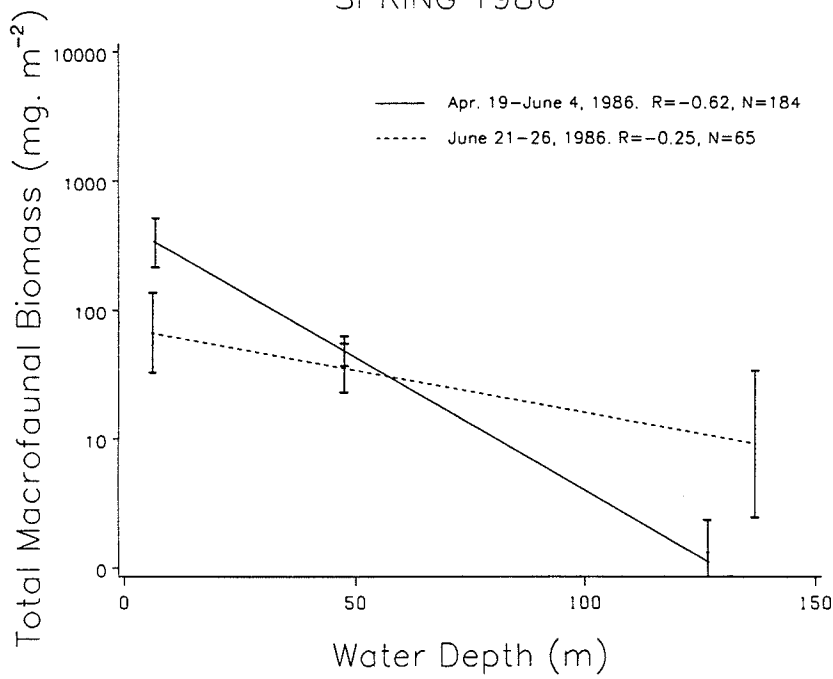
time in the spring.

The short-term variation experiments in which one station was sampled repeatedly with the camera system showed that significant (p<.05) changes in density occurred over a 10 hour period (Figure 15). On June 9, highest densities were observed during the final sampling time between high and low tide. In contrast, highest densities occurred at high and low tide on June 14. Density appeared to decrease with current speed (Figure 16), although this decrease was not consistent over the entire range measured.

iv. Spatial Patterns:

Large-scale spatial variations in sub-ice biomass were investigated by applying ANCOVA with depth as a covariate to the remote surveys and the most temporally proximal Resolute area surveys of 1986. The Wellington channel and McDougall Sound remote surveys were each treated as separate locations, while the survey of April 29 was divided into three locations: Western Bathurst Island, Garret Island and Lowther Shoal (see Figure 6). Significant differences in the water depth – sub-ice biomass slopes across locations (p<.01) precluded the comparison of biomass levels by ANCOVA. Biomass declined much more quickly with depth at Western Bathurst Island and McDougall Sound than in the Resolute area at the same time. Sub-ice biomass levels were not significantly different across locations in the 0-50 m depth interval (ANOVA, p>.05), but mean biomass levels at Garret Island and McDougall

FIGURE 15

Change in mean sub-ice macrofaunal density over a 10 hour period at one station on two occasions. Each point is a mean count of 16 video images, and 95% confidence intervals are shown.

JUNE 8

JUNE 14

Sampling Time
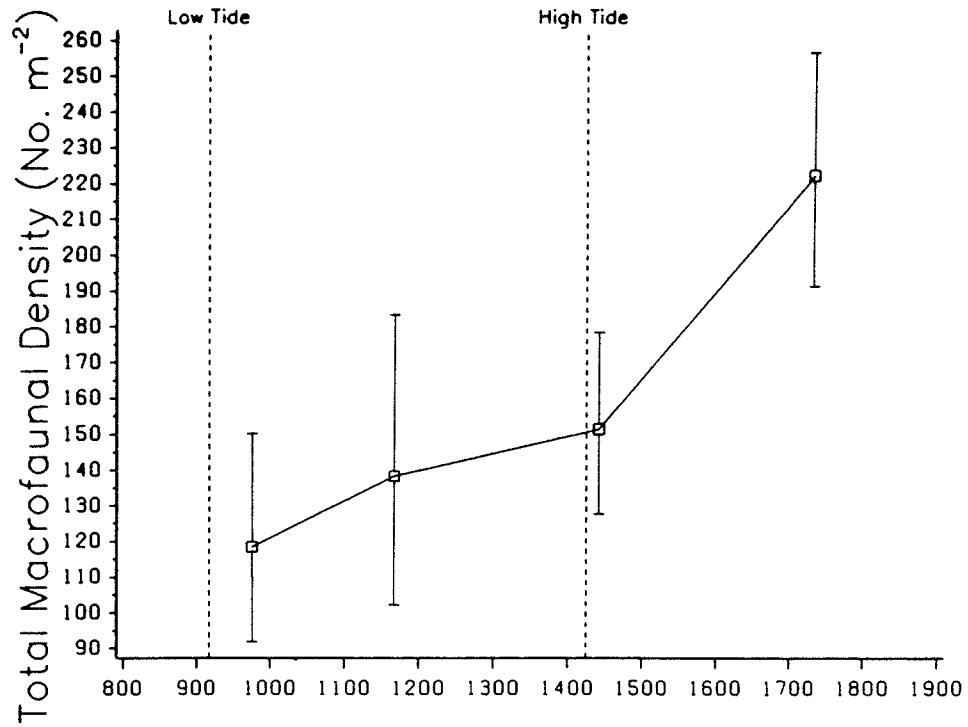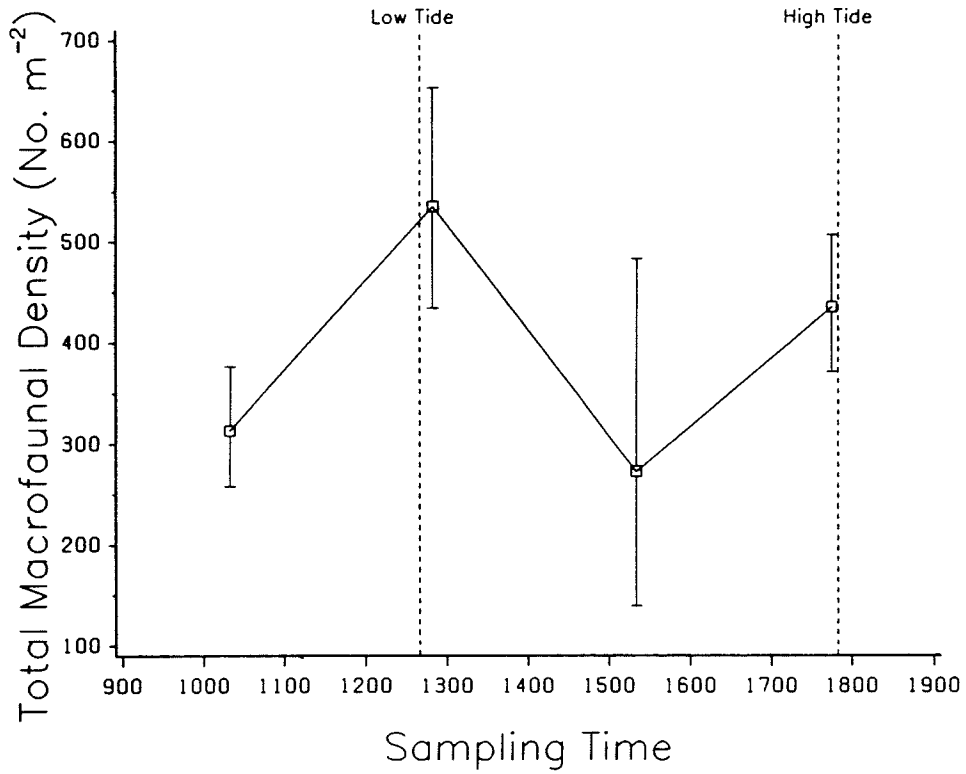
FIGURE 16

Change in mean sub-ice macrofaunal density with current speed at one station over a 10 hour period. Each point is a mean count of 16 video images, and 95% confidence intervals are shown.

Total Macrofaunal Density (No. m^{-2})

Current Speed (cm. sec. $^{-1}$)

JUNE 14
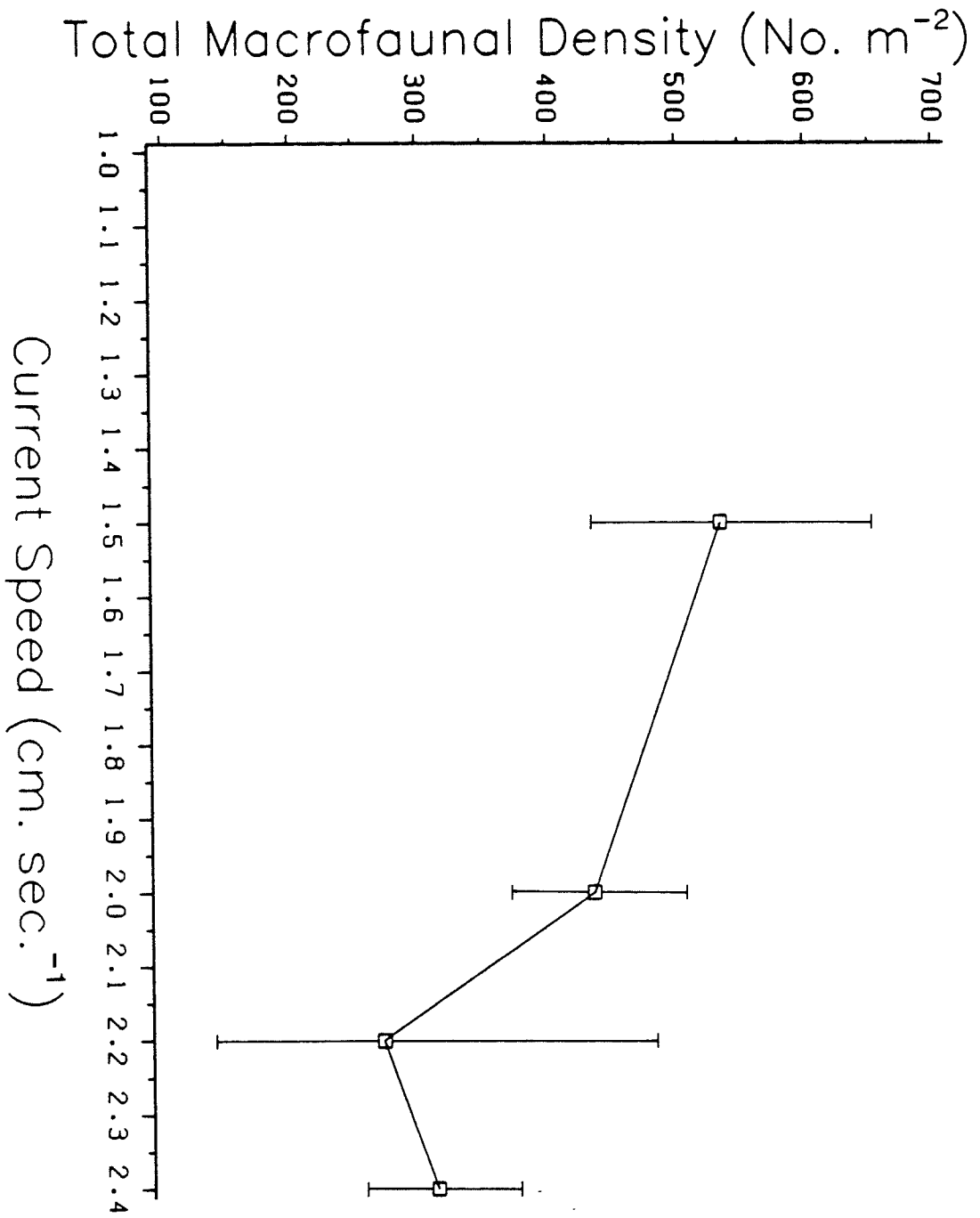
Sound were less than one-tenth and one-half respectively those found in the Resolute area at the same time (Table 6). It seems likely that more precise estimates (ie. more samples) would have revealed significant differences in biomass levels across locations.

4. SPECIES DISTRIBUTION:

Reciprocal averaging was applied to the Resolute area survey data and the Wellington Channel and McDougall Sound remote survey data to determine if gradients in species composition were interpretable in terms of the environmental variables measured. RA axes 1 and 2 together accounted for over half the total variance in most datasets analyzed (Table 7). No annual or seasonal trends in the amount of variance accounted for by each axis were apparent. Scatterplots of the RA axis scores against environmental variables showed obvious linear trends. Linear regression was therefore considered adequate in interpreting the ordinations.

Stepwise multiple regression models relating sample scores on RA axes 1 and 2 to environmental variables (Table 8) consistently revealed a clear inshore-offshore gradient in species distribution. In all but one case, RA axis 1 defined this gradient, being related to water depth, distance from shore or both. For the early May 1986 Resolute area survey, axis 1 functioned as an outlier detector, while axis 2, which accounted for about the same amount of variance, defined the inshore-offshore gradient.

Table 6: Mean total sub-ice macrofaunal biomass in the 0-50 m depth zone at various locations.

Location	Date (1986)	N	Mean Water Depth (m)	Mean Biomass (mg m^{-2})	95% CI^a (mg m^{-2})
Western Bathurst I.	April 19-24	9	35	98	18- 506
Garret I.	"	6	32	9	0- 45
Lowther Shoal	"	3	16	235	24-2269
Wellington Channel	"	12	26	134	26- 705
Resolute Area	"	31	26	105	46- 240
McDougall Sound	May 10-16	12	28	41	5- 295
Resolute Area	"	44	28	141	73- 267

^{a} CI = Confidence Interval

Table 7: Percent of total variance accounted for by first two
          reciprocal averaging (R.A.) axes.

Survey		Axis 1	Axis 2	Total
Date	Location	(%)	(%)	(%)
May 9-17/85	Resolute	30	19	49
June 4-13/85[a]	"	29	24	53
April 19-24/86[b]	"	38	21	59
May 10-16/86[b]	"	24	24	48
May 31-June 4/86[c]	"	35	22	57
June 21-26/86	"	39	21	60
April 26/86	Wellington Channel	30	22	52
May 17/86[b]	McDougall Sound	38	29	66
Mean		33	23	56

[a] _Apherusa glacialis_ deleted

[b] _Parathemisto_ spp. juveniles deleted

[c] _Onisimus_ spp. juveniles deleted

Table 8: Multiple regression models relating R.A. axes 1 and 2 to environmental variables.

* - Coefficient is significant at p < .05 level
** - Coefficient is significant at p < .01 level

	1985				1986											
	Resolute Area				Resolute Area								Wellington		McDougall	
Location / Date	May 9-17		June 4-13		April 19-24		May 10-16		May 31-June 4		June 21-26		April 26		May 17	
R.A. Axis	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Water Depth	**		**			**		**	**	**	**				**	
Distance from Shore					**	**					**		**	*	**	
Snow Depth	*		*					*	**	**	*		**			
Ice Thickness	*							*		**	**	**	**			
N	55	55	50	50	44	44	62	62	67	67	65	65	13	13	14	14
R2	0.37**	0.09*	0.37**	N.S.	0.44**	0.33**	0.13*	0.50**	0.41**	0.25**	0.66**	0.13**	0.72**	0.41*	0.65**	N.S.

Snow depth and ice thickness were inconsistently related to the axis defining the inshore-offshore gradient. In both years, snow depth was important early in the spring, but not at other times. Ice thickness was significantly correlated only in early May 1985 and in the final survey of 1986.

Except in the one case when RA axis 2 defined the inshore-offshore gradient, it was not consistently related to any environmental variables and did not seem to define any interpretable environmental gradient. Higher axes were even less interpretable.

Species were ranked by their scores on the axis defining the inshore-offshore and the regressions between the sample scores on this axis and underlying water depth used to define approximate depth distributions for each species (Table 9). The relative species compositions in the 0-30 m, 30-50 m and >50 m depth zones in both years generally confirmed the RA result (Figure 17). G. setosus and I. anguipes were confined to ice over areas of shallow depth, while O. littoralis and W. pinguis were most abundant over the 30-50 m depth zone. A. glacialis, O. glacialis and P. spp. juveniles were most abundant over deeper waters. O. spp. juveniles changed their pattern of distribution between years, occurring in greatest abundance over waters 30-50 m deep in 1985 and over deeper waters in 1986.

Analysis of scatterplots of the relationship between RA axis 1 and water depth revealed that, in 1985, samples from Allen and Intrepid Bays were clear outliers, tending to have higher scores on axis 1 than other areas of similar depth. These bays were therefore more "offshore" in character than other areas. Species composition in the bays was clearly different in that W. pinguis and G. setosus were far less abundant,

Table 9: Depth distributions of sub-ice amphipods as determined from their mean rankings on the R.A. axes defining an inshore-offshore gradient. Ordinations of Resolute area surveys only used to define rankings.

S - Shallow 0-30 m
M - Mid-depths 20-50 m
D - Deep >40m

Year	1985	1986
Gammarus setosus	S	S
Ischyrocerus anguipes	S	S
Onisimus littoralis	M	M
Weyprechtia pinguis	M	M
Onisimus spp. juveniles	M	
Apherusa glacialis		D
Onisimus glacialis	D	D
Parathemisto spp. juveniles	D	

FIGURE 17

Mean species biomass in three depth intervals as determined from all Resolute area surveys, 1985 and 1986. Biomass levels for each species are adjusted to a common scale (ie. biomass for each species totals 100 over all depths). Species are ordered from left to right by their mean ranking on the reciprocal averaging axis defining an inshore-offshore gradient.
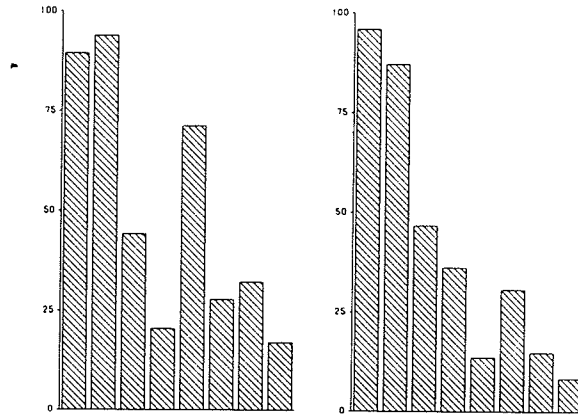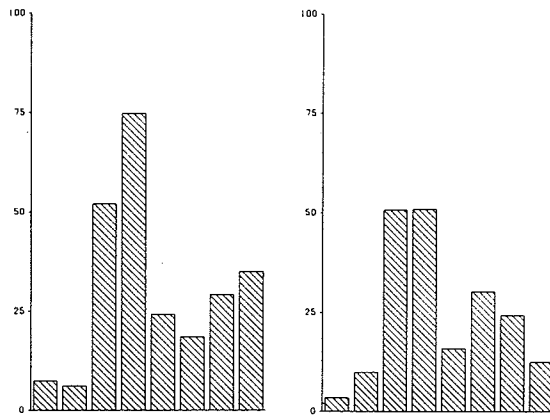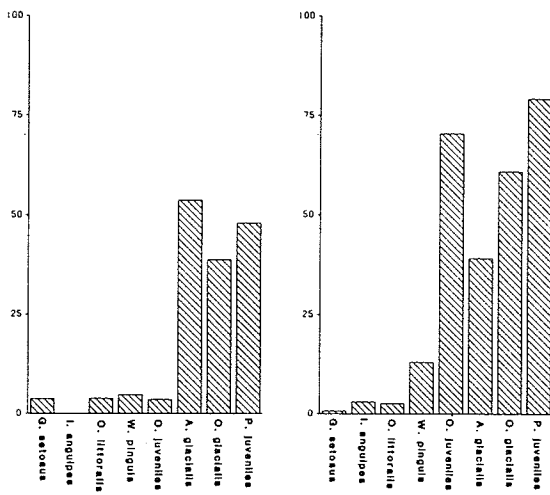
while _Parathemisto_ spp. juveniles were far more abundant than in other areas (Figure 18). Since _W. pinguis_ and _G. setosus_ were nearshore species, while _Parathemisto_ spp. juveniles were usually found over deep waters, this accounts for the resemblance of the communities in the bays to those of deeper areas. _Onisimus_ spp. juveniles were also far more abundant in bays than in other areas. Allen Bay did not have a species composition different from other areas in 1986.

FIGURE 18

Sub-ice macrofaunal species composition in bay and non-bay areas in the Resolute area as determined from Resolute area surveys, spring 1985.
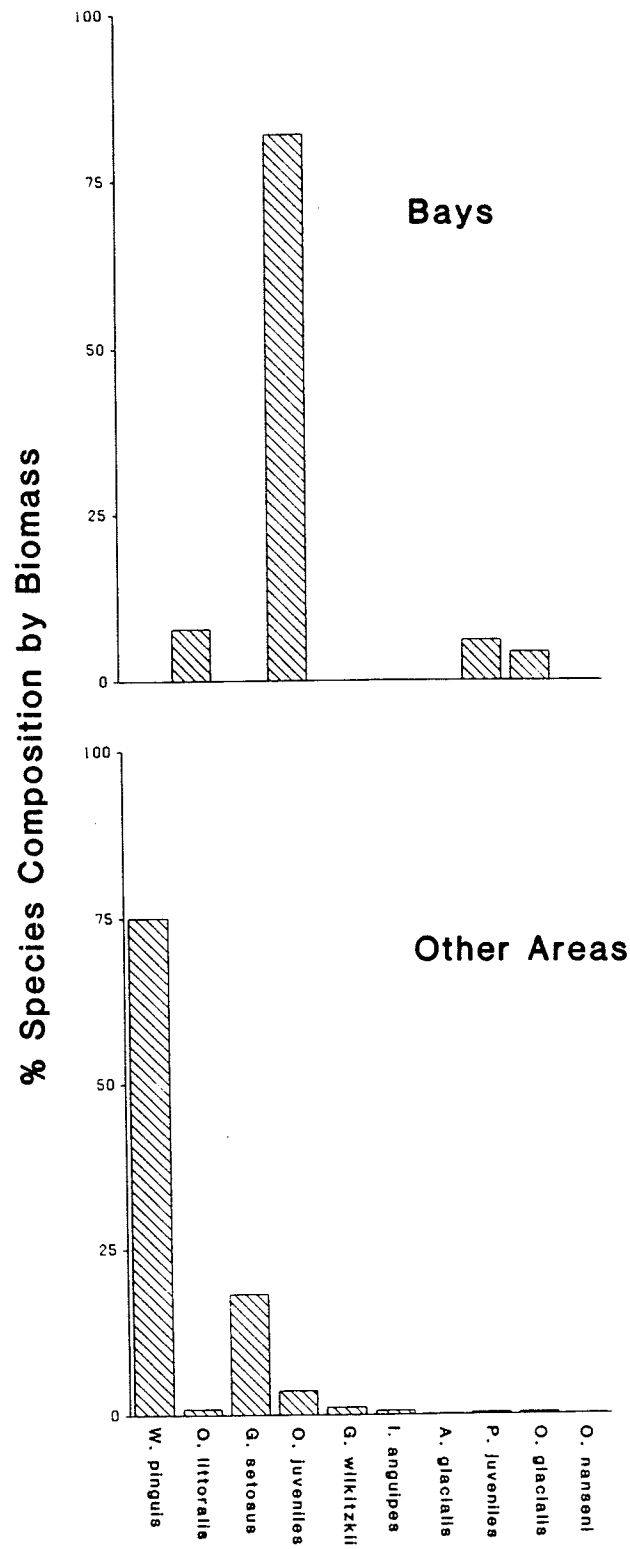
DISCUSSION

1. EVALUATION OF SAMPLING METHODS:

The sampling efficiency of the sweep net used in spring 1986 was estimated at 65%. This estimate was based on a comparison of total macrofaunal density as estimated using the camera system with sweep net catch. It is probable, however, that different species were captured with different efficiencies. This might have resulted in bias, since the species composition of the sub-ice macrofauna was quite variable.

The linear relationship between sweep net catch and macrofaunal density broke down at very high densities, possibly as a result of net clogging. Thus net efficiency was calculated over a limited range of densities. Such high densities were rare, however. The application of the correction factor to sweep net catches at very high densities probably results in an underestimate of true density.

Densities estimated with the video camera system were assumed to be 100% accurate. This assumption may not be completely valid, since organisms may have been embedded in the ice or camouflaged by algae. Resolution was not adequate to speciate macrofauna or to count juveniles.

2. SPATIAL DISTRIBUTION:

i. Relationships to Environmental Factors:

Sub-ice biomass over shallow (0-50 m) waters near Resolute was generally higher than has been previously reported (See Table 10). This could be due to bias in previous surveys, which were carried out using diver operated sub-ice nets, a technique known to underestimate actual densities (Cross and Martin 1983; Gulliksen 1984). Estimates from this study were corrected for net efficiency. Biomass over deeper water was similar to that reported for other areas.

Underlying water depth was the major influence on both total biomass and community structure of the sub-ice macrofauna. Total biomass decreased with underlying water depth at all times and in all areas sampled, and species were distributed along a depth gradient. The influence of water depth on macrofaunal distribution is probably related to the summertime distribution of these species.

Only three of the sub-ice species collected are known to be pelagic or semipelagic in the summer: A. glacialis, O. glacialis and Parathemisto spp. juveniles (Stephensen 1942). The remainder of the species, and by far the largest proportion of the total biomass, originated from the benthos. Thomson (1982), in a survey of the benthos of the eastern Canadian Arctic, found that benthic amphipods were common

Table 10: Total sub-ice macrofaunal biomass levels in various areas.

Location	Month	Community Type	Biomass (mg/m²)	Reference
Cape Hatt	May	Shallow Bays	10-30[a]	Cross&Martin 1983
Bridport Inlet	June	Shallow Bays	10-20[a]	Buchanon et al. 1977
Resolute	April-June	0-50 m, Fast Ice	40-141[b]	This Study
Pond Inlet	May-June	Deepwater,Fast Ice	13[a]	Cross 1982
Barents Sea	August	Deepwater,Pack Ice	10-70[a]	Gulliksen 1984
Resolute	April-June	>50 m, Fast Ice	5-22[b]	This Study

[a] Using Dry wt. = 0.1 (Wet wt.) (Waters 1977)

[b] Range of means of four 1986 Resolute area surveys.

only at depths of less than 50 m and dominant at depths of 10 m or less. Thus the spring distribution of the sub-ice macrofauna, which is composed primarily of amphipods in the Resolute area, appears to be a reflection of the benthic distribution of amphipods at other times of the year.

The distribution of sub-ice amphipod species was also related to their summertime distribution. $\underline{G}$. setosus, an intertidal species (Thomson et al. 1986), was most abundant over shallow water. $\underline{0}$. littoralis and $\underline{W}$. pinguis are of shallow subtidal origin (Cross and Martin 1983; Thomson et al. 1986), and were most abundant over waters of medium depth. Species found over deep waters ($\underline{A}$. glacialis, $\underline{0}$. glacialis and Parathemisto spp. juveniles) are pelagic during the summer, and might therefore be expected to occur in highest areal densities over deep waters. Thus a species' depth distribution during the summer seems to determine its distribution in the sub-ice habitat during the spring. Migration to the ice-water interface must be rapid and direct, and little lateral movement apparently occurs once populations are established. This would facilitate the return of sub-ice species to their summertime habitats late in the spring.

On a smaller scale, snow depth was an important determinant of sub-ice biomass. Total biomass tended to be negatively correlated with snow depth in the Resolute area surveys carried out early in the spring, while the opposite was observed late in the spring. This was more strongly demonstrated by the results of the small scale variance surveys, which showed a strong negative correlation between biomass and snow depth early in May, and a weaker positive correlation late in May. It is probable that the effect of snow depth on sub-ice macrofaunal

distribution is a result of the control snow depth exerts over sub-ice algal concentrations.

Concurrently with this work, Welch et al. (in prep.) have demonstrated that snow depth controls sub-ice algal biomass throughout the spring in the Resolute area. The relationship between snow depth and algal biomass changes over time (Figure 19). Differences in algal concentration between high and low snow areas are greatest early in the spring. For example, on May 9, the date of the first small scale variance survey, the concentration of chlorophyll a under 7 cm of snow was almost an order of magnitude higher than that under 12 cm of snow. This difference was reduced to about 3x by May 29, the date of the second survey, and chlorophyll concentrations under all snow depths were much higher. Later in the spring, chlorophyll concentrations were reduced in low snow areas as the algae sloughed off, while areas with higher snow depths retained algae somewhat longer.

The relationship between snow depth and algal biomass provides a possible explanation for the effect of snow depth on the distribution of sub-ice macrofauna. In April when algal biomass is low, amphipods congregate under low snow areas to graze the higher concentrations of algae found there. In late May when concentrations of algae are high everywhere, food is perhaps not as limiting and the amphipods are more evenly distributed. Once the algae begins to slough off under low snow areas, amphipods congregate under higher snow cover, where the sub-ice algae is retained the longest.

Mean sub-ice macrofaunal biomass was lower within 1 km of the ice edge than in areas further from the ice edge in 1986. Snow depth and ice thickness were also lower near the ice edge (ANOVA, p<.05). This

FIGURE 19

Change in calculated sub-ice chlorophyll $\underline{a}$ concentrations over time at three snow depths in the Resolute area, spring 1986. Each point is based on a separate regression between log(snow depth) and log(chlorophyll $\underline{a}$ concentration), $r>0.90$ and $N=32$ in all cases. Experimental dates refer to small scale subice macrofaunal surveys. Chlorophyll data courtesy of Dr. H. E. Welch.
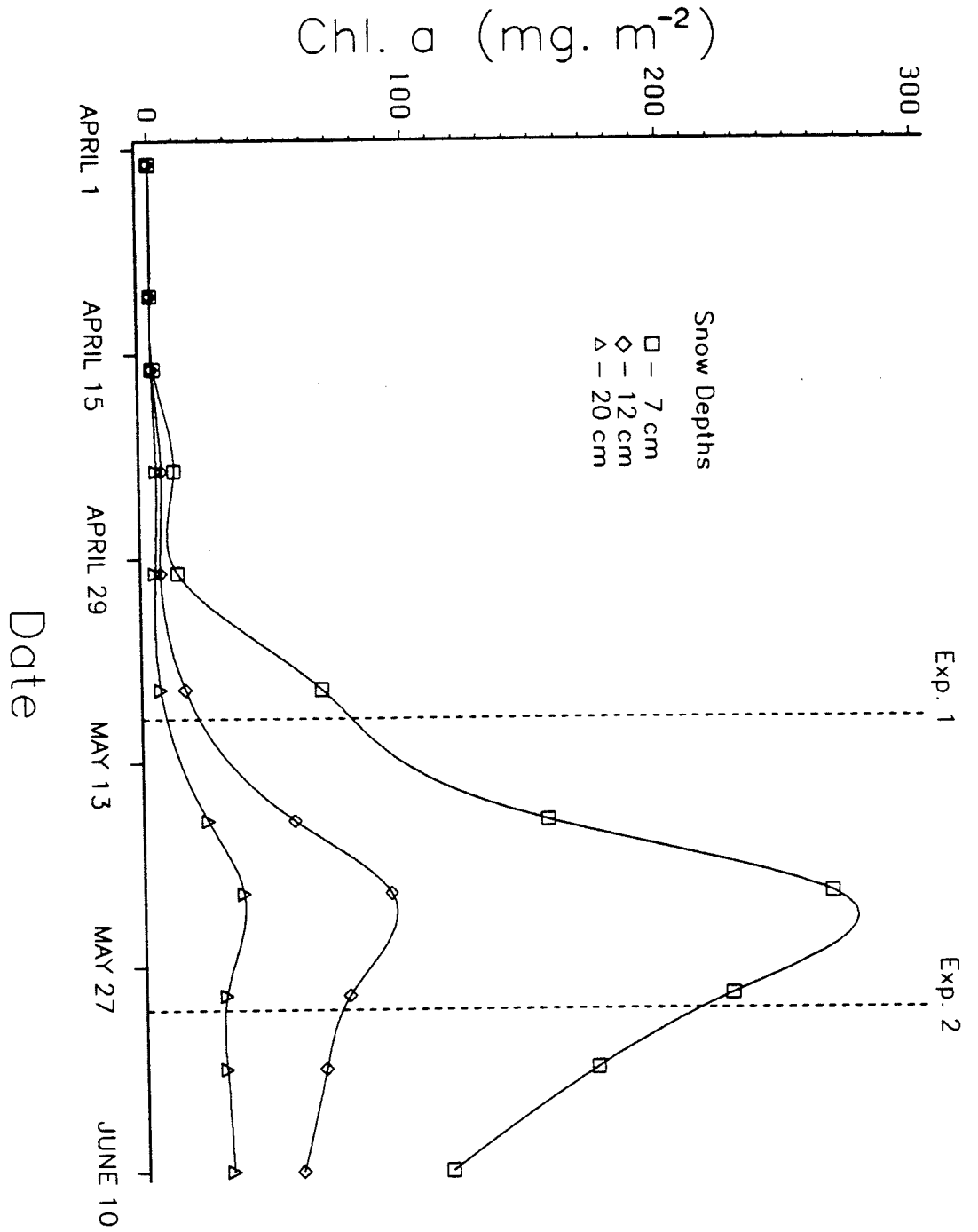
seems unlikely to have been the cause of the depressed biomass levels, however, since lower snow depth and ice thickness should have led to higher concentrations of sub-ice algae, and hence higher sub-ice macrofaunal biomass levels. It is possible that the concentrations of birds and marine mammals reported in ice edge areas (eg. Bradstreet 1982) lead to a higher predation pressure on the sub-ice macrofauna, resulting in lower biomass near the ice edge. The fact that the depression in biomass appears to be confined to within 1 km of the ice edge supports this hypothesis, since diving birds and mammals could penetrate but a short distance beneath the ice.

It is also possible that the movements of the animals themselves may have resulted in decreased abundances near the ice edge. If the amphipods move randomly or periodically drift with the current, a certain percentage would continuously "fall off" the ice edge and thus be lost to the sub-ice community. Since most of the species are benthic in origin, animals lost in this way would presumably not be replenished from open water areas. The result would be a continual net loss of sub-ice biomass from areas near the ice edge, and an eventual reduction in biomass levels in such areas.

This finding contrasts sharply with those of Gulliksen (1984), who observed an elevation in sub-ice macrofaunal biomass near the Barents sea ice edge. This community was quite different from that of Barrow Strait, consisting almost entirely of pelagic amphipods, which may respond differently to the nearby presence of open water than do the predominantly benthic amphipods of the Barrow Strait sub-ice community. Cross (1982) found no relationship between distance from the ice edge and sub-ice biomass levels in the eastern Canadian arctic. The

concentrations of marine mammals and birds observed in ice edge areas are therefore not due to higher sub-ice macrofaunal production, at least in the relatively shallow areas of landfast ice characteristic of the Canadian Arctic Archipelago. The availability of a food source (sub-ice fauna) not normally accessable to these animals seems a more likely explanation.

ii. Large Scale Patterns:

Changes in total biomass and species composition observed over distances of 10-100 km could not be explained by the environmental variables measured. Factors other than those measured in this study must therefore be important determinants of sub-ice macrofaunal distribution.

In 1985, Allen and Intrepid Bays had lower sub-ice biomass and a generally depauperate species composition compared to other areas. These differences were not observed in 1986, despite more intense sampling in Allen Bay. Bays had significantly thicker ice and higher snow depths than other areas (ANOVA, p<.05). This would lead to lower algal biomass in bays, perhaps accounting for the reduced sub-ice fauna. However, the fact that differences in community structure and biomass were not found in 1986, even though snow depth and ice thickness were still greater in Allen Bay, suggests that other factors must be involved.

Thomson et al. (1986) found that bottom type was an important

determinant of arctic intertidal community structure. _Onisimus_ spp. was more common over sandy bottoms, while _G_. _setosus_ was more common on rocky substrates. It is possible that the absence of _W_. _pinguis_, the most important difference between bays and other areas in 1985, was also due to differences in bottom type. _W_. _pinguis_ was not as common in 1986, perhaps explaining why Allen Bay did not have a distinct sub-ice community in that year. More detailed studies would be required to resolve this question.

Striking differences in species composition were observed in areas remote from Resolute sampled in 1986, but the reasons for these variations cannot be determined. Large-scale differences in snow and ice cover were apparent; however, it seems unlikely that these factors could account for differences in species composition, since they were not associated with changes in species composition in the Resolute area. It is probable that other factors, such as bottom type, current speed, pelagic primary production or benthic algal cover, must either directly control spring sub-ice species composition, or influence the species composition of the benthic community at other times of the year.

The observed differences in species composition and total biomass over large areas might affect the distributions of other marine mammals, particularly the ringed seal. Kingsley et al. (1985) observed an east-west gradation in seal densities in the Barrow Strait area that could not be fully accounted for by differences in ice type or water depth. Since seals prey on the ice fauna, it is possible that variations in macrofaunal density and species composition affect seal distributions. Future research effort should be directed towards determining the causes and temporal consistency of these variations.

3. TEMPORAL DISTRIBUTION:

i. Annual:

There were striking differences in species composition between the spring sub-ice communities of 1985 and 1986. The most obvious change was from a community dominated by W. pinguis in 1985 to one dominated by O. littoralis in 1986. O. spp. juveniles contributed significantly to total biomass in 1985 but were extremely rare in 1986, while the relative contribution of G. setosus remained constant over both years. W. pinguis was still an important species in 1986, although considerably less common than in 1985, so the most important change over the two years was in numbers of Onisimus spp., juvenile and adult.

I was unfortunately unable to positively speciate the Onisimus spp. juveniles which were so abundant in 1985, but they most closely resembled O. littoralis. This is the most reasonable identification, since O. littoralis is by far the most numerous representative of its genus in the Resolute area (Green and Steele 1975; Thomson et al. 1986). O. littoralis has a 2 year life cycle, maturing and mating in the fall of its second year and dying after releasing its young the following spring (Steele 1961, cited in Thomson et al. 1986). Hence two cohorts should be present in the spring: one of age 0+ and another of age 1+. However, in both 1985 and 1986, only one cohort was present in the

sub-ice community.

Two possible explanations may be advanced to account for this phenomenon: (i) there are extreme variations in the year-class strength of O. littoralis, or (ii) in any one spring season, one year class inhabits the sub-ice habitat while the other inhabits the benthos. Dunbar (1957) has noted that, in a species with a two year lifecycle, the cohorts are reproductively isolated from one another, as long as each individual breeds only once and none breeds precociously after only one year. Thus, the two cohorts might be genetically quite separate, a situation which could lead to intense intraspecific competition or predation, or to each cohort having different ecological adaptations (ie. rapid speciation). Either explanation is compatible with this hypothesis. Simultaneous sub-ice and benthic sampling must be carried out to resolve this question. The analysis of genetic distances between the two cohorts of this species would be another worthwhile avenue of investigation.

The difference between the pattern of total biomass distribution with depth between spring 1985 and spring 1986 was probably due to the changes in species composition between the two years. Biomass was concentrated over shallower water in 1986 when O. littoralis was dominant than in 1985 when W. pinguis was dominant. O. littoralis adults must remain over shallower water than W. pinguis, either because they originate from shallower water, or because they remain more stationary after migrating to the sub-ice habitat.

ii. Seasonal:

The general patterns of seasonal change in biomass and species composition were similar to those observed by other workers (Carey 1982; Cross and Martin 1983). Lowest biomass and species diversity occurred in winter and early spring. Total biomass increased significantly over spring 1985 but not spring 1986. Of those species whose abundances changed significantly over the course of the spring, most increased in abundance from early to late spring. Limited sampling in early July of both years indicated that no amphipods were present under the ice at this time. This general pattern of seasonal change is probably related to the availability of sub-ice algae.

O. littoralis was the only species which occurred in the sub-ice in January 1986, and total biomass was lower than in spring 1985. It is surprising that there are any inhabitants of the sub-ice during winter, since the lack of sunlight at this time of year precludes any algal production. Although it consumes sub-ice algae during the spring, O. littoralis is omnivorous and consumes crustaceans in the benthos during the summmer (Griffiths and Dillinger 1981). In preliminary examination of gut contents of O. littoralis captured in January 1986, crustacean remains were the only recognizable items. The sub-ice habitat may offer this species either an increased availability of crustaceans for food, or an escape from predation pressures in the benthos.

The increase in total biomass observed over the 1985 spring season

was due primarily to increases in the abundance of _Onisimus_ spp. juveniles and _G. setosus_. In 1986, _G. setosus_ again showed the most quantitatively important change, increasing in abundance from early to late spring. The fact that _Onisimus_ spp. juveniles were not abundant in 1986 perhaps explains why no significant increase in total biomass occurred over the spring of that year. _G. setosus_ appears to be a latecomer to the sub-ice habitat, reaching its peak abundance by late May.

The increase of sub-ice macrofaunal biomass levels over the spring of 1985, and the increases in the abundances of individual species observed in both years, are probably related to the concurrent increases in the abundance of sub-ice algae. Sub-ice chlorophyll a concentrations increased log-linearly from March to late May in 1986 (Welch et al. in prep.; See Figure 19). Hence, food availability might limit grazer populations early in the spring, but probably not by mid-May when algal biomass is much higher. The decline in macrofaunal biomass in late spring and early summer could also be related to falling algal biomass; amphipods may return to a benthic or pelagic existence once the sub-ice habitat no longer offers an abundant source of food. Changes in ice structure and sub-ice salinity caused by freshwater input from melting ice (Percy 1975; pers. obs.) might also play a role in the abandonment of the sub-ice habitat.

iii. Short Term (Diurnal) Changes:

The diurnal fluctuations in amphipod density observed in this study must be considered in future attempts to estimate sub-ice macrofaunal populations. High current speeds appear to reduce amphipod densities, but the mechanism for this remains unclear. Increased current speeds may have enhanced the disturbance to the sub-ice community caused by the camera system, thereby producing artifactual variations in density. Alternatively, high current speeds may dislodge the amphipods from the sub-ice surface or induce them to drift, thus lowering apparent densities.

4. CONCLUSIONS:

Water depth was the major influence on both the community structure and total biomass of the sub-ice macrofauna. Shallow areas (<50 m) are obviously most important in terms of biomass and production. Snow depth also affects sub-ice biomass, probably through its influence on the abundance of sub-ice algae, the major food supply of the macrofaunal community. Geographical variations in species composition and total biomass on a scale of 10-100 km could not be accounted for by the environmental variables measured. These changes could be the result of

large-scale variations in bottom type, current speeds, planktonic and benthic primary production, or other factors.

The species composition of the sub-ice macrofauna changed dramatically over the two years studied. The causes of this annual variation are not known. Biomass was lowest in winter and increased over the spring. This seasonal pattern is probably related to the abundance of sub-ice algae, which also increases over the spring. Short-term fluctuations in macrofaunal densities may be related to daily changes in current speeds, but further work will be neccessary to confirm this.

Since most sub-ice biomass is found over shallow waters, and extensive areas of shallow water are not common in the eastern Canadian arctic, it seems unlikely that the sub-ice macrofauna is of quantitative importance in marine food webs in this area. In other regions, such as the western Canadian arctic and Hudson's Bay, where extensive areas of shallow water do exist, the sub-ice macrofauna may be of much greater importance. It is these areas that might be most susceptable to damage by industrial pollution, especially oil spills beneath the ice (Cross and Martin, 1983). Such occurrences could directly disrupt the food chain through destruction of the macrofauna, or contamination of the food chain could render valuable marine resources unusable. Future research effort should be directed towards determing the susceptability of arctic marine food webs to disruptions of this type, preferably before they occur.

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APPENDIX 1

Taylor's power regressions (Downing 1979; Green 1979) were used to derive a variance stabilizing transformation for the sweep net catch data. Mean biomass levels and variances were calculated for for each species over the entire Resolute survey area for each spring survey. Regressions of log(variance) on log(mean biomass) (Table 11) were significant and had a mean slope (b) of 1.66 over all surveys, indicating a contagious distribution. The variance stabilizing transformation was calculated as:

$$x' = x^{1-b/2} = x^{.17},$$

where x and x' are the untransformed and transformed counts respectively. This is quite close to the log transform used when $b=2$. Since the log transform is commonly applied to species - abundance data (Green 1979), I chose it as the most appropriate variance stabilizing transformation for the sweep net survey data. The actual transformation used was:

$$x' = \log(x+1).$$

Table 11: Power function regressions of variance (s^2) on mean biomass ($\bar{x}$) for all Resolute area surveys, spring 1985 and 1986. Means and variances are calculated for each species over the entire survey area. Regression equations are of the form:

$$s^2 = a\bar{x}^b.$$

Survey Date	N [a]	r^2 [b]	a	b
May 9 - 17/85	8	0.61*	-0.12	2.10
Jun 4 - 13/85	9	0.60**	0.58	1.56
Apr 19 - 24/86	10	0.73**	0.72	1.64
May 10 - 16/86	12	0.76**	0.68	1.50
May 31 - Jun 4/86	12	0.63**	0.94	1.48
Jun 21 - 26/86	11	0.65**	0.57	1.68
				$\bar{b}$ = 1.66

[a] N - number of species present

[b] r^2 - coefficient of determination

* Significant at p<.05

** Significant at p<.01